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Survival Sounds in Insects: Diversity, Function, and Evolution

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Insect defense sounds have been reported for centuries. Yet, aside from the well-studied anti-bat sounds of tiger moths, little is understood about the occurrence, function, and evolution of these sounds. We define a defense sound as an acoustic signal (air- or solid-borne vibration) produced in response to attack or threat of attack by a predator or parasitoid and that promotes survival. Defense sounds have been described in 12 insect orders, across different developmental stages, and between sexes. The mechanisms of defensive sound production include stridulation, percussion, tymbalation, tremulation, and forced air. Signal characteristics vary between species, and we discuss how morphology, the intended receiver, and specific functions of the sounds could explain this variation. Sounds can be directed at predators or non-predators, and proposed functions include startle, aposematism, jamming, and alarm, although experimental evidence for these hypotheses remains scant for many insects. The evolutionary origins of defense sounds in insects have not been rigorously investigated using phylogenetic methodology, but in most cases it is hypothesized that they evolved from incidental sounds associated with non-signaling behaviors such as flight or ventilatory movements. Compared to our understanding of visual defenses in insects, sonic defenses are poorly understood. We recommend that future investigations focus on testing hypotheses explaining the functions and evolution of these survival sounds using predator-prey experiments and comparative phylogenetics.

Keywords: defense, acoustic, mechanism, signal variation, communication, predator, prey, disturbance

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INTRODUCTION

When threatened or attacked by a predator, many insects produce sounds. Familiar examples are hisses of the Death's-head hawkmoth, *Acherontia atropos* (Sphingidae) (Brehm et al., 2015), and the Madagascar hissing cockroach, *Gromphadorhina portentosa* (Blaberidae) (Nelson, 1979), as well as the tymbal clicks of tiger moths (Erebidae: Arctiinae) (e.g., Corcoran et al., 2010). However, insect defense sounds are widespread and diverse, including those produced by small stridulating bark beetles (Lewis and Cane, 1990) and large whistling caterpillars (Bura et al., 2011). Despite centuries of research reporting that insects use sounds for defense (e.g., Lesser, 1738; Sanborn, 1869; Darwin, 1889), we know very little about the roles these sounds play in insect survival (Conner, 2014). How do sounds stop an attack by a predator? Do different sound characteristics serve different functions? Why do only some insects produce defense sounds? To address these questions, we need a review of insect defensive sound production that highlights research to date and identifies what remains to be investigated. Previous reviews of insect defense sounds focused on potential functions (e.g., Conner, 2014), a single mechanism (e.g., stridulation, Masters, 1980), or a specific taxon (e.g., termite alarm signals, Hager et al., 2019; tiger moth anti-bat clicks, Waters, 2003; Conner and Corcoran, 2012). Our review takes a broader approach by exploring the diversity, function, and evolution of defense sounds across the Class Insecta. Specifically, we document which taxa, sexes, and developmental stages are reported to produce defense sounds, the mechanisms by which they produce them, and the diversity of their signal characteristics. We review hypotheses explaining the functions and evolutionary origins of defensive sound production, as well as the adaptive significance of signal variation. While we focus specifically on defense sounds, we recognize that some insects use other forms of acoustic anti-predator strategies such as adaptive silence and acoustic crypsis, and we refer readers to Conner (2014) for further discussion of these strategies.

What Is a Defense Sound?

What do we mean by "defense sound"? Variously called "distress signals" (Ossiannilsson, 1949), "protest sounds" (Alexander, 1956), "disturbance sounds" (Masters, 1979), and "defense sounds" (Bura et al., 2016), the general consensus is that these acoustic signals are produced in response to disturbance and used to repel predators or warn conspecifics (cf. Alexander, 1967). In social insects such as termites and bees, the sounds protect not only the individual, but the colony. We exclude from this review sounds associated with territorial and agonistic behaviors (e.g., those occurring in male-male interactions) as such sounds are generally aimed at competitors rather than predators. We also exclude cases of "incidental" sounds, meaning sounds associated with another defense like the chemical ejections of bombardier beetles (Eisner et al., 2001), unless the sounds are noted by the authors as being part of the defensive display. We recommend the following definition: "A defense sound is an acoustic signal produced in response to attack or threat of attack by a predator (or parasitoid) and that promotes survival." Here we refer to an acoustic signal in the broadest sense, meaning a vibration that is airborne, waterborne (both commonly referred to as sounds), or solid-borne (commonly referred to as vibrations). For simplicity, hereafter we refer to all of these acoustic signals as "sounds" [see Hill (2014) and Yack (2016) for further discussion of acoustic signal nomenclature].

WHICH INSECTS PRODUCE DEFENSE SOUNDS?

Understanding which individuals possess a trait and how it varies is important for testing hypotheses on the function and evolution of that trait. Until now, a review of the distribution of insect defense sounds across taxa, sexes, and developmental stages had not been conducted. Using our definition of defense sounds, we reviewed the literature to identify which insect orders and families include species reported or proposed to produce sonic defenses. Among these examples, we also noted the sex and life stages of the species investigated. Our goal was not to identify every reported occurrence, but to obtain a general overview of the variation between taxa, sexes, and developmental stages to identify gaps in the literature and trends that will inform future studies.

Defensive sound production has been reported in at least 12 of the 28 currently recognized insect orders (**Table 1** and **Figure 1**). However, the number of reports varies between orders, ranging from multiple species within 15 families of Lepidoptera to a single species in Odonata. Coleoptera and Hemiptera have the next most abundant number of reports at 12 and 10 families, respectively. Defense sounds are also commonly described in Blattodea (8 families) and Orthoptera (7 families). The remaining orders have reports from 6 or fewer families, though some of these families contain numerous well-known sound producers [e.g., buzzing in Apidae (Hymenoptera), Kirchner and Röschard, 1999]. Importantly, we cannot conclude based on a single sound-producing species that all members of a given family, or even a given genus, produce defense sounds. For example, not all Phasmatidae (Phasmatodea) stridulate when disturbed (Bedford, 1978), and in Sphingidae (Lepidoptera), both sound- and non-sound-producing larvae occur in the genus *Manduca* (Bura et al., 2016). While defensive sound production appears to be widespread in insects, it is certainly not an even distribution. We discuss why defense sounds might not occur in all species in the next subsection.

Within species that produce defense sounds, the sex that produces these sounds can vary. It is important to note, however, that many studies do not indicate the sex of the specimens tested. Indeed, of the 404 species identified as sound producers in this review, sex was identified in fewer than half the species (194 of 404). In the 152 species for which both sexes were tested, both males and females produce sounds in the majority of cases (126 of 152). Examples include hissing cockroaches (e.g., Nelson and Fraser, 1980) and king crickets (e.g., Field, 1993). Sexual dimorphism of sound features was noted in 21 of these 126 species, and the differences are attributed to morphological traits such as body size (e.g., Coelho, 1998; Hill, 2007), or because the male and female use different mechanisms of sound production (e.g., Kowalski et al., 2014). In the remaining 26 (of 152) species where both sexes were tested, only one sex produces defense sounds. In 20 of these, it's the male sex, and examples include cicadas (e.g., Smith and Langley, 1978) and katydids (e.g., Kowalski and Lakes-Harlan, 2011). In contrast, there are only 6 species where defense sounds are produced solely by the female, including *Heteropteryx dilatata* stick insects (Heteropterygidae) (Carlberg, 1989) and *Ips pini* beetles (Curculionidae) (Dobai et al., 2018). Based on the species investigated to date, when defensive sound production occurs in a species, it is typically produced by both sexes. When only one sex produces sounds, it is usually the male. This male bias could be attributable to males experiencing higher predation risk as they are more mobile when searching for a mate (e.g., Burk, 1982). We recommend that future studies aim to test both sexes wherever possible.

The majority of reports of defensive sound production come from adult insects, but many juvenile life stages, including larvae, nymphs, and pupae, also produce these sounds (**Table 1** and **Figure 1**). We did not, however, find any accounts of insect eggs producing sounds in response to a disturbance. Of the

TABLE 1 | Distribution of insect defense sounds across orders, families, and developmental stages including information on mechanisms and proposed functions. A, adult; N, nymph; L, larva; P, pupa. "**Figure 3** #" refers to the corresponding label on **Figure 3**. Asterisks denote cases where the sound was tested with a predator/receiver in the selected reference.

ORDER Family	Life stage	Sound type	Mechanism	Figure 3 #	Proposed function	Selected references
ODONATA						
Epiophlebiidae	N	Stridulation	Abdomino-femoral	1		Haskell, 1961
ORTHOPTERA						
Acrididae	A	Stridulation	Mandibles	2	Not specified*	Blondheim and Frankenberg, 1983*
Anostostomatidae	A, N	Stridulation	Abdomino-femoral	4		Field, 1993
	A	Stridulation	Mandibular tusks	2		Field, 1993
	A	Stridulation	Tergo-tergal	5		Field, 1993
Gryllacrididae	A	Stridulation	Abdomino-femoral	4	Startle	Field and Bailey, 1997
Gryllidae	A	Stridulation	Tegmino-tegminal	6	Aposematism	Desutter-Grandcolas, 1998
Prophalangopsidae	A	Stridulation	Abdomino-thoracic	7		Gwynne, 2001
Stenopelmatidae	A	Stridulation	Abdomino-femoral	4		Weissman, 2001
Tettigoniidae	A, N	Forced air	Mouthparts	3		Bailey and Sandow, 1983
	A	Stridulation	Tegmino-tegminal	6	Startle	Heller, 1995; Kowalski and Lakes-Harlan, 2011; Kowalski et al., 2014
	A	Stridulation	Legs		Startle	Belwood, 1990
	A	Stridulation	Femoro-alary	8		Rentz, 1993
	A	Stridulation	Abdomino-alary	9, 10	Startle*	Sandow and Bailey, 1978*; Bailey and Sandow, 1983; Heller, 1995
	A	Stridulation	Labrum-mandible	2		Lloyd and Gurney, 1975
PHASMATODEA						
Diapheromeridae	A	Stridulation	Wings		Startle Aposematism	Bedford, 1978 Edmunds, 1974
Heteropterygidae	A	Stridulation	Wings		Mimicry	Carlberg, 1989
Phasmatidae	A	Stridulation	Wings		Startle	Bedford, 1978
Phylliidae	A, N	Stridulation	Antenno-antennal	11		Henry, 1922
MANTODEA						
Empusidae	A	Stridulation	Tegmino-femoral	12	Startle*	Carpenter, 1921*
Hymenopodidae	A	Stridulation	Wings		Startle	Shelford, 1903
	A	Stridulation	Abdomino-alary	13	Startle	Edmunds, 1972
Mantidae	A	Stridulation	Abdomino-alary	13	Startle*	Maldonado, 1970*; Hill, 2007
	A	Stridulation	Pronoto-femoral	14	Startle	Robinson, 1969
BLATTODEA						
Archotermopsidae	A	Percussion	Head		Alarm*	Kirchner et al., 1994*
Blaberidae	A, N	Forced Air	Spiracles	15		Nelson, 1979; Hunsinger et al., 2018
	A	Stridulation	Tergo-tergal	16		Roth and Hartman, 1967
	A	Stridulation	Abdomino-alary			Roth and Hartman, 1967
	A	Stridulation	Pronoto-tegminal	17	Startle* Aposematism	Guthrie, 1966* Roth and Hartman, 1967
Cryptocercidae	A, N	Percussion	Head		Alarm*	Seelinger and Seelinger, 1983*
Ectobiidae	N	Stridulation	Sterno-sternal	18	Aposematism	Schal et al., 1982
Hodotermitidae	A	Percussion	Head		Alarm	Bugnion, 1913
Mastotermitidae	A	Percussion	Abdomen		Alarm*	Delattre et al., 2015*
	A	Tremulation			Alarm*	Delattre et al., 2015*
Rhinotermitidae	A	Percussion	Head		Alarm	Hertel et al., 2011
Termitidae	A	Percussion	Head		Alarm*	Connétable et al., 1999*; Hager and Kirchner, 2013*
	A	Tremulation				Röhrig et al., 1999
HEMIPTERA						
Aphididae	A, N	Stridulation	Abdomino-tibial	19		Broughton and Harris, 1971
Aphrophoridae	A	Tymbalation	Tymbals	20		Ossiannilsson, 1949
Cicadellidae	A	Tymbalation	Tymbals	20		Ossiannilsson, 1949

(Continued)

TABLE 1 | Continued

ORDER Family	Life stage	Sound type	Mechanism	Figure 3 #	Proposed function	Selected references
Cicadidae	A	Tymbalation	Tymbals	20	Startle*	Smith and Langley, 1978*
Cydnidae	A	Stridulation	Abdomino-alary	21		Dupuis, 1953; Gogala, 1970
	A	Tremulation	Abdomen		Not specified*	Nakahira and Kudo, 2008*
Membracidae	A, N				Recruitment*	Cocroft, 1996*; Morales et al., 2008*
Reduviidae	A, N	Stridulation	Prosterno-rostral	22	Startle	Yinon et al., 1972; Schilman et al., 2001
Scutelleridae	A, N	Stridulation	Abdomino-tibial	19		Leston, 1957
Tessaratomidae	A					Leston, 1954
Veliidae		Stridulation				Miyamoto, 1953
HYMENOPTERA						
Apidae	A	Tremulation	Flight muscles		Aposematism* Alarm* Mimicry	Kirchner and Röschard, 1999* Sen Sarma et al., 2002* Seeley et al., 1982
Crabronidae	A	Tremulation	Flight muscles			Coelho, 1998
Formicidae	A	Percussion	Mandibles		Alarm*	Fuchs, 1976*
	A	Percussion	Abdomen		Alarm*	Fuchs, 1976*
	A	Stridulation	Tergo-tergal	23	Alarm Aposematism	Pavan et al., 1997 Ware, 1994
Mutillidae	A	Stridulation	Tergo-tergal	23	Aposematism*	Masters, 1979*; Polidori et al., 2013
Tenthredinidae	L	Stridulation	Abdomen tip	24	Aposematism	Boevé, 2015
Vespidae	A	Percussion	Abdomen tip		Alarm*	Jeanne and Keeping, 1995*
COLEOPTERA						
Carabidae	A	Stridulation	Abdomino-elytral	25, 26	Aposematism*	Wheeler et al., 1970*; Bauer, 1976*
Carabidae: Cicindelinae	A	Stridulation	Alary-elytral	27	Müllerian mimicry	Yager and Spangler, 1997
	A	Stridulation	Elytro-femoral	29		Serrano et al., 2003
Cerambycidae	A	Stridulation	Mesonoto-pronotal	28	Müllerian mimicry Alarm*	Miller, 1971; Schmitt and Traue, 1990 Li et al., 2013*
Chrysomelidae	A	Stridulation	Abdomino-elytral	25		Schmitt and Traue, 1990
	L	Tremulation			Aggregation	Greenfield, 2002
Curculionidae	A	Stridulation	Elytro-femoral	29		Gaiger and Vanin, 2006
	A	Stridulation	Elytro-abdominal	25	Startle	Wilson et al., 1993; Fleming et al., 2013
	A	Stridulation	Vertex-pronotal	30	Startle*	Lewis and Cane, 1990*; Dobai et al., 2018
Dytiscidae	A	Stridulation				Aiken, 1985
	L	Forced Air	Spiracles	31	Startle	Mukerji, 1929
Geotrupidae	A	Stridulation	Elytro-thoracic	32		Palestrini et al., 1988
	A	Stridulation	Coxo-abdominal	33		Palestrini et al., 1988; Carisio et al., 2004
	L	Stridulation	Legs			Pavan et al., 1990
Hydrophilidae	A	Stridulation	Elytro-abdominal	34	Aposematism*	Ryker, 1976; Masters, 1979*; Aiken, 1985
	L					Aiken, 1985
Hygrobiidae	A	Stridulation	Elytro-abdominal	25		Aiken, 1985
Passalidae	A	Stridulation	Abdomino-alary	35	Startle*	Dumortier, 1963b; Buchler et al., 1981*
Scarabaeidae	A	Stridulation	Alary-abdominal	36		Kasper and Hirschberger, 2005
	A	Stridulation	Abdomino-elytral	37		Mini and Prabhu, 1990
	A	Stridulation	Elytro-abdominal	38		Palestrini et al., 1990
	A	Stridulation	Coxo-abdominal	33		Joseph, 1991
	P	Stridulation	Gin traps	39		Dumortier, 1963b
Silphidae	A	Stridulation	Abdomino-elytral	40	Aposematism Müllerian mimicry	Rothschild and Haskell, 1966 Lane and Rothschild, 1965
Tenebrionidae	A	Stridulation	Abdomino-elytral	41	Aposematism	Eisner et al., 1974
TRICHOPTERA						
Hydropsychidae	L	Stridulation	Head-femoral	42	Not specified*	Johnstone, 1964; Jansson and Vuoristo, 1979*

(Continued)

TABLE 1 | Continued

ORDER Family	Life stage	Sound type	Mechanism	Figure 3 #	Proposed function	Selected references
LEPIDOPTERA						
Brahmaeidae	L	Forced air	Alimentary canal	3	Startle	Low, unpublished
Drepanidae	L	Stridulation	Mandibles	2	Not specified*	Guedes et al., 2012*
Erebidae: Arctiinae	A	Tymbalation	Tymbals	44	Aposematism* Batesian mimicry* Müllerian mimicry* Startle* Sonar jamming*	Hristov and Conner, 2005*; Dowdy and Conner, 2016* Barber and Conner, 2007* Barber and Conner, 2007* Bates and Fenton, 1990* Corcoran et al., 2009*, 2011*
Geometridae	A	Tymbalation	Tymbals	45	Batesian mimicry	Corcoran and Hristov, 2014
Heliozelidae	L		Abdomen tip			Low, 2008
Hesperiidae	P	Stridulation	Probosco-abdominal	46		Hinton, 1948
	P	Percussion		n/a		Hinton, 1948
Lycaenidae	P	Stridulation	Tergo-tergal	43		Hinton, 1948; Downey, 1966
	P	Percussion	Anterior end			Hinton, 1948; Downey, 1966
	L	Stridulation			Recruitment*	Pierce et al., 1987*
Nolidae	P	Stridulation	Abdomen tip	47	Startle	Dodd, 1916; Hinton, 1948
Notodontidae	L	Stridulation	Mandibles	2		Federley, 1905
Nymphalidae	A	Tymbalation	Wing buckling	48	Startle*	Møhl and Miller, 1976*; Vallin et al., 2005*; Olofsson et al., 2012*
	A	Stridulation	Wings	49		Dumortier, 1963a
	P	Stridulation	Tergo-tergal	50, 51	Startle	Dolle et al., 2018
Papilionidae	A	Stridulation	Alary-tibial			Jobling, 1936
	P	Stridulation	Sterno-sternal	52	Startle	Dolle et al., 2018
Riodinidae	P	Stridulation	Tergo-tergal	53		Downey, 1966
	L	Stridulation	Vibratory papillae	54	Recruitment*	DeVries, 1991*
Saturniidae	L	Stridulation	Mandibles	2	Aposematism*	Brown et al., 2007*; Bura et al., 2016
	L	Forced air	Spiracles	55	Startle	Bura et al., 2016
	L	Forced air	Alimentary canal	3	Startle	Low, unpublished
Sphingidae	A	Stridulation	Genitalia	56	Sonar jamming*	Kawahara and Barber, 2015*
	A	Forced air	Pharyngeal	3	Startle	Zagorinsky et al., 2012; Brehm et al., 2015
	P	Stridulation	Tergo-tergal	50		Hinton, 1948
	L	Stridulation	Mandibles	2	Aposematism	Bura et al., 2012, 2016
	L	Forced air	Spiracles	55	Startle*	Dookie et al., 2017*; Sugiura and Takanashi, 2018*
	L	Forced air	Alimentary canal	3	Startle	Rosi-Denadai et al., 2018
Yponomeutidae	A	Tymbalation	Wing buckling	57	Müllerian mimicry	O'Reilly et al., 2019
DIPTERA						
Syrphidae	A	Tremulation	Flight muscles		Mimicry*	Brower and Brower, 1965*; Rashed et al., 2009
MECOPTERA						
Meropeidae	A	Stridulation	Jugum-metanotal	58		Sanborne, 1982

References have been selected to include those that best represent the diversity of taxa and developmental stages reported to produce defense sounds. However, it should be noted that this is not a comprehensive list.

69 families identified in our study in which defense sounds occur (**Table 1**), 30 families include reports from juveniles. These examples primarily occur in Lepidoptera (12 families), but also Coleoptera (5), Hemiptera (4), and Blattodea (3). Juvenile sound producers include nymphs in Ectobiidae (Blattodea) (Schal et al., 1982), larvae in Bombycoidea (Lepidoptera) (Bura et al., 2016), and pupae in Lycaenidae and Riodinidae (Lepidoptera) (Hinton, 1948; Downey, 1966). There is no obvious relationship between juvenile and adult defensive sound production within a species. In hemipterans such as Reduviidae (e.g., Yinon et al., 1972) and Membracidae (e.g., Cocroft, 1996), both juveniles and adults can produce defense sounds. However, in Lepidoptera and other holometabolous orders, where a juvenile produces defense sounds, the adult may not. For instance, of the 33 Bombycoidea caterpillar species known to produce defense sounds (Low, unpublished), only two species are reported to produce sounds as adults (e.g., Brehm et al., 2015) and the mechanisms used by the caterpillars and adults differ. Yack (2016) proposed that juvenile insects are under-represented in the literature on acoustic communication, and we argue that this pertains to defensive sound production as well. Juvenile insects are attacked by many predators and parasitoids, and

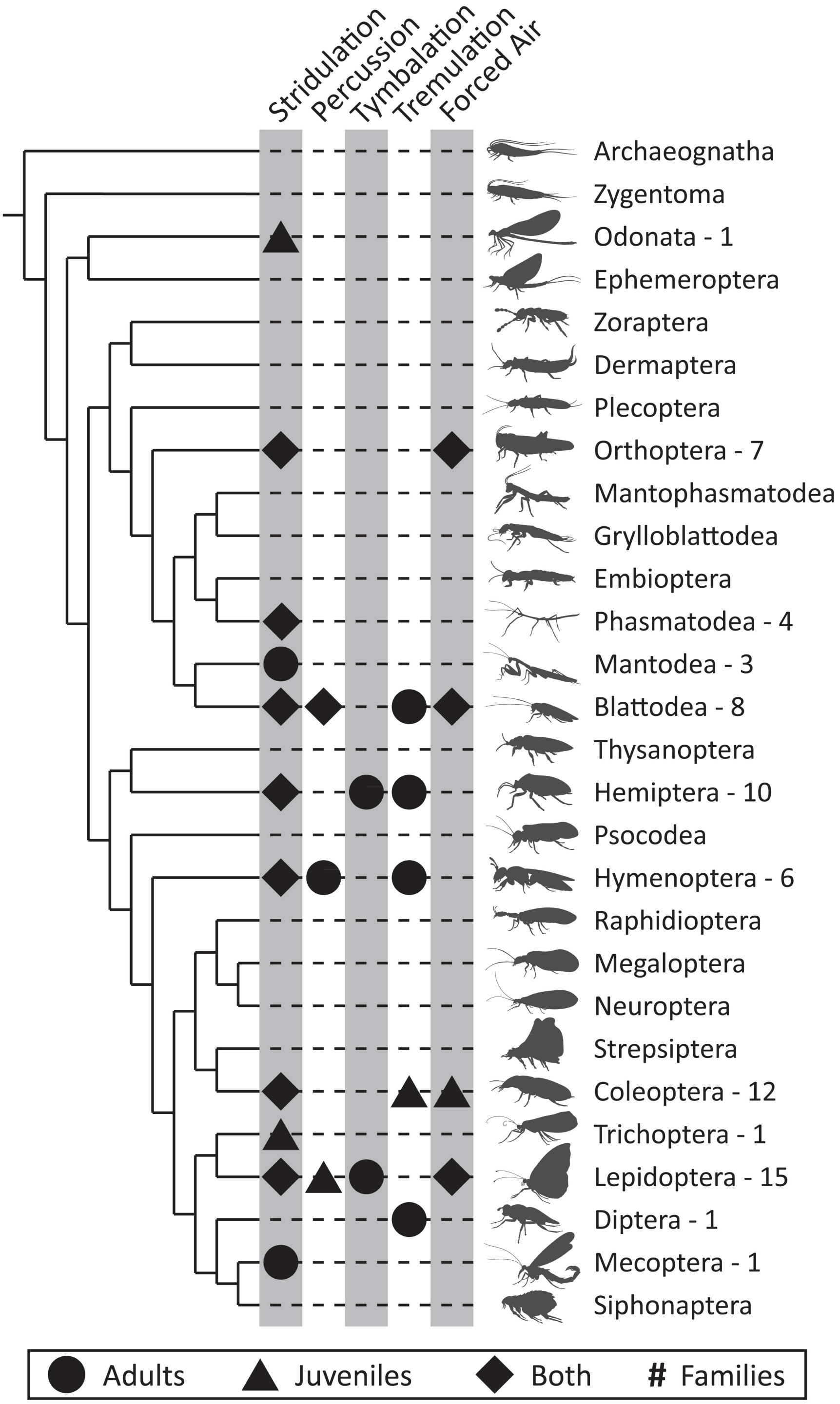

FIGURE 1 | Distribution of defense sounds across orders and life stages of the Class Insecta. The five different mechanisms used to produce defense sounds (stridulation, percussion, tymbalation, tremulation, and forced air) are indicated within their respective columns. Shapes represent the life stage at which defensive sound production occurs, with pupae included under "Juveniles." Numbers represent the number of families within that order where defensive sound production has been noted. Cladogram adapted from Misof et al. (2014).

as such there should be selective pressures to produce defense sounds. Comparative analyses among juvenile sonic defenses would be ideal for testing hypotheses on the functions and evolution of these signals, as in juveniles, defensive sound production is not confounded by sounds used in sexual selection. Future research should focus on identifying the distribution and diversity of defensive sound production in juvenile insects including eggs.

Why Don't All Insects Produce Defense Sounds?

Why is there such diversity with respect to who does and does not produce defense sounds? There are several, non-mutually exclusive explanations. First, morphological or phenotypic traits may enhance or constrain a species' ability to evolve sound production. For example, smaller insects may not produce airborne defense sounds because such sounds could be too quiet for a predator to hear (Bennet-Clark, 1998), and indeed, we did not find any accounts of defensive sound production in orders with tiny insects (e.g., Psocodea, Thysanoptera, and Siphonaptera, **Figure 1**). Sclerotization, or hardness, of an insect's cuticle may restrict sound production to insects with hard exoskeletons (though this would vary by mechanism), and we did find the most defense sound producers in Coleoptera adults and Lepidoptera pupae (**Table 1**). Additionally, some insects may have co-opted a pre-existing mechanism used in a different signaling context, such as cricket and katydid defensive sound production that is thought to have evolved from sexual signaling (Alexander, 1960) (see section "Evolutionary Origins" below). Second, the assemblage of predators may influence who does or does not produce defense sounds. For instance, tymbal click production varies seasonally in tiger moths of south-eastern Canada whereby species that emerge during peak bat foraging season are more likely to click than species that emerge earlier in the year (Ratcliffe and Nydam, 2008). Third, there are costs to producing defense sounds that may preclude some insects from using them due to trade-offs with other defenses. Corcoran and Woods (2015) found that the metabolic rate of the tiger moth *Bertholdia trigona* (Arctiinae) is 66% higher when producing sonar jamming sounds than when at rest, but is negligible when compared to the 277% higher rate of flight. If defense sounds are costly to produce, perhaps insects that have already invested in other costly defenses (e.g., chemical defenses, Zvereva and Kozlov, 2015; Knapp et al., 2020) will not produce them. Fourth, the insect's habitat may not be conducive to transmitting sounds effectively due to interference with sound propagation from absorption, scattering, or masking by background noise (Römer, 2020). For example, insects may be living in wood or soil where the distance that sounds can travel is heavily influenced by both the source amplitude and the properties of the substrate that can absorb or interfere with the sound wave. Hager and Kirchner (2013) found termite vibrational signals produced by an individual have a range of only 0.4 m due to attenuation properties of the soil that dampen the signal amplitude. Despite this limited range, the signals can be propagated through the rest of the nest by receiving termites that relay the signal onward. Finally, sampling biases may explain differences in reports of defensive sound production between taxa, sexes, or developmental stages. For instance, Lepidoptera, Coleoptera, and Hemiptera are not only speciose orders, but also generally well-studied, thereby increasing the likelihood of researchers encountering species that produce defense sounds. Also, some signals may go undetected without the use of specialized recording equipment, such as laser vibrometers that are required to record solid-borne defense sounds. Similarly, in many instances, defense sounds are intended for close range communication with a predator and do not travel long distances (e.g., Bura et al., 2016). In these cases, unless a researcher is explicitly attacking an insect and recording sounds, the signals may not be noticed. For example, Walters et al. (2001) investigated the antipredator defenses of *Manduca sexta* caterpillars (Sphingidae), but overlooked their defensive clicking [subsequently reported by Bura et al. (2012)] by not recording sounds during their trials. Hypotheses to explain the evolution and variation of traits such as communication signals are being increasingly tested using phylogenetic comparative methods (e.g., acoustic communication in Orthoptera, Song et al., 2020). We believe that using phylogenetic comparative analyses that incorporate morphological traits, predator types, habitats, and other defenses will be particularly insightful for testing and developing hypotheses explaining why some species produce defense sounds while others do not.

DIVERSITY OF MECHANISMS

Insects are highly acoustic animals and have evolved numerous mechanisms of sound production that occur on all different body parts. The hardened exoskeleton of insects has enabled the evolution of this range of mechanisms, although even soft-bodied insects such as caterpillars can produce sounds using forced air or limited sclerotized body parts (e.g., Bura et al., 2016). Sound-producing mechanisms in insects have been reviewed by several authors, including Haskell (1961), Dumortier (1963b), Ewing (1989), and Hill (2008). These authors use a variety of terms to describe different mechanisms, including stridulation, percussion, vibration, click mechanisms, air expulsion, frictional mechanisms, and vibrating membranes. Even though sound production in insects has been reviewed, sounds produced specifically in a defensive context have not. Here, we describe the various mechanisms used for producing defense sounds as well as the locations on the body where these mechanisms occur.

We recognize five categories of sound-producing mechanisms derived from terms used by Ewing (1989) and Hill (2014): stridulation, percussion, tymbalation, tremulation, and forced air (**Figure 2**). Stridulation involves the rubbing of two body parts together or one body part on the substrate to produce sounds. The body parts may be unspecialized, such as mandibles rubbing against one another (e.g., Brown et al., 2007), or specialized, such as a file and scraper (e.g., Dobai et al., 2018, **Figure 2A**). Coleoptera exhibit the greatest diversity of stridulatory mechanisms (**Figure 3**). Percussion, which involves "tapping" or "drumming" the substrate, is common among ants (e.g., Fuchs, 1976) and termites (e.g., Hager and Kirchner, 2013, **Figure 2B**) that use these sounds as alarm signals. Tymbalation occurs via the buckling action of specialized body parts, often called tymbals, and is found in Lepidoptera and Hemiptera. This mechanism is well-known in moths that produce anti-bat

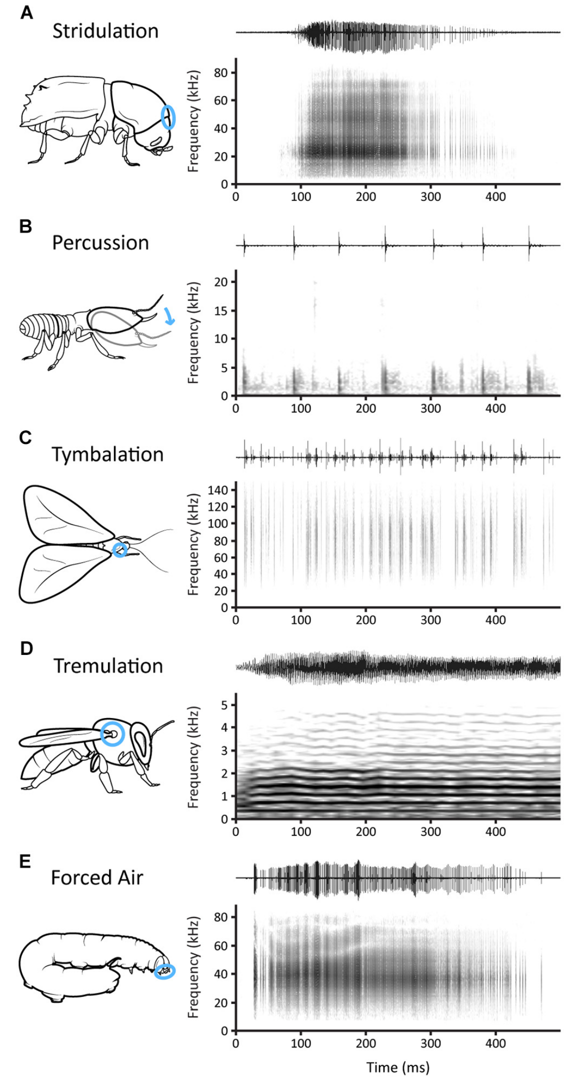

FIGURE 2 | The five types of mechanisms that insects use to produce defense sounds, illustrated by examples from five different insects. Blue circles correspond to the location of the mechanism in the chosen example. Waveforms and corresponding spectrograms show 500 ms of sound from each species. **(A)** Stridulation: a single chirp produced by an *Ips pini* bark beetle. Chirps are produced using a file and scraper mechanism located between the head and pronotum. **(B)** Percussion: a series of drumming signals by a *Macrotermes natalensis* termite. The signals are produced by tapping the substrate with its head. **(C)** Tymbalation: a series of clicks produced by a *Eubaphe unicolor* moth. Clicks are produced via a pair of tymbals located one on each side of the prothorax. **(D)** Tremulation: a group piping signal produced by *Apis florea* bees. Piping sounds are produced through vibrations of the flight muscles. **(E)** Forced Air: a single vocalization produced by an *Amphion floridensis* caterpillar. Vocalizations are made by airflow from the alimentary canal. Sound files were contributed by the Yack Lab (*I. pini* and *A. floridensis*), F. Hager (*M. natalensis*), A. Corcoran (*E. unicolor*), and S. Fuchs (*A. florea*). See text and **Table 1** for further details on these examples.

clicks (e.g., Conner and Corcoran, 2012; Corcoran and Hristov, 2014, **Figure 2C**), and in cicada anti-predator squawks (e.g., Smith and Langley, 1978). Tremulation involves bodily motions that are transmitted as vibrations through the substrate and is usually produced by bobbing movements (Virant-Doberlet and Čokl, 2004). We broaden this definition of tremulation to include the vibration of flight muscles of both Diptera (e.g., Rashed et al., 2009) and Hymenoptera (e.g., Sen Sarma et al., 2002, **Figure 2D**). Forced air mechanisms are produced via airflow from an orifice such as spiracles (e.g., Bura et al., 2011) or the alimentary canal (e.g., Brehm et al., 2015; Rosi-Denadai et al., 2018, **Figure 2E**). All five of these broad categories are used by different insects for defense sounds, but the locations where each is found varies.

Mechanisms used to produce defense sounds have evolved on almost every part of the body, as illustrated in **Figure 3**. We excluded percussion and tremulation from the figure as these usually involve large undifferentiated regions of the body, such as the head of termites and the flight muscles of flies (**Table 1**). Also excluded from the figure are mechanisms such as "rustling of the wings" where no specific location is mentioned. Our results show that mechanisms of defensive sound production occur on numerous different body regions in both adults (**Figure 3A**) and juveniles (**Figures 3B–D**). Of the 58 mechanisms illustrated, 49 are stridulatory. Stridulatory mechanisms predominantly occur either between neighboring segments (e.g., #7, **Figure 3A**; #52, **Figure 3C**), or on a section of the body that can be rubbed by appendages such as the hind legs (e.g., #19, **Figures 3A,B**) or, in adults only, the wings (e.g., #26, **Figure 3A**). Tymbals used to produce defense sounds are only noted in adults. These are located on the prothorax (#45, **Figure 3A**) or metathorax (#44, **Figure 3A**) in Lepidoptera, and on the first abdominal segment in Hemiptera (#20, **Figure 3A**). However, some Nymphalidae butterflies use a portion of their forewing membrane as a tymbal-like structure that buckles to produce clicks (#48, **Figure 3A**) (Møhl and Miller, 1976), and some Yponomeutidae moths use a part of their hind wing in a similar manner (#57, **Figure 3A**) (O'Reilly et al., 2019). Forced air mechanisms are found in both adults and juveniles. Spiracles are used for air expulsion in larvae of Coleoptera (#31, **Figure 3D**) and Lepidoptera (#55, **Figure 3D**), as well as both adults and nymphs in Blattodea (#15, **Figures 3A,B**). Airflow via the alimentary canal is found in both adults and juveniles of Orthoptera (#3, **Figures 3A,B**) and Lepidoptera (#3, **Figures 3A,D**).

Why might a mechanism evolve where it does on a given insect? For stridulation, the mechanisms are found where body parts can be easily rubbed together (Dumortier, 1963b) and the neuromuscular control is likely already available. In hard-bodied insect adults, the site possibilities are vast as demonstrated by the diversity within Coleoptera. In soft-bodied insect larvae, stridulatory mechanisms are restricted to sclerotized areas such as the head and legs (**Figure 3D**). Tymbalation requires a flexible region of the exoskeleton as well as a method of buckling this region. Tymbals located on the main body occur on or near the thorax where locomotory muscles can be used to pull the tymbal in and out (Wessel et al., 2014). On the other hand, tymbal-like mechanisms on wings will require either an opposing structure to press against (e.g., Møhl and Miller, 1976), or rely on movement of the wings themselves to buckle the flexible wing membrane (e.g., O'Reilly et al., 2019). For forced air, which

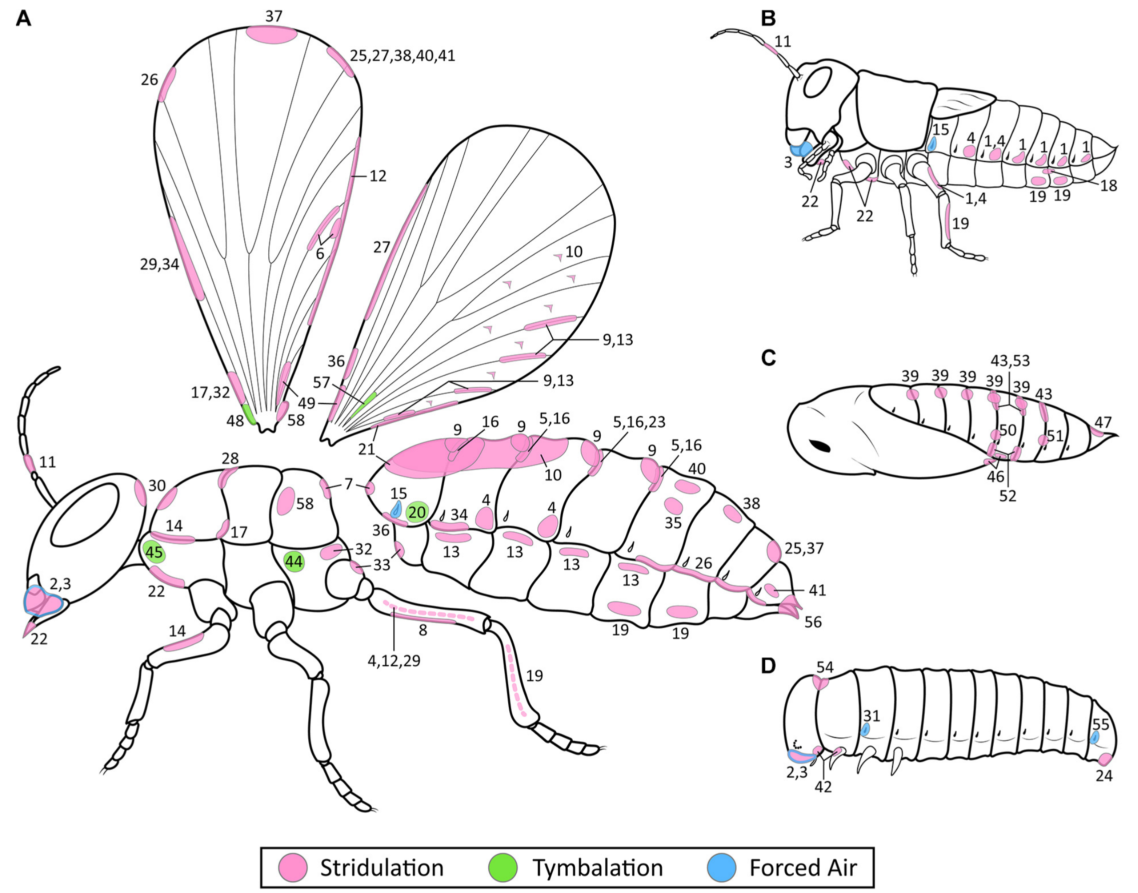

FIGURE 3 | Location of stridulation, tymbalation, and forced air mechanisms used for producing defense sounds in adult and juvenile insects. Percussion and tremulation were excluded as they generally employ undifferentiated body parts. Each number represents a position where a sound-producing mechanism has been recorded in the literature. **(A)** Generic adult insect. **(B)** Generic nymph. **(C)** Generic pupa. **(D)** Generic larva. The numbers correspond to their order of appearance in **Table 1**, which includes information on the orders, families, and literature citations. Mechanisms by insect order are as follows: 1: Odonata. 2–3: Orthoptera and Lepidoptera. 4–10: Orthoptera. 11: Phasmatodea. 12–14: Mantodea. 15–18: Blattodea. 19–22: Hemiptera. 23–24: Hymenoptera. 25–41: Coleoptera. 42: Trichoptera. 43–57: Lepidoptera. 58: Mecoptera. Tymbal mechanisms (numbers 20, 44, 45, 48, and 57) are in green. Forced air mechanisms (numbers 3, 15, 31, and 55) are in blue. Stridulatory mechanisms (all other numbers) are in pink. In stridulatory mechanisms that involve two rubbing parts, both parts are given the same number. A dotted line represents a mechanism located on the inner surface of that appendage. Note that numbers 8 and 35 do not have a corresponding location marked on the wings as the entire wing is used in these mechanisms.

pair of spiracles evolved for sound production likely depends on the underlying control of airflow within each insect's tracheal system. Directional airflow is controlled by the coordinated action of the spiracles and ventilatory movements (Heinrich et al., 2013). A spiracle used for sound production likely evolved from one originally used in air output, as demonstrated in hissing cockroaches (Nelson, 1979). The alimentary canal mechanism of forced air may originate from a sucking-pump as proposed for *Acherontia atropos* moths (Brehm et al., 2015), or from regurgitation as proposed in *Amphion floridensis* caterpillars (Sphingidae) (Rosi-Denadai et al., 2018). Percussion mechanisms use body parts already equipped with the flexibility to drum on a surface, while for tremulation the only described mechanisms used for defense sounds are flight muscles that can be decoupled from the wings to prevent flight. The morphological variation among and between these mechanisms creates a diversity of signal characteristics, and we explore this relationship in the next section.

HOW AND WHY DEFENSE SOUNDS VARY

Insect defense sounds demonstrate wide variation in their physical characteristics. Sound unit durations (unit being an individual sound as perceived by the human ear, Broughton, 1976) range from 250 μs (tiger beetle clicking, Yager and Spangler, 1997) to periods of over a minute (bee hissing and their mimics, Sen Sarma et al., 2002). Dominant frequencies range from 152 Hz (wasp buzzing, Coelho, 1998) to 90 kHz (hawkmoth stridulation, Kawahara and Barber, 2015). The loudest sound level reported is 110 dB SPL at 8–10 cm (butterfly clicks, Møhl and Miller, 1976) while the quietest reported is 49.8 dB SPL at 2 cm (caterpillar whistling, Sugiura and Takanashi, 2018). This wide variation in signal characteristics disagrees with past proposals that defense sounds tend to share similar characteristics (e.g., Masters, 1980; Schmitt and Traue, 1990; Field, 2001). So why do defense sounds vary? While there are many factors that could explain this variation, we consider the following: morphological influences, the sensory system of the receiver, and the information content of the signal.

An insect's morphological features can impact their signal characteristics. First, the physical structure of the mechanism itself directly influences the traits of the sound produced (Dumortier, 1963c). For example, the number of ridges on a tiger moth's tymbal correlates to the maximum click rate of their sounds (Dowdy and Conner, 2019). Second, sound production and propagation are highly affected by body size. Smaller insects not only have less muscle power available to produce sounds, but also have smaller resonating structures that are more efficient at transmitting high frequency than low frequency airborne sounds (Bennet-Clark, 1998). Third, the form of the resonating structures influences the frequencies that are transmitted. For instance, the unspecialized gaster of ants provides a resonating structure that transmits broadband alarm signals (Masters et al., 1983). Crickets on the other hand use a specialized portion of their forewing called the "harp," and the frequency and bandwidth of the sounds produced depend on how well the harp is coupled to the sound-producing mechanism (Montealegre-Z et al., 2011). However, the latter example has only been studied in a mating context. Fourth, properties of the insect's exoskeleton will influence the sounds produced. For example, a certain degree of sclerotization is necessary for both percussion and stridulation. Perhaps this is why soft-bodied larvae use fewer of these mechanisms, and why the mechanisms are isolated to sclerotized body parts (see **Figure 3D**). Researchers should take into account morphological factors when testing hypotheses to explain why defense sounds differ in their physical characteristics.

Just as the hearing of prey insects is shaped by the sounds of their predators (see Yack et al., 2020), the defense sounds of prey should be shaped by their receivers. A receiver may be a predator (vertebrate or invertebrate), parasitoid, or non-predator (conspecific or heterospecific). If the receiver is very specific, then we might expect these signals to be specialized to that receiver. Tiger moth tymbal clicks are an example of targeted defense sounds. The dominant frequency of these clicks is usually ultrasonic, ranging from 28 to 82 kHz (Corcoran et al., 2010), and matches the ultrasonic hearing of insectivorous bats (Sales and Pye, 1974). Similarly, vibratory signals in termites that function to warn colony members of a threat contain most energy between 1 and 5 kHz, matching the frequencies that initiate conspecific behavioral responses (Hager and Kirchner, 2013). In contrast, a defense sound may target a wide range of predators each with different acoustic sensitivities. In such cases, we might expect the sounds to be of broader bandwidth and simpler temporal structure to reflect a range in sensory processing and cognitive skills (Masters, 1980). For instance, stridulation of *Dasymutilla* sp. wasps (Mutillidae) is broadband, simple, and shown to inhibit attacks by both mice and spiders (Masters, 1979, 1980). Additionally, *Antheraea polyphemus* caterpillars (Saturniidae) are attacked by a range of invertebrate and vertebrate predators, and their stridulatory defense sounds are broadband and simple in temporal structure (Brown et al., 2007).

Comparing characteristics of sounds produced within a species but in different contexts can lend insights into the selective pressures on defense sounds enacted by receivers. **Figure 4** illustrates a few examples of insects that produce sound in both defensive and reproductive contexts. *Dendroctonus valens* and *I. pini* bark beetles (Curculionidae) as well as *Cyphoderris monstrosa* orthopterans (Prophalangopsidae) produce defense sounds that are simpler in temporal structure (e.g., lower pulse rates and shorter durations) than their songs aimed at potential mates (Mason, 1991; Lindeman and Yack, 2015; Dobai et al., 2018; Mason, pers. comm.). One possible explanation for defense sounds being simpler in these species is that they target a broad predator audience, whereas songs directed at potential mates advertise individual characteristics (e.g., skill, health, size, and energy reserves) that are communicated by signal traits. For example, *D. valens* courtship sounds consist of interrupted chirps proposed to advertise male body size and condition to females, and females prefer more complex interrupted chirps than simpler ones (**Figure 4**) (Lindeman and Yack, 2015). In *Manulea japonica* tiger moths (Arctiinae), the opposite is true, as courtship songs produced by males are simpler in temporal structure than defense sounds (Nakano et al., 2013). Females must distinguish between courtship songs and bat sounds as the latter induces a defensive response in females including sound production and/or escape. Perhaps courtship songs evolved to be simpler in temporal structure to prevent the female from responding with an evasive response. At present, there are few studies in insects that compare signal traits of sounds produced in different behavioral contexts (e.g., defense, reproduction, and aggression). In addition to the above-mentioned examples, see also Kowalski and Lakes-Harlan (2010) on ground crickets, and Stölting et al. (2004) on cicadas. We encourage more such studies to better understand receiver selective pressures on defense sound characteristics.

Defense sound characteristics are also proposed to vary according to the message being conveyed (Bura et al., 2016). However, only two authors have tested this hypothesis in insects. Corcoran et al. (2010) found that the signal characteristics of tiger moth anti-bat clicks cluster into two groups: sound units with low duty cycle (proportion of time occupied by sound) are proposed to function as warning sounds, and high duty cycle units as sonar jamming sounds. In Bombycoidea caterpillars, short duration sounds are associated more with chemical defense than longer sounds, which are instead proposed to function in deimatic displays (Bura et al., 2016). The functional implications of different signal characteristics in conveying different messages to receivers are discussed further in the next section.

PROPOSED FUNCTIONS OF DEFENSE SOUNDS

A defense sound can be directed at either the attacker or a conspecific. Proposed functions of sounds directed at the attacker

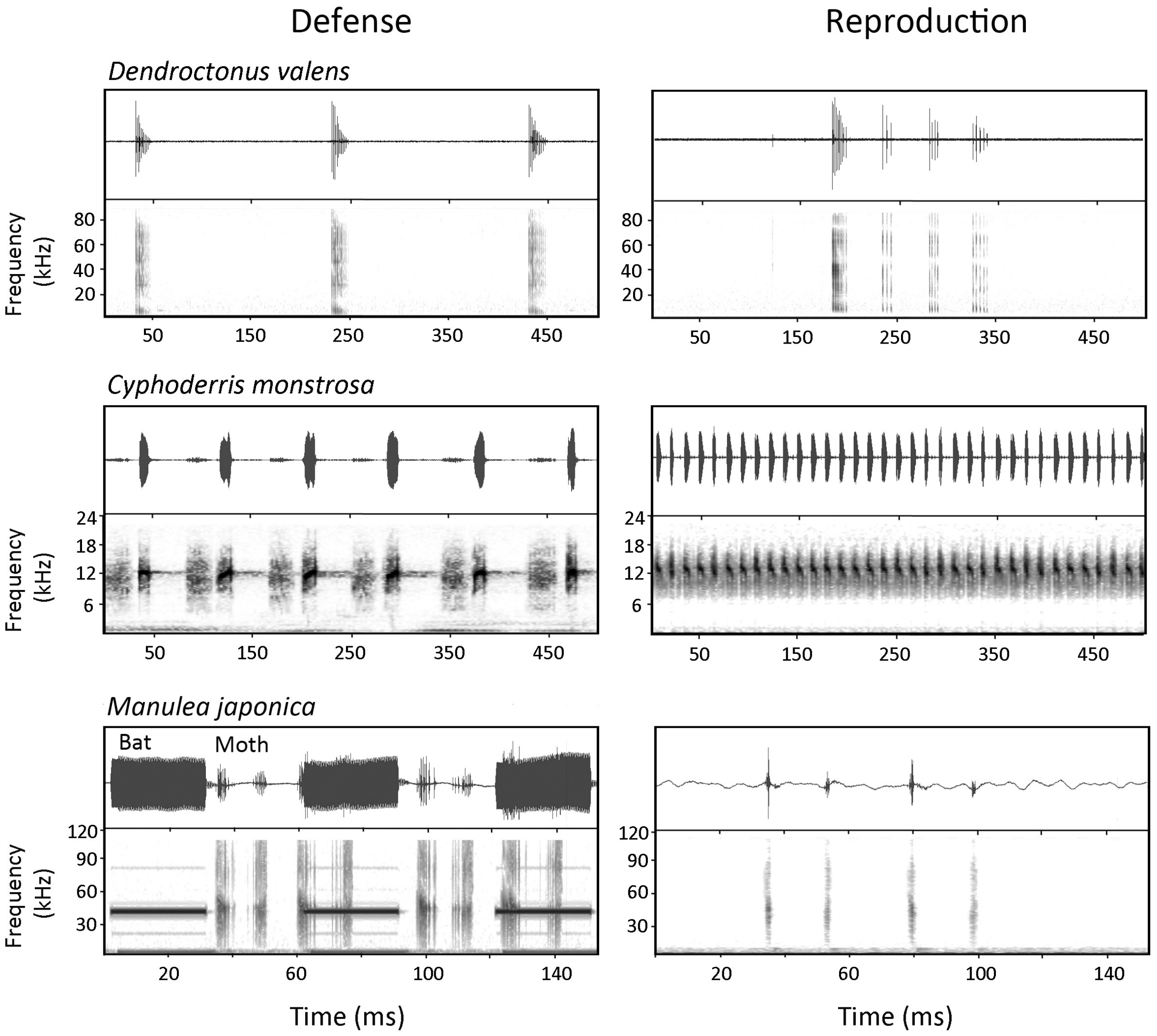

FIGURE 4 | Sounds produced by insects in both defense and reproduction to illustrate contextual differences in signal characteristics. In a defensive context, the male bark beetle *Dendroctonus valens* produces 'simple' chirps that are temporally simple compared to the more complex 'interrupted' chirps that are predominant during courtship displays. The male orthopteran *Cyphoderris monstrosa* produces a series of disyllabic chirps as defense sounds while the calling song is a continuous series of rapid trills. The male *Manulea japonica* tiger moth produces a burst of tymbal clicks in response to simulated bat calls (simulated bat calls in the spectrogram are shown as longer duration calls at ~40 kHz that precede the moth clicks), while the courtship tymbal clicks are simpler in structure. Sound files were contributed by the Yack Lab (*D. valens*), A. Mason (*C. monstrosa*), and R. Nakano (*M. japonica*). See text and **Table 1** for further details on these examples.

include deimatism, aposematism, mimicry, or interference, while those aimed at conspecifics (and sometimes heterospecifics) are usually alarm signals. We define each of these proposed functions based on the broader defense literature (Ruxton et al., 2018) and provide examples if available. We also summarize the predicted receiver responses and defense sound characteristics for each functional category in **Figure 5**.

Signals Directed at Predators

Deimatic Displays

Deimatic displays have been defined as signals that act on the innate startle response of a predator (Skelhorn et al., 2016; Umbers et al., 2017). Although there has been debate on what comprises a deimatic display and how a predator will react (see Umbers et al., 2015; Skelhorn et al., 2016; Umbers and Mappes, 2016), predicted predator responses typically include the predator fleeing from the prey or hesitating long enough for the prey to escape, as well as habituation to the signal with repeated exposure, provided the prey is not otherwise defended (**Figure 5**) (Skelhorn et al., 2016; Umbers et al., 2017). In the visual realm for example, eyespots in butterflies and caterpillars are often recognized as a form of deimatic display that can cause predators to retreat (e.g., Vallin et al., 2005; Hossie and Sherratt, 2013) and habituate with repeated exposure (e.g., Blest, 1957). In the acoustic realm, there are few

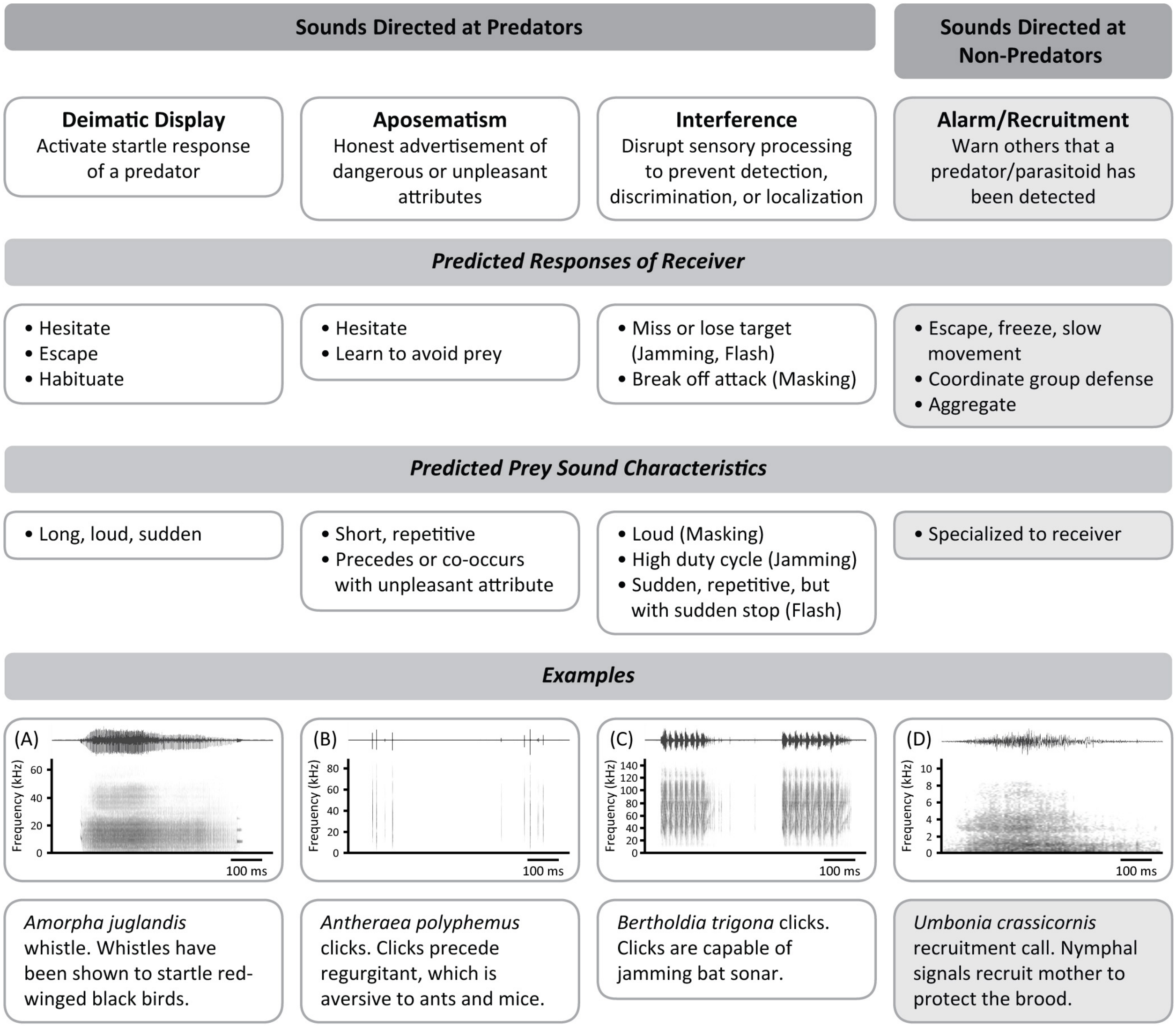

FIGURE 5 | Hypotheses explaining the function of insect defense sounds with corresponding predictions of both prey characteristics and receiver responses. Sound files **(A–D)**, shown as examples, were contributed by the Yack Lab (*A. juglandis* and *A. polyphemus*), A. Corcoran (*B. trigona*), and R. Cocroft (*Umbonia crassicornis*). See text for further discussion of these functions and corresponding examples.

experimentally tested examples of deimatic sounds involving predator responses (**Table 1**). Stridulation in *Henschoutedenia epilamproides* cockroaches (Blaberidae) startles rats and voles, causing them to withdraw (Guthrie, 1966). Clicking in *Aglais io* butterflies (Nymphalidae) causes bats to scream, jump, and retreat (Møhl and Miller, 1976), and causes mice to run away without attacking (Olofsson et al., 2012). Whistling in *Amorpha juglandis* caterpillars (Sphingidae) startles birds, causing them to dive and fly away (Bura et al., 2011; Dookie et al., 2017, **Figure 5A**), though birds habituate with repeated exposure to the sounds (Dookie et al., 2017). Deimatic sounds in insects have been characterized as being long, loud, and sudden – physical characteristics that are proposed to activate the predator's startle response (e.g., Hill, 2007; Kowalski et al., 2014). For instance, *A. juglandis* whistles are 440 ± 272 ms long, 69 to 82 dB SPL at 5 cm, and elicited upon contact (Bura et al., 2011). While insect defense sounds are sometimes proposed to be deimatic based on their signal characteristics alone (e.g., Kowalski et al., 2014; Bura et al., 2016), it is key when assessing any defensive function that the predator's responses be recorded (Skelhorn et al., 2016). Also, some insects combine deimatic sounds with visual displays, and the components of such multimodal defenses may operate synergistically, or individually to target different predators (Rowe and Halpin, 2013). For example, while clicks alone in *A. io* butterflies startle bats and mice, it is the hidden eyespots alone (which are revealed simultaneously with the sounds) that have a startling effect on birds (Vallin et al., 2005). This example highlights the necessity of studying responses to defense sounds by different predators. Future research should involve experiments with predators (and not focus only on signal characteristics of the prey) as well as investigate potential synergistic effects of the insect's entire defensive display.

Aposematism

Aposematism is the honest advertisement of dangerous or unpleasant attributes (Edmunds, 1974; Ruxton et al., 2018; Caro and Ruxton, 2019). These attributes include not only distastefulness or toxicity, but also stinging spines, ability to fight back, and a vicious bite. Naïve predators are predicted to hesitate prior to sampling novel aposematic prey, while experienced predators will have learned to associate the signal with the unpleasant attribute and reject such prey based on the signal alone (**Figure 5**) (Speed, 2000). For example, red is a common aposematic color that can cause naïve predators to hesitate (Exnerová et al., 2007) and also facilitates learning more so than other colors (Rönkä et al., 2018). *A. polyphemus* caterpillars (Saturniidae) provide strong evidence for their sounds being aposematic. After simulated attacks or attacks from chicks, caterpillars produce clicking sounds followed by regurgitation. The regurgitant is aversive to ants and mice, and chicks stop their attacks following the caterpillar's regurgitation (Brown et al., 2007, **Figure 5B**). In another caterpillar, *Saturnia pyri* (Saturniidae), short chirping sounds are induced by simulated predator attacks and these sounds precede or accompany the secretion of defensive phenolic chemicals from scoli (bristle-bearing outgrowths) (Bura et al., 2009). These chemicals were shown in previous studies to be aversive to birds and ants (Deml and Dettner, 1993, 1995). Learned avoidance to an aposematic sound has been demonstrated in bats. Bats learn to associate tiger moth tymbal clicks with distastefulness in as few as two exposures to clicking moths, and will thereafter avoid the moths in a lab setting (Hristov and Conner, 2005). Similar to acoustic deimatism, some defended insects may combine sounds with warning coloration or odors, and such multimodal displays may increase the efficacy of an aposematic display or improve predator's learning of defended prey (Rowe and Halpin, 2013).

While it has been hypothesized that some sound characteristics may be more effective as aposematic signals than others (e.g., Bura et al., 2016), this has not yet been experimentally validated. However, we can draw on visual aposematic characteristics to make predictions. To improve prey discrimination and enhance learning, visual aposematic signals are predicted to be simple, symmetrically patterned, and conspicuous (Forsman and Merilaita, 1999; Ruxton et al., 2018). Simple visual signals such as bold patterns and few colors may be more reliably recognized than complex patterns (Cott, 1940), while symmetric patterns are easier to detect, learn, and remember than asymmetric patterns (Forsman and Merilaita, 1999). We predict the equivalent acoustic traits to be short (simple) and repetitive (symmetrical) sound units that are distinct from the background noise (conspicuous). For example, *A. polyphemus* aposematic clicks are short (24.7 ± 17.2 ms in duration), repetitive (52.7 ± 82.2 clicks in a train of sound), and distinct (ranging from 58.1 to 78.8 dB SPL at 10 cm) (Brown et al., 2007). Additionally, Masters (1980) noted a short and repetitive trend among disturbance stridulations of beetles, true bugs, and velvet ants, and Bura et al. (2016) found that short sounds correspond to the presence of chemical defenses (regurgitation or secretions from scoli) in caterpillars. These traits may aid in learning and memory retention as reported for clicker training with vertebrates (Smith and Davis, 2008). It has been reported that some moths produce ultrasonic aposematic sounds continually during flight (O'Reilly et al., 2019). Such proposed warning sounds that are always turned 'on,' analogous to warning coloration, would be interesting to explore further with live predators. We recommend that future studies focus on identifying effective aposematic sound characteristics and their impacts on a predator's psychology.

Mimicry

Defensive mimicry occurs when one individual (the mimic) copies the appearance or behavior of another (the model) to gain a selective advantage (Jamie, 2017). There are several ways that mimicry may be used for protective measures, but how a predator is predicted to respond depends primarily on its experience with the model. We address three forms of acoustic mimicry. First, in Müllerian mimicry both the mimic and model are defended, and the predator is predicted to respond as it would to an aposematic signal (**Figure 5**). Müllerian mimicry may also facilitate a predator's learning and memory retention of aposematic signals (Bradbury and Vehrencamp, 2011; Ruxton et al., 2018). Acoustic Müllerian mimicry is proposed to occur among defended clicking tiger moth species (Barber and Conner, 2007) and between defended clicking tiger moths and tiger beetles (Yager and Spangler, 1997). Second, in Batesian mimicry an undefended mimic copies an aposematic model. The predicted response of a predator that has had previous experience with the model is to avoid the mimic, whereas if the mimic is encountered prior to the model, then we would not expect a naïve predator to learn to avoid the signal. For example, Barber and Conner (2007) reported that after having sampled *Cycnia tenera*, a noxious clicking tiger moth (Arctiinae), red and big brown bats refuse palatable, clicking *Euchaetes egle* tiger moths. Another proposed acoustic Batesian mimic is *Eubaphe unicolor* (Geometridae), a palatable moth that produces tymbal clicks very similar to its sympatric, unpalatable tiger moth species (Corcoran and Hristov, 2014). Third, it has been proposed that insects can mimic the alarm calls of their predators. In vertebrates, such calls signal danger to conspecifics who react by increasing their vigilance or seeking cover (Fallow et al., 2013). An example of acoustic mimicry in insects is whistling in *A. juglandis* (Sphingidae) that is proposed to mimic the alarm calls of the caterpillar's avian predator (Dookie et al., 2017). Further studies on acoustic mimicry in insects should include comparisons of acoustic characteristics between models and mimics to determine their degree of similarity, playback studies to monitor predator responses, and palatability trials using different predators.

Interference Signals

Another way that insects may thwart attack is to interfere with a predator's sensory processing capabilities by impeding detection, discrimination, or localization of prey. For example, flash coloration (a form of flash behavior) can cause a predator to lose track of its original target when a flash of color is revealed while fleeing, then hidden when stopped (Loeffler-Henry et al., 2018; Caro et al., 2020). Predicted predator responses to interference signals vary based on how the signals affect their cognitive processing. To date, three types of acoustic interference have been described in insects: sonar jamming, flash noise, and masking (**Figure 5**). Sonar jamming prevents prey localization by disrupting the returning echolocation signals of bats and causing the bats to miss their target (Corcoran et al., 2011). Jamming sounds are predicted to have a high duty cycle (proportion of time occupied by sound) to effectively disrupt echoes (Corcoran et al., 2009), and indeed, *B. trigona* tiger moths (Arctiinae) produce tymbal sounds with a 44% duty cycle (Corcoran et al., 2011, **Figure 5C**). However, after reporting that hawkmoths produce jamming sounds via genital stridulation with duty cycles as low as 18%, Kawahara and Barber (2015) proposed that a duty cycle threshold of about 20% or higher is necessary to jam bat sonar. The second type of acoustic interference is flash noise. Similar to flash coloration, flash noise occurs when the prey produces a sound that a predator can track acoustically (Edmunds, 1974). The predator is predicted to lose track of the prey when the signaler falls silent. For instance, a disturbed grasshopper (species unspecified) may be tracked via its wing-beat sounds, but when it lands and is again silent, the predator is unable to pinpoint its location (Edmunds, 1974). We believe that this would be especially true if the grasshopper stops flapping before it hits the ground, leaving a gap between where the sound was last heard and where the insect lands. However, the function of flash noises in hindering predators remains speculative. Masking, the third type of acoustic interference, occurs when one sound makes other sounds difficult to hear (Carterette and Friedman, 1978). Smith and Langley (1978) proposed that cicada disturbance squawks decrease the auditory acuity of a mouse by being loud, possibly preventing the mouse from hearing its own predators while handling the cicada. This could thereby make the cicada unprofitable to pursue, and the mouse would be predicted to break off the attack.

Signals Directed at Non-predators

Alarm Signals

Defense sounds directed at non-predators are referred to as alarm signals and are used to warn conspecifics, and sometimes heterospecifics, that a predator or parasitoid has been detected (Bradbury and Vehrencamp, 2011). Thus, alarm signals are usually found in group-living animals. Acoustic alarm signals in insects are predominantly transmitted and perceived through the substrate as vibrations, though some may have an airborne component (Hunt and Richard, 2013). Generally, receivers of an alarm signal respond by escaping, slowing their movement, coordinating a group defense, or approaching the signaler to provide aid (**Figure 5**). For example, drumming in *Camponotus* spp. carpenter ants (Formicidae) induces a context-dependent response where workers that were mostly still prior to the signal will freeze altogether, but those that were already in motion begin moving faster (Fuchs, 1976). Piping by returning foragers of *Apis florea* honeybees (Apidae) alerts the colony to a nearby threat and initiates coordinated hissing among the whole colony (Sen Sarma et al., 2002). The hissing in turn is thought to be an aposematic signal to approaching predators. Coordinated group responses to alarm signals also include tapping within nests by *Parachartergus colobopterus* (Vespidae) that calls the wasps outside to spray venom at intruders (Jeanne and Keeping, 1995). Alarm signals can also coordinate group formation, as observed in disturbed *Stolas* sp. beetle larvae (Chrysomelidae) where vibrational signals recruit other larvae to form a circle (Greenfield, 2002). This coordinated response may offer a survival advantage through safety in numbers (Dury et al., 2014). A rather unique type of alarm signal is the "stop" signal of honeybees (Apidae). When *Apis cerana* bees encounter danger at a foraging site, they prevent further recruitment to the site by using vibratory signals to stop any waggle dance that would otherwise recruit bees to that site (Dong et al., 2019). Insects that use alarm signals to recruit help to the signaler include *Umbonia* sp. treehopper nymphs (Membracidae) that produce vibrations when disturbed by a predator (Cocroft, 1996; Ramaswamy and Cocroft, 2009, **Figure 5D**). As the vibrational signals are transmitted across the brood, the mother responds by approaching the disturbance and often succeeds in repelling the attacker. Recruitment calls can also be directed toward heterospecifics, as seen in Lycaenidae and Riodinidae caterpillars that use solid-borne vibrations to induce ants to attend to them (Pierce et al., 2002). Tending by ants offers protection from predators and parasitoids, with untended caterpillars facing more predation by wasps than tended ones (Pierce et al., 1987; DeVries, 1991). Despite the examples that demonstrate the benefits of acoustic alarm signals to a colony, these signals have mostly been studied in the eusocial Hymenoptera and Blattodea. However, as many other substrate-bound insects (e.g., caterpillars and sawfly larvae) form groups (see Costa, 2006), the role of vibratory communication in mediating group defensive responses should be further explored in these insects.

EVOLUTIONARY ORIGINS

How did defense sounds evolve in the first place? There are two possibilities discussed in the literature: (1) they evolved from non-signaling behaviors; or (2) they were co-opted from acoustic signals that evolved for another function. Ideally, testing hypotheses on the evolutionary origins of a trait are conducted using a phylogenetic comparative approach which requires examples of homologous traits at various stages of evolution as well as a robust phylogeny (Petak, 2019). However, to the best of our knowledge this approach has not been used to test hypotheses explaining the origins of insect defense sounds. Nonetheless, we can speculate on the evolutionary origins of sonic defenses given the limited evidence available.

A communication signal can evolve from a non-signaling behavior through the process of ritualization (Scott et al., 2010; Petak, 2019). Non-signaling behaviors such as walking, flying, or using a spray apparatus can produce incidental sounds which act as cues, meaning traits that have not evolved to alter a recipient's behavior (Yack et al., 2020). Cues can evolve into signals through ritualization whereby they become more conspicuous and stereotyped (Petak, 2019). Ritualization seems the most likely explanation for how sonic defenses evolved, especially when a defense sound is the only form of acoustic communication in a species. Several such hypotheses have been proposed for insects. Alexander (1956) suggested that defense sounds evolved from incidental sounds produced during a struggle with a predator. Nelson and Fraser (1980) proposed that hissing in cockroaches evolved from a spray apparatus since some insects produce defensive froths from their spiracles or other body openings, and can even produce incidental sounds while doing so (e.g., Carpenter, 1938). Tiger moth tymbals and the clicks they produce are proposed to have evolved through modification of the thoracic pleura which buckle when the moth is walking or flying, and so may have been associated with escape behaviors (Fullard, 1992).

A communication signal can also evolve secondarily from a pre-existing signal. For example, ultrasonic courtship signals were co-opted from anti-bat clicks in several tiger moth species (Simmons and Conner, 1996; Weller et al., 1999). Though evolving from a pre-existing signal has been less commonly proposed for defense sounds, there are a few examples. Defense sounds in crickets and katydids are proposed to have evolved from sexual signals due to the ubiquity of acoustic sexual signals in this group and the relative lack of defensive sound production (Alexander, 1960). Cases where only one sex produces both sexual and defense sounds may also indicate that the sonic defenses evolved from a pre-existing sexual signal. For instance, many species of bark beetles show sexual dimorphism in sound production whereby only one sex produces sounds in both sexual and defensive contexts (Bedoya et al., 2019). In cicadas, Smith and Langley (1978) proposed that disturbance squawks evolved secondarily to courtship sounds as both sound types, when produced via tymbals, are found only in males. If signals evolved initially for defense, it is difficult to explain the lack of tymbal sound production in the opposite sex (Smith and Langley, 1978). Territorial signals may provide another origin for some defense sounds, possibly in caddisfly larvae (Hydropsychidae) that produce sounds both when poked with forceps and when other larvae attempt to enter their shelter (Johnstone, 1964). To the best of our knowledge, co-opting a pre-existing acoustic communication signal for use in defensive sound production has yet to be formally investigated.

Future research on the evolutionary origins of defense sounds must involve phylogenetic comparative studies. Such studies require documentation of a series of variable, but homologous, morphological and associated behavioral traits within extant species, as well as a robust phylogeny to assess which traits are ancestral or derived. Behavioral traits are more challenging to document than morphological traits as they must be studied in living specimens. Consequently, there are currently few phylogenetic comparative analyses on the evolution of insect defensive displays (but see Vidal-García et al., 2020). This review has identified several insect groups that are promising for studying evolutionary origins of defense sounds in that the groups display variable sonic defenses and recent phylogenies are available. These insect groups include praying mantids (e.g., Vidal-García et al., 2020), tiger moths (e.g., Zaspel et al., 2014; Dowdy and Conner, 2019), Lepidoptera pupae (e.g., Dolle et al., 2018; Espeland et al., 2018), and Bombycoidea caterpillars (e.g., Bura et al., 2016). These model systems will allow us not only to test hypotheses on evolutionary origins of defense sounds, but also test hypotheses on why some insects evolve sonic defenses and others do not.

CONCLUSION

Defense sounds occur widely in insects. Yet, compared to our understanding of visual defenses, there are major gaps in our understanding of which insects produce defense sounds, how these sounds promote survival, and how they evolved. Here, we recommend some key, non-mutually exclusive lines of investigation and questions to focus on in future research. First, further testing is necessary to better document the extent of defensive sound production throughout the Class Insecta. Because defense sounds often occur only during close encounters with predators and thus may be "quiet," they may go unnoticed unless "attacked" by the experimenter. Also, defense sounds that are ultrasonic, or transmitted as solid-borne vibrations, can easily be overlooked by scientists not using specialized equipment. We recommend conducting experiments on those orders that are not well-represented in the literature, being careful to document any differences in the sex of the species being assessed. We also recommend further investigations on juvenile stages such as larvae, nymphs, pupae, and eggs. Second, what are the key selective pressures that led to the evolution of defense sounds? Variables including the types of predators, the presence of other defenses, body size, and life history traits should be documented and analyzed using phylogenetic comparative methods, meta-analyses, and developmental studies to address this question. Third, what explains the wide variation in signal characteristics? How much of this variation is related to factors such as the type of mechanism, the type of message being conveyed, and the hearing of the receiver(s)? We encourage experimental investigations to test the hypothesis that different acoustic characteristics are more efficient at conveying different messages, such as aposematism or deimatism. Fourth, how did defensive sound production evolve originally? Did it evolve from escape or fighting behaviors, or from pre-existing signals used in another context? To understand the evolutionary origins of defense sounds, phylogenetic comparative analyses are necessary. Fifth, and perhaps most important, testing hypotheses on the survival benefits of these sounds requires experiments with natural predators. Most studies have been conducted by humans pinching insects and reporting the sounds. While these studies are important, experiments with a diversity of natural predators are necessary to record the effectiveness of sonic defenses. Such studies should monitor the initial predator responses as well as the effects over time, such as habituation and learning rates. Additionally, the behavior of the prey should be closely monitored to determine how long the display lasts, if the prey tries to escape, and if there are other behaviors associated with sound production. While predator-prey experiments can be challenging to conduct, they are essential to furthering our understanding of the efficacy of survival sounds in insects. Defense sounds clearly play an important role in the survival strategies of many insects, and further research on acoustic communication is critical for establishing a comprehensive understanding of insect predator-prey interactions.

AUTHOR CONTRIBUTIONS

ML led the project and wrote the first draft. All authors contributed to data collection, editing the manuscript, and figure and table preparation. All authors approved the final version of the manuscript.

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