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# Synonyms

Animal communication; Information theory; Information transmission; Signaling

#### **Definition**

Exchange of information between a sender and receiver in insects

## Introduction

Broadly, communication refers to any exchange of information between individuals. The individual transmitting the information is the "sender," while the individual to whom the information is transmitted is the "receiver." The sender can be a single individual or a group of individuals, just as the receiver may be an individual or a group of individuals. Often, the information transmitted is meant to influence the current or future behavior of the receiver. This information is referred to as a "signal"; the sender is the "signaler." Theory

predicts that for a signal to evolve, both the sender(s) and receiver(s) should benefit from their interaction (Bradbury and Vehrencamp 1998). Thus, there should be tight coevolution between signal production and subsequent perception and response.

Insects communicate in various contexts, both between and within species. These contexts include but are not limited to mate choice, competition with conspecifics for access to mates, avoiding predators, locating resources, and kin recognition.

Mate choice: Individuals (typically males) attempt to attract potential mates with conspicuous visual displays, sounds, and smells. The responsive sex (typically females) can respond to mating advances with similar displays of their own.

**Competition**: Individuals signal to others in agonistic interactions to secure mates, territories, or other resources.

**Predator avoidance**: Insects send alarm signals to warn others against nearby predators or warning signals to deter predators themselves.

**Resource localization**: Members of the same species or colony share information about accessing food and other resources.

**Kin recognition**: Some signals are species- or kin-specific and allow insects to identify intruders, avoid inbreeding, and prioritize the safety of close kin.

#### **Modalities of Insect Communication**

**Visual signaling** involves the display of distinct body parts, typically referred to as the signal. Of all insects, butterflies, flies, dragonflies, and damselflies use visual signals most often.

Mate choice: Many insects use visual signals, especially colorful wings, to attract mates. The red admiral butterfly, Vanessa atalanta, uses bright coloration on the dorsal wing surface that gains the attention of potential mates.

Predator avoidance: The ventral side of the aforementioned red admiral butterfly is drab, camouflaging the species from predators (Opler and Krizek 1984). Some insects have bright advertisement signals, called aposematic signals, that warn predators of their unpalatability (Mappes et al. 2005). Lady beetles, tiger moths, and blister beetles all broadcast long wavelength colors like red and orange colors that advertise the bitter-tasting chemicals in their bodies. Many butterfly and moth species have large round eyespots on their wings. In some cases, these spots mimic the eyes of another, potentially more dangerous animal. For example, Hemeroplanes triptolemus larvae expand the front segments of their bodies, mimicking a snake and scaring off predators. Otherwise, the spots encourage a predator to attack a part of the insect's body that is less vital to its survival. When a predator attacks, it will go for the eyespots located on the wings, avoiding the thorax or abdomen.

Resource localization: One of the biggest discoveries in animal communication is that honeybees, Apis mellifera, use visual communication to share information about nearby resources. These bees use two forms of dance behavior, the waggle dance and the round dance, that share information with other members of the colony about the direction and distance to patches of flowers yielding nectar and pollen, water sources, or new nest-site locations (Riley et al. 2005). As the distance between the resource and the hive increases, the round dance transforms into variations of a transitional dance, which, when communicating resources at even greater distances, becomes the waggle dance (Seeley et al. 2006).

Kin recognition: Visual signals can be used to identify individuals living among a group. Paper wasps, *Polistes fuscatus*, have highly variable yellow facial and abdominal markings that are signals of individual identity. Queens and workers form a linear dominance hierarchy that determines how food, work, and reproduction are divided within the colony. This stable hierarchy is facilitated by individual recognition between the different ranks (Tibbets 2002).

There are many advantages to visual signals. This form of communication is long range and effective in all directions, regardless of wind speed. Since visual signals travel at the speed of light, they are the fastest of all signaling types. If the signal is passive, like many aposematic signals, they require little to no energy to broadcast. There are some disadvantages to visual signaling, such as the requirement for the receiver to have a clear view of the signaler. Since visual signals are only effective when they are visible to the receiver, many insects display only when the sun is out. Bioluminescence is an exception to this rule, where some insects such as adult Photuris fireflies, glowing click beetles and cockroaches, and railroad worm larvae produce their own light and signal at night. Lastly, active signals, like sexual signals, can be metabolically expensive to produce, and visual signals can be broadcast to unintended receivers like predators who can more easily spot prey adorning these elaborate signals.

Acoustic signaling involves the production and propagation of sound toward a receiver. In the absence of the vocal structures reserved to vertebrates, insects have evolved diverse mechanisms for sound production. Crickets and katydids sing by stridulating or rubbing together specialized wing structures to generate pulses of sound (Alexander 1961). Similarly, grasshoppers rub their hind legs against hardened forewings, creating sound like a bow on a violin. Cicadas have specialized organs called tymbals that generate sound when flexed back and forth (Young and Bennet-Clark 1995). Several beetle species make sounds by rubbing body parts together or on an external source. For example, deathwatch beetles bang their heads repeatedly on hard surfaces to generate a ticking noise (White et al. 1993). Other

insects, such as Madagascar hissing roaches, produce hissing sounds by expelling air through spiracles (Nelson 1979). Like other terrestrial animals, most insects use a thin membrane known as the tympanum to process sounds. Insect tympana can be located anywhere on the body, including the legs (crickets and katydids), wings (butterflies), mouthparts (sphingid moths), abdomen (cicadas), and thorax (tachinid flies, praying mantis) (Greenfield 2016).

Mate choice and competition: Male crickets, katydids, grasshoppers, and cicadas produce songs that attract females in mate choice. In some families (such as katydids), females may respond to mating attempts with songs of their own (Villarreal and Gilbert 2013). Males of these species can also employ sound in competition to establish dominance or warn other males not to approach (Alexander 1961).

Predator-prey dynamics: Sounds also play a role in predator avoidance and prey localization. For example, cicadas emit a distress call when disturbed, warning others of a potential predator (Young and Bennet-Clark 1995). Some moth species emit sounds that jam a predatory bat's echolocation sense (Corcoran et al. 2009). Predators and parasites such as tachinid flies use their exceptional hearing to find prey (Lehmann 2003).

Acoustic signaling provides several advantages for insects. Since sound is easily manipulated, slight changes in sound characteristics (amplitude, frequency, periodicity) can produce a wide range of signals conveying different kinds of information. Sound waves also move relatively quickly to receivers. However, sound can be metabolically expensive to produce, and acoustic signals can often reach deadly targets such as predators and parasites. Sound also attenuates (reduces in intensity), and the strength of the signal is lost over long distances. In noisy environments, receivers may have trouble perceiving an acoustic signal.

Chemical signaling is one of the oldest and most common forms of insect communication. Insects regularly signal with **pheromones** (within species) and **allelochemicals** or **allomones** (between species) (Regnier and Law 1968; Ali and Morgan 1990). Many also use

nonvolatile, short-range hydrocarbons as chemical signals (Singer 1998). Individuals generally sense long-range chemical signals with olfactory reception and short range with forms of contact reception, such as taste. Chemical communication is most famously studied in group-living and social insects such as hymenopterans (ants, bees, wasps), aphids, and termites.

Resource localization: As picnic-goers often notice, ants use pheromone trails that lead nest mates toward food sources in a behavior known as tandem running. This behavior is also commonly found in termites, which lay chemical trails that facilitate group foraging (Kaib 2013). Solitary insects also use chemicals in resource communication; bark beetles use pheromones that convey the location of a new host tree to their conspecifics.

Predator avoidance: Termites, alongside social bees and wasps, also use alarm pheromones that recruit their kin into attacking predators (Kaib 2013). More defensively, several ant and aphid species employ chemical alarm signals that warn nest mates to scatter as a predator approaches (Yamaoka et al. 2006). Many solitary insects either exude unappealing scents or directly chemically incapacitate a predator. The aptly named brown marmorated stinkbug produces foul smells that deter its predators. Several beetles, flies, and moths use chemical repellants in areas where they lay eggs to divert potential predators or competitors. Cockroaches secrete chemicals onto their dorsal side that harden like glue in a predator's mouth, allowing the roach time to escape (Farine et al. 2002). Bombardier beetles famously expel fatal chemical steam from their abdomens when threatened (Eisner 2003).

Kin recognition: The ability to recognize kin often facilitates an extreme division of physical and reproductive labor in social insects. Ants, social bees, and social wasps use colony-level chemical "profiles" to identify relatives and expel intruders without the same cues, avoiding exploitation by outsiders. Pheromones can also directly mediate the reproductive division of labor. Queen honeybees produce pheromones that both limit the development of ovaries in workers and attract drones (males) to mate

(Hoover et al. 2003). These chemicals ensure that only queens reproduce in a colony.

*Mate choice*: In social insects, mating behavior is generally limited to the queen (ants and social bees), king (termites), and reproductive workers (semisocial wasps). There are few such limitations in solitary insects, where males and females alike use pheromones to attract and locate mates. When the chemical causes searching behavior, it is referred to as a sex attractant; when it induces mating behavior, it is called an aphrodisiac. Moth sex attractants are particularly well studied, as females release long-distance pheromones (30+ miles in some silkworm families) that signal availability to receptive males. In tiger moths, females select males based on pheromone production, which acts as an honest indicator of male fitness (Lofstedt 1993). In species with multiply-mating females, males use chemicals to ensure paternity. For example, tsetse fly sperm contains chemicals that act as an anti-aphrodisiac, discouraging other males from mating with a female (Carlson and Schlein 1991).

There are several advantages to chemical communication in insects. Most chemicals are highly effective in low doses, meaning that small quantities can provoke behavioral responses. Chemical signaling is therefore less metabolically expensive than many other forms of communication. Chemicals do not degrade quickly or become harder to sense in different visual conditions; they are effective across long distances and many environments. However, since longdistance signals depend on air transmission, chemical communication may not be as effective if a receiver is upwind of a signaler. Chemical signals are also not as variable as acoustic signals, and thus do not carry as much information about the signaler. While less conspicuous than visual and acoustic signals, predators can still exploit chemical cues. For example, parasitoid wasps can mimic the scent of their prey to infiltrate habitats and lay parasitic eggs and larvae.

Vibratory signaling involves the use of low-frequency, substrate-borne (rather than air-borne) vibrations to communicate. Insects produce vibrations in diverse combinations of percussive drumming, tremulation or abdominal and body jerking, tymbal clicking, and stridulation.

Predator avoidance: Many termite species produce vibrational signals to warn nest mates of predator disturbances or pathogenic fungal spores in the nest (Kirchner 1997; Rosengaus et al. 1999).

Resource localization: Interestingly, vibrational communication plays a large role in the evolution of some mutualisms between different insect species. Larvae and pupae of ant-associated butterflies produce substrate-borne signals that attract high numbers of ants, thereby increasing their protection against predators (Travassos and Pierce 2000). Perhaps the best example of vibratory insect communication is in group-living treehoppers, which communicate almost exclusively using vibratory signals. Vibratory signals are associated with defense and parental care (Cocroft 1999) and are used to locate feeding sites (Cocroft 2001). Similarly, gregariously living sawfly larvae use vibrational signals that maintain colony cohesion and locate fresh food sources (Cocroft 2001).

Mate choice: Male treehoppers send vibrations that attract females, and responsive females will signal in return. Before mating, males and females will engage in vibrational duetting, with the male and female signaling back and forth. Some crickets and katydids also use vibrations to attract mates.

Vibrations are an essential form of communication for many small insects. In order to effectively communicate with air-borne acoustic signals, smaller insects need to produce very high-frequency signals, which are prone to greater degradation (Bennet-Clark 1998). Thus, smaller insects use vibrational signals because they are far-reaching and relatively low cost. Propagation of vibrational signals is also less diffuse, and the signal is confined to the substrate through which it is being sent. Therefore, it is easier to locate, but less likely to attract aerial predators. As long as the continuity of the substrate is maintained, the transmission of a vibratory signal is not greatly affected by obstacles in its path. Substrate-borne communication has some disadvantages. Primarily, vibratory signals are distorted in time and frequency, and vibrations become more degraded with increasing distance between the signaler and the receiver.

**Multimodal communication**, or the use of signals in two or more modalities, is ubiquitous in insects. In fact, unimodal signaling may be the exception rather than the norm. These signals can either convey different messages about the signaler or redundant information to reinforce the impact of one message (Hebets and Papaj 2005).

Resource localization: Honeybees use visuals, vibrations, and chemicals in different parts of the waggle dance to elicit foraging behavior from their hive mates (Hölldobler 1999).

Predator avoidance: Wood tiger moths use both aposematic coloration and chemical signals to warn blue tits against eating them; the combination of signals is a more effective deterrent than either in isolation (Rojas et al. 2019). Similarly, some species of ants use a combination of vibrational tapping and alarm pheromones to warn hive mates of danger (Hölldobler 1999). Alarm chemicals are more effective than vibrations, but the combination has the most impact.

Mate choice: Male field crickets use both courtship songs and contact chemicals to attract mates, conveying different information about male fitness in each one (Simmons et al. 2013). Similarly, some katydids use air-borne sounds and substrate vibrations during courtship to improve the localization of a stridulating male (Kalmring et al. 1997). In some chorusing insects, like those in the family Gryllotalpidae, the vibrational component of the male advertisement call determines how far apart calling males are from each other in the wild (Hill and Shadley 2001). Male Drosophila also use vibrational tapping and chemical aphrodisiacs to attract mates (Butlin et al. 2011).

#### Conclusion

The world around us is full of insect signals – the electric iridescence of the emerald green ash borer, the soothing song of a serenading cricket, the marching ants directing each other with chemicals, and the vibrational duetting of treehoppers. Insects have evolved incredible means of communicating in many contexts. In addition to representing the spectacular diversity of signal evolution, the study of insect communication has

many implications for the overall study of animal behavior. Like most animals, insects can communicate information about identity, status, future actions, environmental discoveries, etc. to multiple receivers (Bradbury and Vehrencamp 1998). Studying how such signals evolve across insect taxa can help elucidate general evolutionary principles. The many modalities that insects use to communicate also inform the creation of human biomimetic devices. For example, the incredible sound localizing abilities of the tachinid fly Ormia ochracea prompted the development of a new line of hearing aids (Kuntzman and Hall 2014). Studying insect communication also has various practical implications. The field of forensic entomology relies on understanding how insect localize and communicate resources to glean important information at crime scenes. Studying the signals requisite to mate attraction and other biologically relevant function can inform conservation practices for endangered insect species. Lastly, researchers have used mating and resource localization signals to develop reproductive suppression and biological control plans in pest management.

## **Cross-References**

- ► Aposematism
- ► Arthropod Communication
- ► Arthropod Sensory Systems
- ► Chemical Signals
- ▶ Chemoreception
- **▶** Communication
- **▶** Gustatory Perception
- ► Hymenoptera Sensory Systems
- **▶** Insect Cognition
- ► Insect Sensory Systems
- **►** Modality
- ► Olfactory Perception
- ▶ Ornamentation
- ▶ Predator Defense
- ▶ Predator Detection
- ► Secondary Sex Characteristics
- ► Sensory Adaptation
- ► Sensory Receptors
- ► Sexual Dimorphism

- ► Sexual Selection
- ► Visual Recognition of Prey and Predators

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