

Behavior of the House Cricket, *Acheta domesticus*

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Background

The Study of Animal Behavior

All animals interact with their environment, including individuals or groups of either the same or different species. These behavioral interactions, whether with the environment or other animals, have fascinated researchers for a long time. However, it was not until the early decades of the 20th century when the study of animal behavior gained a coherent conceptual framework and a clearly spelled out research program, which eventually developed into a discipline that we now call “classical ethology”. This field was internationally recognized in 1973 when the Nobel Prize in Physiology or Medicine was awarded to Karl von Frisch, Konrad Lorenz, and Nikolaas Tinbergen “for their discoveries concerning organization and elicitation of individual and social behavior patterns”. Many would argue that these three are the most prominent historical figures in the field of behavioral biology. Karl von Frisch pioneered the research on the communication mechanisms amongst bees about a food source, discovering the honeybee “dance language” (von Frisch, 1967). Konrad Lorenz conducted many studies examining instinctual and fixed action patterns of behaviors in animals as well as imprinting (Lorenz, 1952). Nikolaas Tinbergen examined the degree of behavioral responses to various stimuli in many animals; some behavioral responses could be elicited more strongly using an exaggerated stimulus (supernormal stimulus) compared to the natural stimulus (Tinbergen, 1951).

Tinbergen’s Four Questions

In 1963, Tinbergen proposed a framework that united all aspects of animal behavior research. To this day it inspires students of animal behavior, as it delineates very clearly the approaches that are necessary to answer the seemingly simple question: Why do animals behave the way they do? According to this framework, the mechanisms underlying animal behavior can be broadly divided into four categories, also known as **Tinbergen’s (1963) four questions: Causation, Ontogeny, Survival Value (Function) and Evolution**. The processes underlying causation and ontogeny (development) of behavior are considered to be proximate mechanisms, whereas the processes underlying survival value (function) and evolution of behavior are known as ultimate mechanisms. Studying causal mechanisms aims to understand the underlying internal factors (e.g. neural, genetic, hormonal) for a behavior. Ontogenetic mechanisms of behavior examine how behavior develops in relation to genetic and experiential factors. A behavior is said to have survival value if it has important survival and fitness consequences. Finally, research into the evolutionary mechanisms of behavior requires an understanding of the origins of the behavior in question within a comparative and phylogenetic context. Although Tinbergen proposed these four categories as useful guidelines for research, he emphasized that these areas are not mutually exclusive in explaining animal behavior. In order to get a complete understanding of an animal’s behavior, we need to understand both proximate and ultimate mechanisms (Figure 1). It is this integration across levels of biological organization where modern approaches have opened exciting new avenues of research (for review, see Wong & Hofmann, 2010).

Behavioral biologists use Tinbergen's "Four Questions" as a framework within which to ask testable questions about why an animal behaves in a certain way. Consider the question of "why is this cricket chirping?" While this may seem a simple question it becomes much more interesting once we begin to break it down into its components. For example, we might ask:

- How does the cricket generate its characteristic "song"? And how do other crickets (as well as other animals, including humans) perceive this signal? (Causation)

- How does chirping behavior arise throughout the development of the cricket? Is the cricket's song fully formed when it first appears? (Development)

- Why does the cricket sing in the first place? To entertain us humans (an idea put forward in earlier centuries)? To attract a mate? To threaten competitors? Who else might attend to – and possibly take advantage of – this acoustic signal? (Survival value, function)

- When we compare the songs of different cricket species, what differences, if any, are there? How did the song of an ancestral cricket species diversify into the multitude of song structures we observe in nature? (Evolution)

As you can see, it is essential to parse questions about animal behavior (including our own!) carefully before beginning to formulate hypotheses and design experiments with which to examine the behavior in question.

Sensory Physiology and Orientation

Animals gather information about their environment and themselves via sensory systems. This allows them to interact with the world and orient in it. Sensory information first comes into contact with the nervous system via its receptors. The receptors can be divided into four general categories.

1. Photoreception: response to variations in the radiant energy received by a photoreceptor.
2. Thermoreception: response to radiant thermal energy.
3. Mechanoreception: response to kinetic energy (e.g., sound, touch)
4. Chemoreception: response to chemicals (e.g., smell, taste)

What can animals do with this sensory information? In this exercise, we will look at two often related aspects of behavior, **communication** and **orientation**. We can distinguish four basic forms of orienting responses:

1. **Tropism**: Directed turning or bending movement (or growth) of (part of) sessile organisms toward or away from an external stimulus, such as light, heat, or gravity. Examples include phototropism, thermotropism, and gravitropism.
2. **Kinesis**: A movement in response to a stimulus that is not oriented with respect to the source of stimulation. For example, undirected locomotor activity is lowest in preferred environments and highest in hostile environments (usually in reference to light intensity, temperature, humidity, etc.).
3. **Taxis**: The directed movement of a free-moving organism or cell toward (positive) or away from (negative) an external stimulus. Examples: Phototaxis, chemotaxis, phonotaxis.
4. **Long-distance orientation**: Animals move towards a goal that they do not (yet) perceive with their senses. We can distinguish three types of long-distance orientation: Compass orientation (direction of movement in a constant angle relative to a stimulus, such as the sun or the earth magnetic field); landmark orientation (based on learned sign posts throughout space); and navigation (current position and direction of movement can be determined from any point in space based on sensory cues).

Communication

Animal communication is ubiquitous and a conspicuous aspect of the behavior of all animals. Communication is the result of any action or display by one individual – the **sender** – that functions as a **signal** and affects the current or future actions/displays of another individual – the **receiver**. For example, females may use the colorful plumage or melodious song (or racy car!) displayed by males to choose a mate among a number of suitors. Also, females may make their choice based on the quality of acoustic signals (e.g., songs) or other kinds of displays. Such behavior patterns often, but not always, provide information about the health or condition of an available male (the so-called “good genes hypothesis”). Displays also play an important role in competition between males. By carefully analyzing the displays performed by males during the breeding season, either while fighting or when courting females provides a basic understanding of their function (e.g., female choice, male-male competition, or both) and underlying proximate mechanisms (e.g., biomechanics of signal production, neural basis of behavior).

Every sensory channel can be used for communication, including those not easily accessible to our senses. Thus, when designing a study of animal behavior one needs to always keep in mind possible information that might be available to the animal, even though it is hidden from the experimenter. How animals communicate is a fundamental problem in the study of behavior, as it can be a window into the cognitive world of animals.

Acoustic Communication and Auditory Processing in Crickets

Acoustic communication among animals utilizes sound to signal information from one individual to another. From the perspective of causation, we can ask how these signals are generated by the sender and how the receiver processes them in order to recognize and localize the sender. Many animals use acoustic signals for intraspecific (within species) communication. For example, birds produce song, frogs croak, and crickets chirp.

In crickets, males produce their song by rubbing their forewings (elytra) against each other. We can distinguish three song types:

- 1) The **calling song** is a regularly patterned, fairly loud signal that attracts females. This is the chirping you will have heard many times during summer nights,
- 2) The courtship song is used when a male attempts to mate with a female. It sounds more like a scraping noise of low intensity
- 3) The aggressive song (also called rivalry or triumph song) – a very loud trill - is produced during or after combat with another cricket.

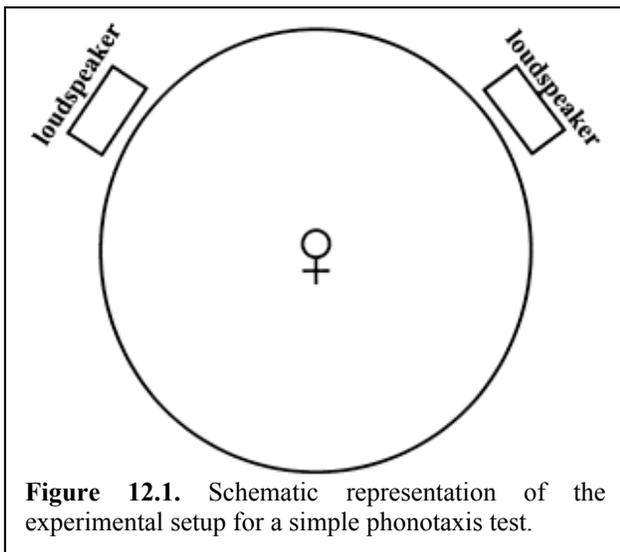


Figure 12.1. Schematic representation of the experimental setup for a simple phonotaxis test.

Cricket females do not sing; however, they are attracted to this signal and will approach it in a directed orienting response towards the source of the song, a process that is called (positive) phonotaxis (see above). This behavior can be investigated in a simple circular arena, equipped with one or two loudspeakers from which various kinds of songs (conspecific [of same species], heterospecific [of different species], or synthetic) can be broadcast (Figure 12.1). If there is only one loudspeaker, the animal can approach the

sound stimulus (loudspeaker), avoid it, or not respond at all. In a two-choice paradigm (with two speakers), the test animal can exhibit a choice between two song stimuli (e.g., conspecific *vs.* heterospecific).

For successful phonotaxis to occur, females need to be able to *recognize* the acoustic signal as that of a conspecific (and potentially attractive) male, and they need to be able to *localize* it in space. How can they do this? Crickets carry their ears below the knees of their front legs. From there, a well-studied auditory pathway decodes the acoustic signals in the central nervous system (Hedwig, 2001). Researchers have discovered that certain auditory neurons, which can be individually identified, are involved in this process. Specifically, the response properties and the structure of these neurons can be analyzed in tethered animals with the central nervous system exposed for intracellular electrophysiological recordings or optical imaging. Because these fundamental processes are relatively accessible in crickets, they have become an important model system for studying the mechanisms underlying auditory processing and the control of motor patterns at the systems and cellular level.

Eavesdropping

As we all know from experience, communication signals may be received not only by the intended recipient, but also by other individuals whose interests might be opposed to our own. For example, a chirping cricket not only attracts females, but may also attract potential predators (such as birds and bats) and parasites. A spectacular example is the parasitic tachinid fly *Ormia ochracea*, which can localize a singing cricket without a problem. Once the fly has found its victim, it will deposit her eggs on it. Once the eggs hatch, the maggots enter the host's body, using it as a living pantry until it dies and the maggots eclose as adult flies (Cade, 1975). When first discovered, the behavior of this eavesdropping fly was the only example of a natural parasite exploiting the mating signal of its host! In a particularly compelling example of rapid evolutionary change as a consequence of strong selective pressure (by the parasitic fly), a genetic mutation leaving males unable to produce song has spread through a population of field crickets on the Hawaiian island of Kauai (Zuk, 1994). To perform phonotactic behavior, *Ormia* has evolved a remarkable and unusual "ear", which has inspired the development of "biomimetic" (i.e., applying biological systems to the design of engineering systems) hearing aids that considerably improve hearing in a noisy environment (Mason et al., 2001).

Animal Conflict

Over the last four decades, fighting behavior has been studied extensively from an evolutionary point of view using evolutionary game theory (Maynard Smith, 1974). The *war of attrition* as well as the *hawk-dove game* represent two models that have provided the basis for understanding how nonstrategic factors like fighting ability can shape the evolution of fighting behavior. One animal contest model suggested that 'conventional fighting' is used by animals to assess the 'resource holding power' (RHP) of the opponent. Although a number of important predictions have been made from these early models, they were not based on realistic behavioral mechanisms (i.e. they did not take into account the existence of escalating sequences of behavior as a result of external and internal signals).

The observation that threat displays are ubiquitous has been a longstanding puzzle in the understanding of animal conflict (Tinbergen 1951; Andersson 1980). Displays may transmit information about fighting ability, but may also serve other functions. For example, they could signal aggressive motivation and intentions, or contain specific contextual information. Classical ethologists saw cooperation as the basis for honest signals that are performed at a 'typical intensity'

and become ritualized during the process of ‘adaptive formalization’. This evolutionary process was suggested to result in an optimal signal form that minimizes distortion during propagation between sender and receiver. There are many examples where direct assessment has been shown. However, such stereotypy may preclude the extraction of honest information about the sender, an interpretation put forward by behavioral ecologists, who assert that animals may benefit from concealing information about their fighting ability and the value of a resource they might be holding. Originally, it was also assumed that honest signals, especially if they are energetically cheap and not a direct indicator of RHP, would be vulnerable to cheating and thus could not be evolutionarily stable. However, we now know that a signal does not always have to be costly to be reliable and evolutionarily stable.

Should animals communicate information about their intentions to enter or continue a fight? The sequential assessment game (Enquist & Leimar 1983, 1987) showed that assessment of fighting ability and resource value in animal contests can be evolutionarily stable, and displays may serve specific functions. It seems now that the assessment of intentions is compatible with an adaptive interpretation of motivation (an animal’s willingness to fight). That is, animals can be expected to assess each other’s motivational states during interactions, and on the basis of that information, in conjunction with assessment of strength, they decide whether to escalate or give up. Probing and retaliation would keep the levels of ‘bluffing’ about intentions low. While there are many studies of

signals that allow assessment of fighting ability or strength, signals that convey information about resource value and/or motivation have received much less attention (but see Hofmann & Schildberger, 2001).

Aggressive Behavior in Crickets

Crickets are a convenient and powerful model system for examining aggressive behavior. In many cricket species, males compete for territorial shelters and females, and their aggressive behavior has been described extensively in the ethological literature (Alexander, 1961; Adamo & Hoy 1995; Hofmann & Stevenson 2000). Although crickets can perform a number of different behaviors during agonistic interactions, the actual fighting behavior can be characterized as an escalating contest following a more or less fixed sequence of events. The typical sequence observed in the Mediterranean Field Cricket, *Gryllus bimaculatus* is shown in Figure 12.2.

While the sequence can be repeated and sometimes interrupted by bouts of rivalry song, displays are performed

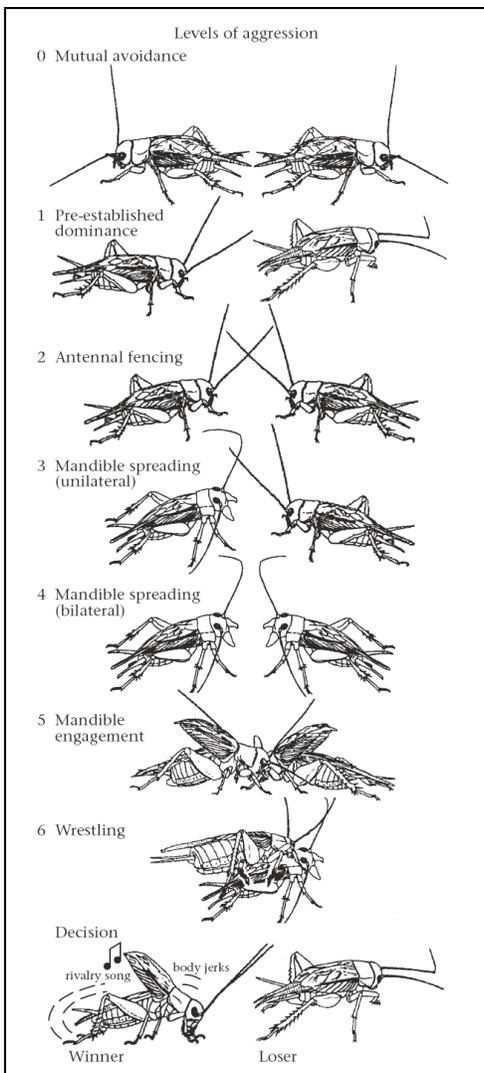


Figure 12.2. Pictogram illustrating the stereotyped escalating sequence of motor performances (Level 0–6) characteristic for aggressive encounters between male crickets. Level 0: mutual avoidance: no aggressive interaction. Level 1: pre-established dominance: one cricket attacks, the other retreats. Level 2: antennal fencing: the two crickets lash with their antennae. Level 3: mandible spreading (unilateral): one cricket displays broadly spread mandibles. Level 4: mandible spreading (bilateral): both crickets display their spread mandibles. Level 5: mandible engagement: the mandibles interlock and the animals push against each other. Level 6: wrestling: an all-out fight where the animals may repeatedly disengage, struggle for position, bite other body parts, and re-engage mandibles. Decision: the fight can be concluded at any of the Levels 1–6 by one opponent, the loser, retreating, upon which the established winner typically produces the rivalry song together with characteristic body tremulation (jerking)

mutually and the actual behavioral repertoire used is rather small. Other displays may be used in different contexts (e.g. the maintenance of an established rank order or a situation where one sensory channel cannot be used). For example, it has been shown that the production of both aggressive song and body jerks can be an important social communication tool in male cricket encounters (Judge & Bonanno, 2008). In addition, pheromones allow sex recognition. It has also been shown (Hofmann & Schildberger, 2001; Rillich et al., 2007) that two display behaviors – antennal fencing and mandible spreading – are parts of an assessment sequence that occurs during fights between male crickets, where antennal fencing is an energetically inexpensive signal that carries mostly motivational information about resource value, whereas mandible spreading indicates strength.

Evolution of Aggressive Displays in Crickets

It is important to realize that these aggressive displays can vary substantially across species. For example, the fighting behavior of male house crickets, *Acheta domestica* – the species you will be working with in this Exercise – is somewhat different from the sequence shown in Figure 12.2, as you might discover if you decide to test a hypothesis about aggressive behavior in this week’s lab. Why might this be? We know that *G. bimaculatus* is a mostly solitary species, i.e., animals of this species avoid contact, except for resolving conflicts over resources (e.g., territory/shelter, food or mate – mostly between territorial males) and for reproduction (e.g., approaching a singing male – mostly exhibited by females). *A. domestica*, on the other hand, is a gregarious species: The animals live in groups of usually five to 20 individuals in a relatively small space (such as the basements of lab buildings!). Based on this difference, you may already be able to predict that the solitary and territorial *G. bimaculatus* males are much more likely to escalate when encountering another male. Interestingly, when males of *A. domestica* are individually housed (isolated) for a number of days, they too become more aggressive. This phenomenon, that animals become more aggressive in isolation, is widespread across the animal kingdom.

Overall aggressiveness and display patterns vary considerably across cricket species (Jang et al., 2008; Judge & Bonanno, 2008). While some species only rarely escalate to physical combat, others almost always escalate. Interestingly, “victory displays”, such as rivalry song and body jerking (tremulation), also vary considerably, possibly as a consequence of ecological factors (such as the presence of a phonotactically operating predator). These results strongly suggest that both overall aggressiveness and the behavioural patterns used during and after combat have shaped the evolution of cricket species.

The Neurobiological Mechanisms Underlying Cricket Aggression

Once a fight between two crickets (or almost any animal species) has been decided, there is a winner and a loser. While winners usually will show increased aggressive motivation and be more likely to win their next encounter as well (the so-called “winner effect”), losers will avoid interactions with other individuals for some time (more than twelve hours in the case of the Mediterranean field cricket, *Gryllus bimaculatus*). However, it was discovered that this “loser effect” can be erased, and aggressive motivation reset, by allowing the loser animal to fly for a short period of time (Hofmann & Stevenson, 2000). In the laboratory, this can be accomplished by flying a tethered cricket in a simple wind tunnel. As an interesting aside, this work was inspired by “folk science” in ancient China, where the raising of crickets for fighting has a long tradition (Hofmann, 1996).

What are the proximate mechanisms that underlie aggressive behavior in crickets? Using the flight-induced reset of aggressive motivation in losers (described above), researchers have

discovered that **biogenic amines** play an important role. Amines – such as dopamine, norepinephrine and serotonin – are neurochemicals that act as **neuromodulators** in the brain, i.e., they alter the overall activity thresholds of neural circuits underlying behavior, thus making it more (or less) likely for a behavior to occur. In the case of cricket aggression, it is the biogenic amine octopamine (the invertebrate version of norepinephrine) that is necessary for the reset to occur (Stevenson et al., 2001, 2005).

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