

Chapter 14. Predator and Prey Interactions

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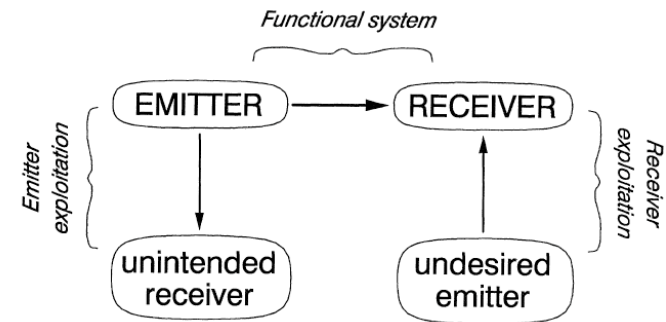


Figure 14.1. Basic elements of a communication system (after Otte 1974). The emitting individual generates a signal and transmits it to a receiver. An individual can be both an emitter and a receiver (e.g., bats), and networks of emitters are found in species such as frogs and crickets. There are two forms of exploitation in which: (i) emitter is taken advantage of by unintended receivers (eavesdropping bats on frogs), and (ii) the receiver is deceived by an undesirable emitter (e.g., Batesian mimicry, discussed below) (from Endler 1993).

In chapter 13, we focused on sensory systems and introduced the concepts of sensory drive and sensory exploitation. Here we delve deeper in eavesdropping by predators, and prey counter strategies like mimicry. A schema for understanding the interactions between predator and prey is presented in Figure 14.1. This loop can be embedded in a coevolutionary process generating correlational selection on each of the two participants, which results in a coevolutionary arms race. For example, the aposematic newt-garter snake arms discussed in Chapter 3 leads to an ever-escalating response by prey (evolve TTX and resistance to TTX) to predator counter-strategies (evolve TTX resistance counterstrategy). Such interactions are called Red Queen dynamics. Here we also consider the diversity of prey strategies including crypticity, evasion and escape tactics. In the absence of a viable prey counterstrategy, flight can also switch to fight (see Chapter 7, Huey and Hertz 1981).

Vision and Motion Detectors

Predator Motion Detectors

Many prey have evolved to be cryptic and thus the challenge for many predators is locating unmoving and concealed prey. Development of a

[search image](#) greatly aids in locating cryptic prey during a birds active foraging flight (see Chapter 5). Other organisms that forage actively use olfactory cues to locate concealed prey.

However, the challenge for other predators is not so difficult. Many predators are sit-and-wait rather than **widely foraging** (Huey and Pianka 1976). **Sit-and-wait** predators remain motionless for long periods of time. When a prey item moves in their receptive field, the predator lunges with great speed (relative to the prey) and snaps it up. We will consider the visual system of a classic sit-and-wait predator, the toad.

The key to the toads motion-based prey detector is the **receptive field**, the fundamental unit of its perception machinery. Each of the thousands of receptive fields in the toad eye consist of the following components:

1. a single **ganglion cell** that integrates information from the receptive field and relays a response back through the optic nerve,
2. **bipolar cells** that are all connected to the single ganglion cell on one synapse and connected on the other side to one or more receptor cells,
3. a circular cluster of receptor cells, the **receptive field**, that consist of
4. **central excitatory photoreceptors** that are loosely tethered together through bipolar cells,
5. **peripheral inhibitory photoreceptors** that are connected to a single bipolar cell.

This is the smallest *neural unit* of **stimulus filtering** found in the visual system. Other stimulus filtering is found at the level of the specific photoreceptors. Individual neurons can integrate certain signals (e.g., cones vary in photopigment found, see Chapter 13). The opponency generating machinery discussed in Chapter 13 (Side Box 13.1) reflects a simple stimulus filtering system. The stimulus filtering found in receptor sensitivity is hard-wired by evolution. However, a receptive field has special cellular interactions built into it that result in certain information being ignored and other information being acted upon. In the toad's motion detector the receptive field is the smallest unit of filtering. The

excitatory and inhibitory cells of the receptive field act in unison to either filter or detect objects from higher centers such as the optic tectum. The stimulus filtering in the receptive field is also capable of being modified by the animal's internal state -- food satiated or hungry.

If a **large object** casts an image over the visual field, the light intensity changes on the photoreceptors. Both excitatory and inhibitory cells from many receptive fields are triggered. Because the ganglion receives impulses from both the excitatory and inhibitory cells (i.e., through their respective bipolar cells) the effect of the inhibitory cells cancels out the effect of excitatory cells. No impulse is sent from the ganglion cell to the optic tectum.

However, if a **small image** passes over the visual field, the small image tends to trigger fewer receptive fields. The small image will also tend to excite some of these fields because the image hits many of the central excitatory cells, but only a few peripheral inhibitory cells. The ganglion cell receives impulses from the excitatory cells (through their bipolar cells), but with little inhibitory feedback, the action potential is relayed on to the optic tectum for further integration.

The optic tectum receives inputs from ganglion cells. Several clusters of ganglion cells form a higher-order receptive field at the level of the optic tectum that integrates information from the clusters of receptive fields.

Consider objects of different shapes that might strike receptive fields. Receptive fields come in a variety of "flavors" or shapes. Some are used for detecting long thin objects, others large objects, etc. One of the toad's favorite foods consists of worms -- long thin objects. There are receptive fields that are tuned to fire when long thin objects pass across them. When several "long-thin" receptive field detectors have the image of a bar pass over the receptors, their ganglion cells will relay the information to the optic tectum. The visual grasp reflex then takes hold, and the toad orients with both eyes. Once both eyes are locked on, other motor neurons cause the toad to lean forward, open it's mouth, and eat the worm. (N.B. This is also called a Fixed Action Pattern, Chapter 17).

Side Box 14.1. The toad's receptive field

Ewert (1974, 1980) mapped out the fundamental unit by which stimuli are filtered by a visual system using the European toad and its feeding response and anti-predator response. The ganglion cells integrate the action potentials created by a large number of bi-polar cells, some of which generate negative influences and others positive influences, which are integrated by bi-polar cells. A net negative effect integrated by ganglion cells generates an anti-predator fixed action pattern, while a net positive effect integrated by the ganglion cells generates a feeding fixed action pattern.

Figure 14.2. The visual system of all vertebrates, toads included, consists of a retina (see Chapter 13), by which nervous inputs cross from one eye to the opposing brain hemisphere, into the optic tectum, and then into the thalamus and cerebellum. (From Alcock 1998).

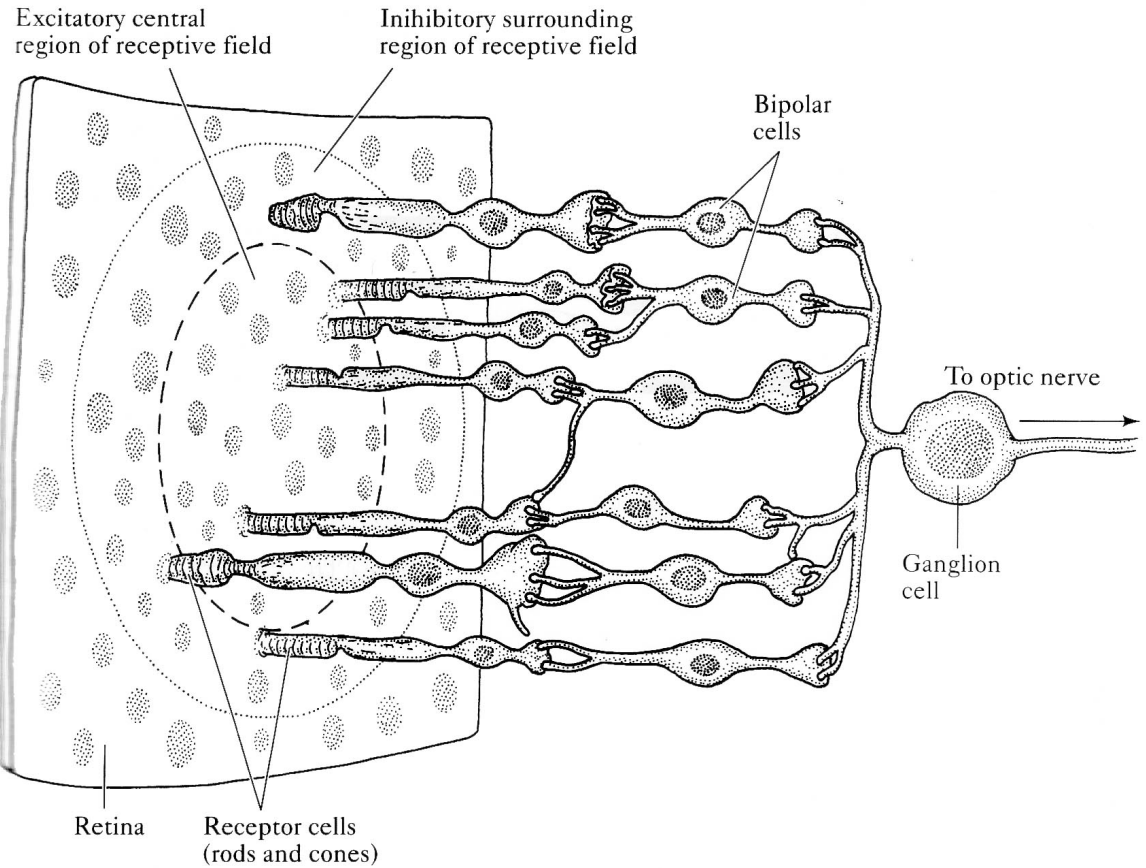
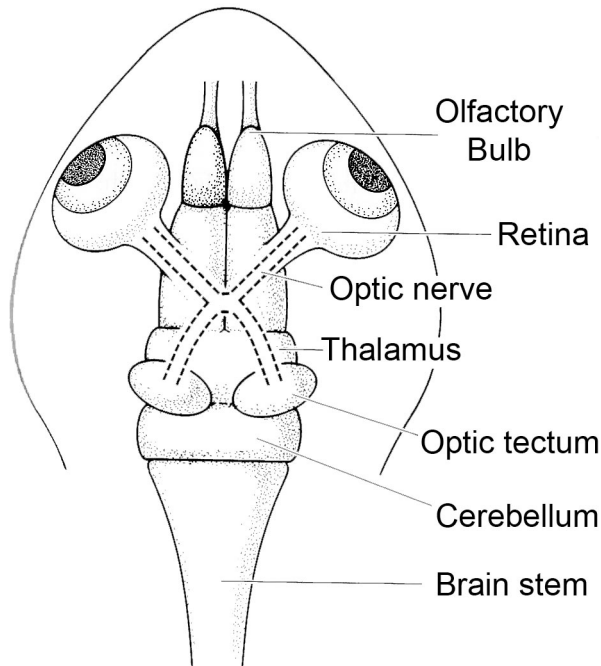


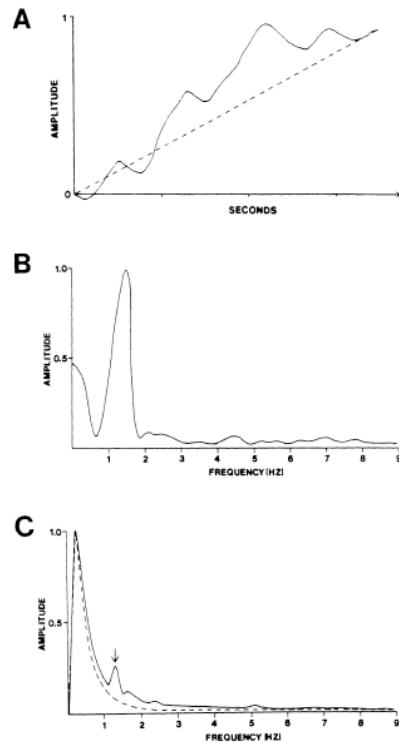
Figure 14.3. The fundamental structure of the stimulus filtering system of the toad consists of receptor cells (rods and cones) and many receptor cells are tied into bi-polar cells. The bi-polar cells can either receive inputs from the inhibitory field, or the excitatory field. When an object passes in front of the toad and drops the light intensity to inhibitory neurons they generate a suppressive effect on feeding behavior. When an object passes in front of the toad and drops the light intensity to inhibitory neurons they generate an excitatory effect on feeding behavior. The ganglion cell integrates the relative number of inhibitory versus excitatory inputs. If the object is long and skinny and horizontal, many excitatory cells in the interior of the receptive field will fire, generating an orienting and feeding response (a fixed action pattern, FAP – see Chapter 16). The same object, if oriented in a vertical direction and passed in front of the toad will trigger more peripheral inhibitory neurons first, which swamp out the excitatory effect of neurons in the central region of the receptive field. Toads recoil away from such stimuli, an anti-predator response. In this way shape detectors built into the receptive field are stimulated by light from objects and generate the primary filtering of the nervous system. (Alcock 1998).

Sensory Exploitation of a Prey's Motion Habituation Mechanisms

Recall that the motion detectors of *Anolis* lizards rapidly become habituated to the sinusoidal frequencies of branches swaying in the wind (Chapter 13). In contrast, *Anolis* lizards are extremely sensitive to the square-wave like patterns that are found in signature displays and challenge displays of conspecific males and females. Receptive female lizards move towards the square-wave displays of males. Thus, males use the displays to attract females to their territory and also repel other

males. The dual function signal also has a sinister third side to it.

Figure 14.3. A) Motion of a vine snake, *Oxybellis aeneus*, as it moves from location 0 to 1. B) Fourier transform of branch blowing in the breeze. C) Fourier transform of the vine snake. Note conspicuous peaks that mimic the movement of wind blowing vines.



Consider the vine snake, *Oxybellis aeneus*, which is a voracious predator on *Anolis* lizards. Fleishman (1989) has done careful laboratory studies where the wind conditions and swaying of plant vegetation were manipulated, their motions recorded on video, and their motion patterns analyzed for their **spectral properties** (waves).

First, vine snakes prefer to move when the wind is blowing. Moreover, when the snake moves, it not only slithers in a forward direction, but it also sways its head back and forth. In addition, the frequency of the snakes swaying body seems to correspond to the natural resonance frequencies of swaying branches and vines. The vine snake appears to exploit a weakness of the *Anolis* motion detector system. *Anolis* must habituate to swaying branches in order to see conspecific displays.

Vine snakes have evolved a motion that slithers into the "habituation zone" of the motion stimulus filters that *Anolis* uses in its optic system.

Sound

Male Frogs and Eavesdropping Bats

Even though the signaler may receive some benefit, many animals can receive the signal. An unintended receiver is often a predatory species. Sexual ornaments are intended for the female. However, the ornaments also make the male more obvious to a predator and thus they entail costs. Advertising calls make males of many species vulnerable to a predator's prey-detection mechanisms, resulting in costs to the signaler. As we will discover below, the bat has exquisite acoustical transmission and receptive organs. However, there are bats that do not have to echolocate to find their prey in the dark -- they need only listen to calling male frogs.

Species of tungara frogs produce two sounds when they are trying to attract mates. The first is a whine, which may or may not be followed by a chuck. Mike Ryan and his colleagues have shown that females of many species in this group strongly prefer males that produce a chuck (Chapter 13, Figure 13.17c).

The fringe-lipped bat does not have to call to find its prey by echolocation, rather it listens for male Tungara Frog calls. The bat then swoops down and captures a male. Bats also strongly prefer speakers that are projecting a chuck at the end of the whine in a 2 to 1 ratio compared to speakers with only the whine and no chucks. Thus, male frogs are caught in the middle of their own **sensory exploitation** of females, which prefer chucks (see Chapter 13), and the interception of such signals by their bat predator, which also prefer males with chucks. When calling alone, male frogs only use the whine as there are no other males to compete with. The whine may be sufficient to attract a female under these conditions. When calling in a group, they are forced to use the chuck, and risk the chance of being taken by a fringe-lipped bat.

Echolocation in Bats

The ability of bats to locate prey in flight even in the face of the evasive maneuvers by prey is simply amazing. A bat repertoire is as follows:

1. they can locate their target with an echo pulse,
2. they figure out how fast the target is moving,
3. some bats can discriminate the "shape" of the target,
4. some bats can determine if the target is beating its wings,
5. all within the span of one second from detection to capture.

Bats with a nose leaf emit sound through their nose, but most bats emit sound through their mouths. Bats typically emit short chirps 0.5-10 milliseconds (thousandths of a second long) with a long period of time between chirps. The signals are **frequency modulated** in the 15-150 kHz range. Some species of bats drop the interval between chirps to smaller and smaller times as they target their prey. These bats use the information from the broad band of frequencies and the **echo delay** (time between emission and return), and form images of the prey by using the echo information from a broad range of frequencies.

Resolving distance information

To process these echo returns, bats rely on some elaborate neural

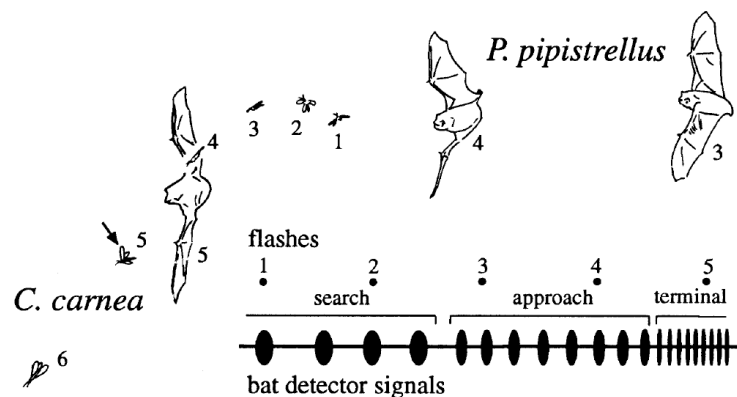


Fig. 14.4. Attack sequence of a bat approaching a lacewing. Speed of the target can be determined by differences in any pair of pulses and their return echoes.

circuits that are tuned to the information coming back from their ears. Bats possess special echo detector neurons that are sensitive to a sound delay (its echo). Neurons are sensitized by the 1st pulse. If the sensitized neurons are stimulated again within the specified time, the bat registers this information. Certain **echo neurons** are **range tuned** to long echo delays (e.g., far away), others are range tuned to shorter and shorter delays. In this sequence of echo detection, range-tuned neurons are arranged in a linear sequence back into the brain, such that they form a brain map of the bats attack pattern at the prey. From such neural maps, bats can compute other information on speed of prey. Most of the basic echo time delay between ears (e.g., location information) is processed by the **binaural system**, while the **monaural system** processes more detailed information of frequency shapes. Additional details on the binaural and monaural systems and the critical role of built in **time delays** in the neural circuits are given in Side Box 14.2. The monaural and binaural systems pass neural impulses to the **inferior colliculus (IC)** for processing and integration (analogous to the role of the toad optic tectum in integrating data processed during prey capture). In bats, frequency processing of sound is mapped in a precise spatial fashion (**tonotopic**; tones + topic = space) across the IC (Figure 14. 5).

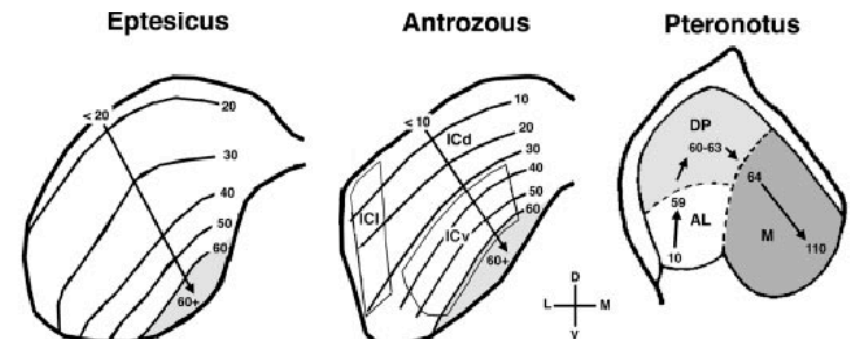


Figure 14.5. Comparison of tonotopic organization in the IC of 3 species of bats. White areas, frequencies below 60 kHz; grey areas, frequencies above 60 kHz. In *Pteronotus*, the light gray area represents the expanded 60-83 kHz region corresponding to the acoustic fovea (analogous to the optic fovea), and the dark gray area represents frequencies higher than 63 kHz. AL, anterolateral region of the IC; DP, dorsal posterior region of IC; M, medial region of IC. In *Antrozous*, ICd, dorsal region of IC; ICl, later region of IC; ICv, ventral region of IC. Arrows indicate the tonotopic axis from low to high frequencies. (Covey and Carr 2004).

Resolving shape information

To detect the shape of the object, other neurons decode the distortion of the echo. A small dimple in the returning echo describes the size of the head/thorax relative to wing placement of the insect. A bat with **frequency-modulated chirps** has special **frequency-tuned neurons** that fire when they detect the specific frequency of its own voice. This information is stored in the neurons for a given amount of time after the chirp and such neurons are referred to as having a long latency -- the neurons take a while before they decay from an activated state and re-polarized. The bat is actually storing a **neural template** of its own frequency-modulated chirp with each group of frequency tuned neurons holding the information for their own unique frequency (each of which was emitted at a slightly different time because the bat modulates the frequency of the chirp during the course of the attack sequence).

When the echo returns, short-latency neurons fire that are also frequency-tuned and a set of higher order integrating neurons compares the two populations of short and long latency neurons. The shape of the object distorts the echo return. Some of the original frequencies are so attenuated that they do not fire the short-latency neurons. The difference between the long and short latency neurons firing patterns leads to a crude "image" of an object's shape being formed. Eventually the long and short-latency neurons return to ground state and the bat is ready to resolve more shape information on the next chirp and echo return set.

Resolving wing beat frequency

Rather than use a frequency-modulated chirp, other bats use a compound signal, which has a **constant frequency** (~80 kHz) component (100 milliseconds) that is longer and tacked onto the end of the frequency-modulated component (see Side Box 14.1, Fig. 14.9). Bats that use such compound signals can measure the wing beat frequencies of their prey (Kober & Schnitzler 1990, Neuweiler 1990). The motion of the wings of prey causes glints in the echo return that is used by the bats to compute wing frequency. Neurons sensitive to resolving such "glints" decode the wing frequency information by even more complex spectral analysis (Fig. 14.10). Bats prefer fluttering targets similar to flying insect.

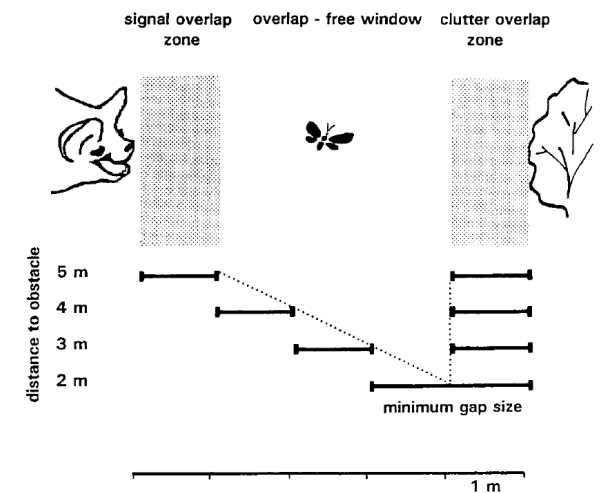
Visualize the echo hitting the flying target. At the instant that the first wave of sound hits the target, some of the surfaces of the target are moving away and others are moving towards the target (e.g., body vs. wing beat). Such differences in body and wing motion cause the **constant frequency signal** to becoming "Doppler shifted" in which the frequency is increased or decreased. A **Doppler shift** in any waveform (e.g., light or sound) occurs when an object has apparent motion relative to the observer. In this case the insects wings and body are moving relative to the bat. As the pulse of the constant frequency chirp strikes the insect, parts of it are Doppler-shifted down in frequency, while others are Doppler shifted up in frequency. This distorts the pure constant frequency signal coming from the bat and creates higher and lower frequencies when the pulses are reflected back as an echo.

As the bat comes in for the attack, it drops the constant frequency signal by a few kHz, and it shortens the interval between signals. By dropping the frequency, it avoids interference that might come from other signals as it gets closer and closer to the target. The environment also interferes.

Environmental constraints on echolocation

The exquisite resolving power CF bats are constrained by environment. The separation of target echo from interfering signals is an important task facing echolocating bats. The evaluation of sonar echoes from a target is hampered when clutter echoes evoke neuronal activity.

Fig. 14.6. Schematic of the masking situation for a bat foraging near vegetation. The prey echo overlaps the emitted signal when the insect flies in the signal-overlap zone, and it overlaps the clutter echoes when it flies in the clutter-overlap zone. No overlap occurs when the insect flies in the overlap-free window. At a distance of 2 m the overlap-free window is closed, and for the given signal duration the bat has reached the minimum gap size where overlap-free echolocation is impossible (Schnitzler and Kalko 2001).



Side Box 14.2. Sensory drive and bat sonar

In Endler's (1993) theory of **sensory drive** (see Chapter 13), the role of environment plays a paramount role in constraining the kinds of signals and communication in animals. In the *self-communication* of echo returns the acoustic environment has an enormous impact on which kind of biosonar a given bat species adopts. CF bats have only a brief downward FM component and prefer to hunt in open areas free from the

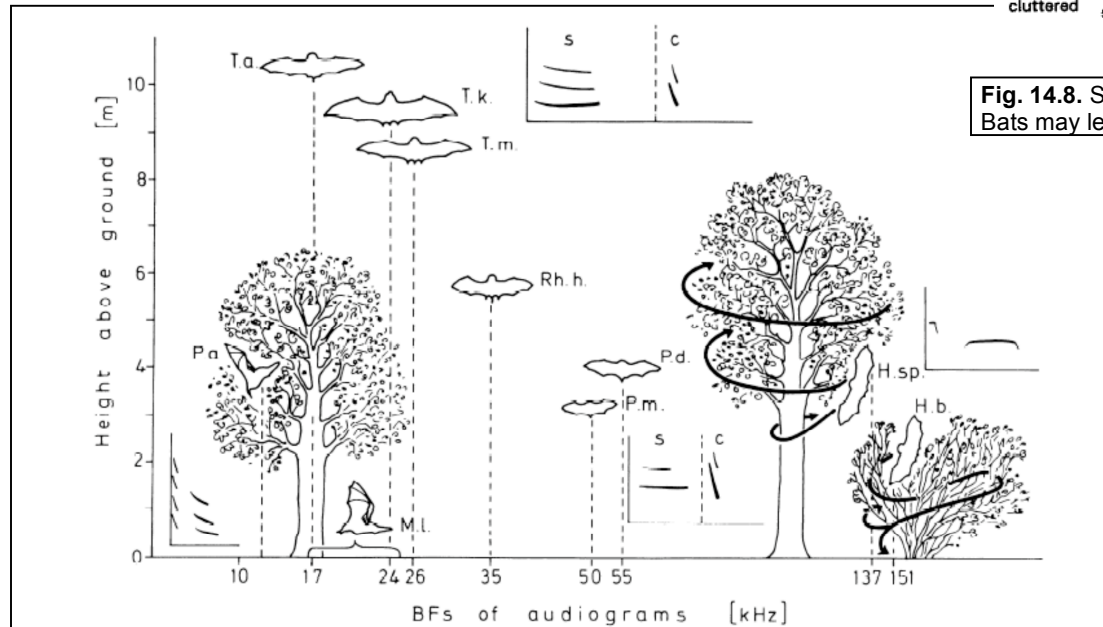


Fig. 14.7. Correlation between preferred foraging habitat and best frequency (BF) of audition in echolocating bats. Bats gleaning prey from ground (Ml, *Megaderma lyra*) or foliage (Pa, *Plecotus auritus*) are most sensitive at 10 and 20 kHz frequencies, well below echo frequencies. Bats foraging for flying insects above vegetation (Ta, *Tadarida aegyptiaca*, Tk, *Tophozous kachlensis*, use low-frequency echolocation for detecting insects over long distances. Bat species catching flying insects between vegetation (Pd, *Pipistrellus drmeri*, Pm, *Pipistrellus mumus*, Rhh, *Rhinopoma hardurkeri*) have sensitive audition in a medium ultrasonic frequency range. Bat species foraging in open spaces use CF-like signals for searching (s) and brief, broadband signals for catching (c) prey. Hipposiderid (Hb, *Hopposideros bicolor*, Hsp, *Hopposideros speoris*) and rhinolophid bat species often hunt close to or within vegetation and are specialized for fluttering-target detection. Bats foraging in this habitat may use echolocation with high frequencies. *Inset*: types of sounds used for echolocation in specific habitat (from Neuweiler 1990).

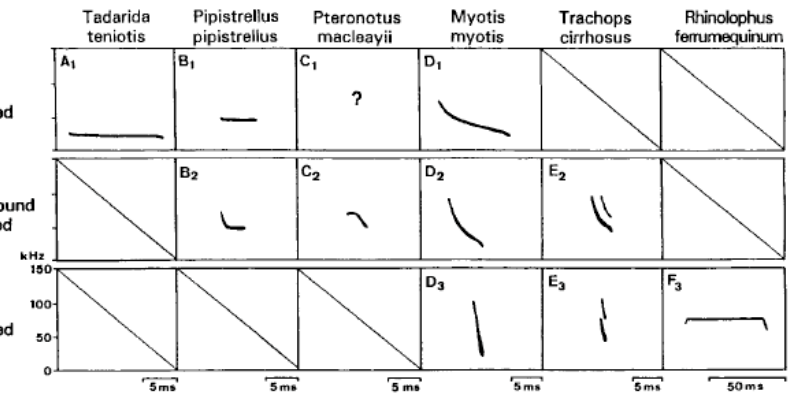


Fig. 14.8. Summary of the various search signals and associated habitat types. Bats may leave a preferred space for less-cluttered space but not the reverse.

clutter of vegetation. The difference in complexity of the acoustic signals is thought to be an adaptation to habitat (Fenton 1995, Neuweiler and Fenton 1988) (Fig. 14.7-9)

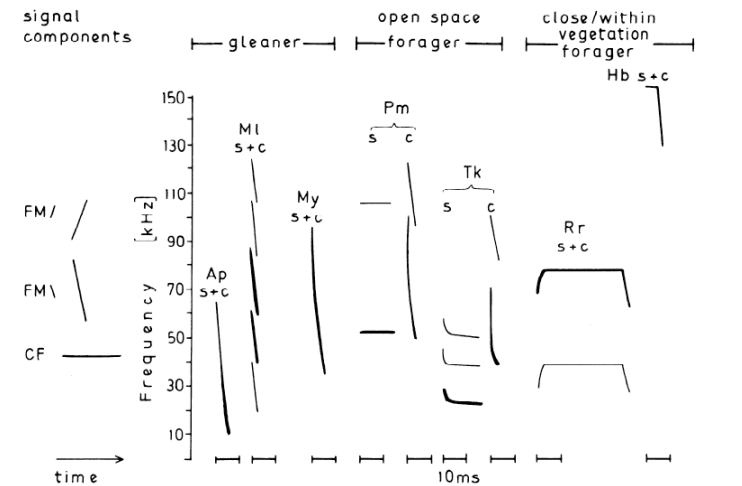


Fig. 14.9. Signal components and types of echolocation emitted by bats echolocating in different habitats. Left column: echolocation sounds only consist of 3 components: downward (FM/) or upward (FM\) frequency modulated or constant-frequency tone (CF). The CF tones may include from 1 to several harmonics. Types of echolocation vary in their utility, depending on habitat. Sound for searching is labeled s. Sound for catching a target is labeled c. (Neuweiler 1990).

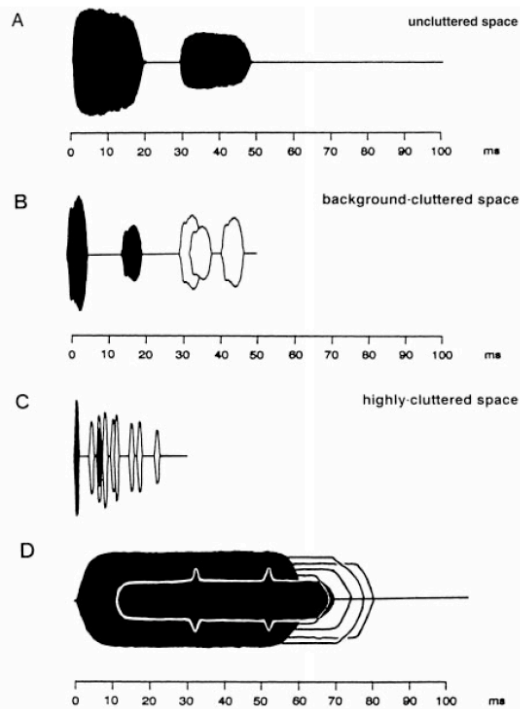


Fig. 14.10. The input into the auditory system of bats that forage in different clutter situations. The emitted pulse and returning insect echo are depicted in black. (a) In uncluttered space, pulse echo-pairs are far from clutter echoes. (b) In background-cluttered space, the pulse-echo pair is followed by clutter echoes (depicted in white). (c, d) In highly cluttered space, the target echo overlaps with clutter echoes. Sound duration and envelope form correspond to search signals typical for different spaces: (a) QCF signal of open-space forager; (b) broadband FM-QCF signal of an edge and gap forager; (c) broadband FM signal of a narrow-space “FM” forager; (d) long CF-FM signal of narrow-space “CF” forager; echo shows amplitude modulations, or glints, created by beating insect wings (Schnitzler and Kalko 2001).

Likewise the bats own emitted signal can interfere with the activity evoked by the target echo (Figure 14.6). Interfering signals that precede the target echo, such as the emitted signal, produce a *forward-masking effect*. Interfering signals that follow the target echo, such as clutter echoes, produce a *backward-masking effect*. Depending on the signal type, several strategies are used to avoid masking (Fig. 14.10, and Side Box 14.1). Narrowband signals (e.g., CF bats) are good for target detection but less well suited for target localization. Broadband FM signals (e.g., FM bats), however, are good for localization but less well suited for detection. This trade-off between detectability and accuracy of localization creates a sensory drive on the kinds of signals used by different bats. In different environments, a specific kind of pulse is more efficient, reflecting **sensory drive** (Side Box 14.1). Relatively long narrowband signals (i.e., CF bats) are adapted for long-range detection of insects in open space and may also deliver some information based on glints produced by the fluttering wings of an insect (Fig. 14.11).

Are bats all that different from other small mammals?

The kinds of sounds that bats can detect are within the limits observed in other small mammals like rodents. Thus, the ancestral bat was well imbued with a broad frequency range. Echolocating bats do exhibit the lowest threshold sensitivity observed among this class of mammals suggesting that there is indeed some refining selection on sensitivity thresholds for acoustic detection in echo-locating bats (Fig. 14.11).

Neural circuits need time to return to ground state before they can be used. The brainstem in bats and dolphins has obvious anatomical specializations that appear to play a role in analyzing the temporal structure of echolocation sounds. Monaural pathways are highly modified, because they are especially highly developed in echolocating bats (Side Box 14.2), and these pathways seem to play an important role in the initial stages of processing temporal patterns of pulse and echo.

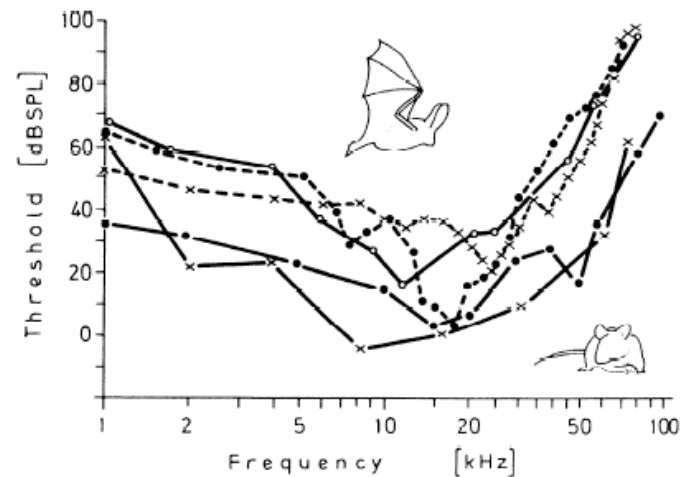


Figure 14.11. Comparison of audiograms of nonecholocating ground-dwelling mammals and bats (continuous lines) and of echolocating bats (dashed lines). There is no difference in frequency range heard between 2 groups, and auditory sensitivity to ultrasound (> 20 kHz) is not specific to echolocation. Behavioral audiograms: ●—●, house mouse; ○—○, cotton rat. Neuronal audiograms: ○—○, non-echolocating, fruit eating bat, *Cynopterus spinx*, x - - x, echolocating insectivorous bat *Taphazous kachensis*; and ● - - ●, echolocating insectivorous bat *Tadarida aegyptiaca*.

Side Box 14.2. The Neural architecture of sonar processing

The processing of information contained in sounds begins in the cochlea and continues in the auditory structures of the lower brainstem. The auditory system between the cochlea and the midbrain consists of multiple parallel pathways that provide multiple transformations of the cochlear signal. These transformations include changes from *excitatory* input to *inhibitory* output, changes in the temporal patterns of neural discharge, and the creation of **delay lines**. The parallel pathways of the lower brainstem can be grouped into two broad classes, a binaural system that receives input from both ears and a monaural system that receives input only from the contralateral ear. The **binaural pathways** of the brainstem have been studied in sufficient detail to show that they perform the

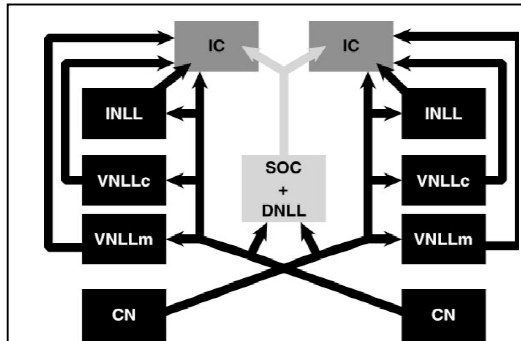


Fig. 14.12. Diagram showing monaural and binaural auditory pathways in the brainstem of an echolocating bat. Each cochlear nucleus (CN) receives input from the ipsilateral ear via the auditory nerve. Binaural pathways: The CN projects bilaterally to the superior olivary complex (SOC); the SOC, in turn, projects bilaterally to the dorsal nucleus of the lateral lemniscus (DNLL) and the inferior colliculus (IC). The DNLL also projects bilaterally to the IC. Monaural pathways: The CN projects directly to the contralateral IC; in addition, it projects to the contralateral nuclei of the lateral lemniscus, including the multipolar cell region of the ventral nucleus (VNLLm), the columnar region of the ventral nucleus (VNLLc), and the intermediate nucleus (INLL), each of which in turn projects to the IC. Thus, the IC receives direct and indirect monaural inputs from the contralateral ear. (Covey and Casseday 1999).

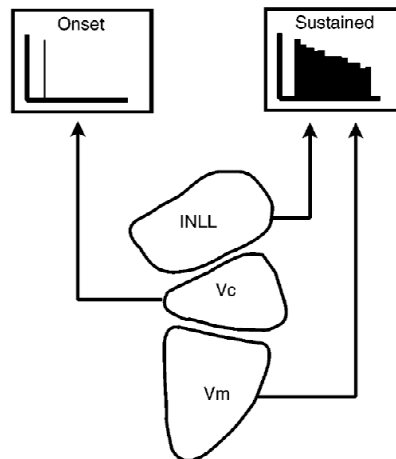
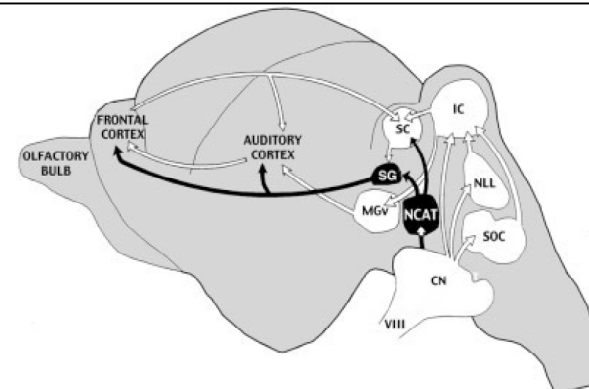


Fig. 14.13. How to time delay neurons. The monaural nuclei of the lateral lemniscus provide two functionally distinct streams of input to the inferior colliculus. The first stream (onset) originates in units that respond transiently with a single action potential and provide a time marker for the start of sound pulses (Vc). The Vc responds to periodic frequency modulations, but poorly or not at all to periodic amplitude modulations. The second stream (sustained pulses) originates in units that respond throughout the duration of a sound (Vm and INLL). These units respond well to periodic amplitude modulations and provide information about sound duration and intensity.

initial computations for sound localization (e.g., differences in timing from one side to the other). As in other mammals, the anteroventral cochlear nucleus is the main source of projections to the superior olivary complex (SOC) (see Fig. 14.12, 14.14). In all species of bats, the structure, connections, and response properties of neurons in the medial superior olive (MSO), part of the SOC, have been modified for echolocation. The general structure of MSO in bats is reminiscent of the barn owl's MSO analog, the nucleus laminaris, which is relatively thick and nonlaminar compared to that of diurnal birds such as chickens that do not depend on hearing to capture prey. Kubke et al. (2002) suggest that this adaptation is related to the owl's need to perform fine temporal discriminations to localize prey in the dark.

Monaural neurons are excited by sound at the contralateral ear and unaffected by sound at the ipsilateral ear. The **monaural pathways** from the brainstem to the inferior colliculus (IC) can be divided into two streams of processing, one of which transmits information about stimulus onset and the other of which transmits information about stimulus duration and intensity (Figure 14.12). In both of these streams of processing, neural activity corresponds to real-time features of the stimulus, such as onset, offset, duration, rate and depth of amplitude modulation, and rate of frequency modulation. Combining excitatory and inhibitory inputs with these different patterns provides a means of creating tuning for simple temporal patterns of sound. However, for this mechanism to be effective, the inputs must also be offset from one another in time. This offset requires delay lines (see Fig. 14.13). The IC in bats, as in other mammals, is the major source of auditory input to the thalamocortical pathway. In addition, the IC of echolocating bats is a major source of input to areas involved in motor coordination, including the superior colliculus (SC), an area responsible for orienting movements and from the SC coordination is further relayed to the auditory cortex and frontal cortex (see Fig. 14.14).

Fig. 14.14. Schematic parasagittal view of the bat brain showing the lemniscal pathway (white) and the extralemniscal pathway via NCAT and supragenulate nucleus (black). CN, cochlear nucleus; IC, inferior colliculus; MGv, medial geniculate nucleus, ventral division; NCAT, nucleus of the central acoustic tract; NLL, nuclei of the lateral lemniscus; SC, superior colliculus; SG, supragenulate nucleus; SOC, superior olivary complex. (from Covey 2005).



The **inferior colliculus** (IC) of bats is remarkably similar to that of other mammals in its basic structure (Box 14.2) except that it is large relative to brain size. Many IC neurons are tuned to one or more temporal parameters of sound. Temporal parameters include sound duration, FM sweep direction, and modulation rate. Many IC neurons are selective in that they are tuned to a specific range within one of these parameters, and they respond poorly or not at all to sounds outside this parameter range. For example, some IC neurons respond only to FM sweeps and not to other types of stimuli, such as pure tones or noise. In addition to being selective for FM sweeps, these neurons may be tuned to a specific direction, rate, and depth of frequency change. It seems likely that the temporal processing mechanisms described above are examples of general principles of the operation of the vertebrate midbrain. The first principle is that inhibitory and excitatory inputs, which themselves have different temporal properties, interact to produce filters for temporal features of sounds. The second principle is that filters are mainly for biologically salient sounds, especially sounds produced by prey.

The most rapidly produced echolocation sounds of big brown bat have a repetition rate of about 150/s. Wing beat frequencies of flying insects that the bat hunts are much less. Bats need built in **time delays**. If it is the job of the IC of the bat to filter for these kinds of sounds, then its operation must become slower to accommodate the filtering. Duration tuning is a good example. To measure the duration of sound, the neurons that do so cannot respond until the end of the sound. Thus a byproduct of filtering for biologically important sounds is that inhibitory mechanisms reduce the rate of temporal operations in the IC to match the rate at which the sounds can be analyzed. These kinds of time delays are built into the neural architecture by a simple neuron that first makes a time check (one pulse), while at the same time other neurons keep pulsing until the sound is finished (See Side Box 14.2, Fig. 14.13). The consequence of the processes that occur in the IC is a temporal window or multiple windows during which the neuron can or cannot fire.

The bat's neural circuitry provides a model of neural mechanisms for the analysis of temporal patterns. The computational processes that occur in the IC result in a slowing of the rate of neural processing to the speeds at which biological sounds of prey are produced.

Bat versus Dolphin Sonar

By virtue of their small size and availability for use in a laboratory, bat sonar has been very well studied. Dolphin sonar has also been studied for both reasons of pure science, as well as for the practical implications in commerce and warfare. The principles used in bat and dolphin sonar are very similar and the contrast between the two media, air *versus* water, is useful to highlight the constraints that the medium imposes on signal design and decoding.

As discussed above, the constant frequency signal of bats can be used to analyze the Doppler shift of the prey. In contrast, the frequency-modulated signal of bats is Doppler Intolerant in that the bat or the prey's motion does not significantly alter the signal. Dolphins tend to produce frequency-modulated signals and dolphins cannot decode the information that might be encoded in a Doppler shift.

Whereas bats produce sound from the larynx and emit it from either the mouth or nose, dolphins produce sounds with their nasal sacs. Whereas bats receive sound in their ears, dolphins detect return echoes through the lower jaw back into the stirrup and anvil of the inner ear.

Despite these gross anatomical differences, bats and dolphins seem to resolve a similar range of sounds frequencies. In addition, bats have a special muscle response, which locks down the ears and reduces the intensity of sound received at the level of the ear during signal transmission. This gain control prevents damage to the sensitive ears. It is unclear whether dolphins possess similar gain control.

Bats and dolphins differ in the target detection range owing to the properties of air versus water. Consider the ability of a bat or dolphin to resolve a ~one inch sphere. Bats can correctly target such a sphere 75% of the time at a distance of 5 m. Thereafter, their ability to target falls way off. Below this distance, targeting success rises slowly to 90%. Dolphins on the other hand can resolve the sphere at 75 m.

The lower detection distances for bats arise because air absorbs a considerable amount of the **acoustical energy** in the ultrasonic

frequencies that bats use. In contrast absorption of these frequencies in water is two orders of magnitude lower for dolphins. In addition, dolphins can simply produce much more energy in their signal compared to bats because of their much larger size.

Finally, water and air transmission differ one important aspect. The impedance in air is very high. Sound waves bounce back from relatively solid objects in the air and they are not distorted by traveling into the object because of the dramatic difference between the densities of the wave (air) and the object. In contrast, the density of a fluid filled body in water is very comparable to the density of waves traveling through the water, and this low impedance allows dolphins to potentially resolve information regarding the structure of the object. Some of the energy of sonar is bouncing off the object, but other energy penetrates a little before being reflected back. Bats can resolve differences between plastic versus wood or metal objects when they are trained for target discrimination, but cannot resolve differences between metal types. Dolphins in contrast can even resolve the subtle density differences between metals (e.g., iron versus brass).

Signal Detection by Moths and Crickets and Evasive Maneuvers

The prey is by no means helpless in their encounters with bats. Moths, grasshoppers, and mantids have all evolved neural circuitry that aids them in eluding the bats. The bat must send out a signal to echolocate, while the prey can receive this signal and begin evasive maneuvers. Insects can be broadly grouped into those taxa that are adapted specifically for hearing bats (e.g., moths) and those that have secondarily adapted for hearing bats, largely because they may also use sound in sexual selection (e.g., crickets) (Fig. 14.9, next page).

Moths receive the ultrasonic bat vocalizations with two ears on each side of the thorax. When pressure waves from the high-energy bat vocalizations strike the ears and vibrate the membranes of the moth ears, two **sensory receptors** (A1 and A2) can fire depending on the energy of the sound.

The sensory neurons trigger an action potential in the **sensory interneurons**, which conduct the electrical impulses to the next synapse. The next neuron in the chain after the first synapse is triggered by **neurotransmitters**, which are released and cross the synaptic junction and trigger a new action potential. The impulse can travel to the brain in this manner, or to ganglia in the thorax. Neurons in the ganglia or brain can integrate the information and send an action potential on to **motor neurons** that cause muscles to fire. The differential sensitivity of the A1 and A2 sensory neurons leads to a **stimulus filtering** of the bat sounds that gives the moth two options:

1. long distance evasion tactics when the bat is far away
2. short distance evasion tactics when the bat is at extremely close range.

The A1 cell is sensitive to low energy sounds (e.g., distant bat calls), and the A2 is sensitive to high-energy sounds (e.g., close bat calls), however, the frequency of the sounds for both neurons must be in the ultrasonic range of bat calls (>20 kHz).

When A1 is stimulated, the firing rate of the neuron is proportional to the intensity of sound, and the moth can detect whether the bat is approaching. A1 fires more and more rapidly as the sound gets louder and louder. By comparing the time delay between right and left ears, the moth can tell which direction the bat is coming from. The wings can also obscure the sound from above or reflect it from below, thus the moth can also assess the bats altitude. The moth can use all of this "long range information" to alter its flight path to avoid being detected (recall that the bats detection distance is < 5 m).

If all these evasive Maneuvers fail, and the bat is about to collide, the A2 neuron begins firing because of the high energy reaching the moth ear. The A2 cells send a message to the thoracic ganglia, and this seems to shut down wing beats or cause them to fire erratically. This leads to erratic flight which may be a last ditch attempt to elude the ranging and speed computing neurons of the bats brain.

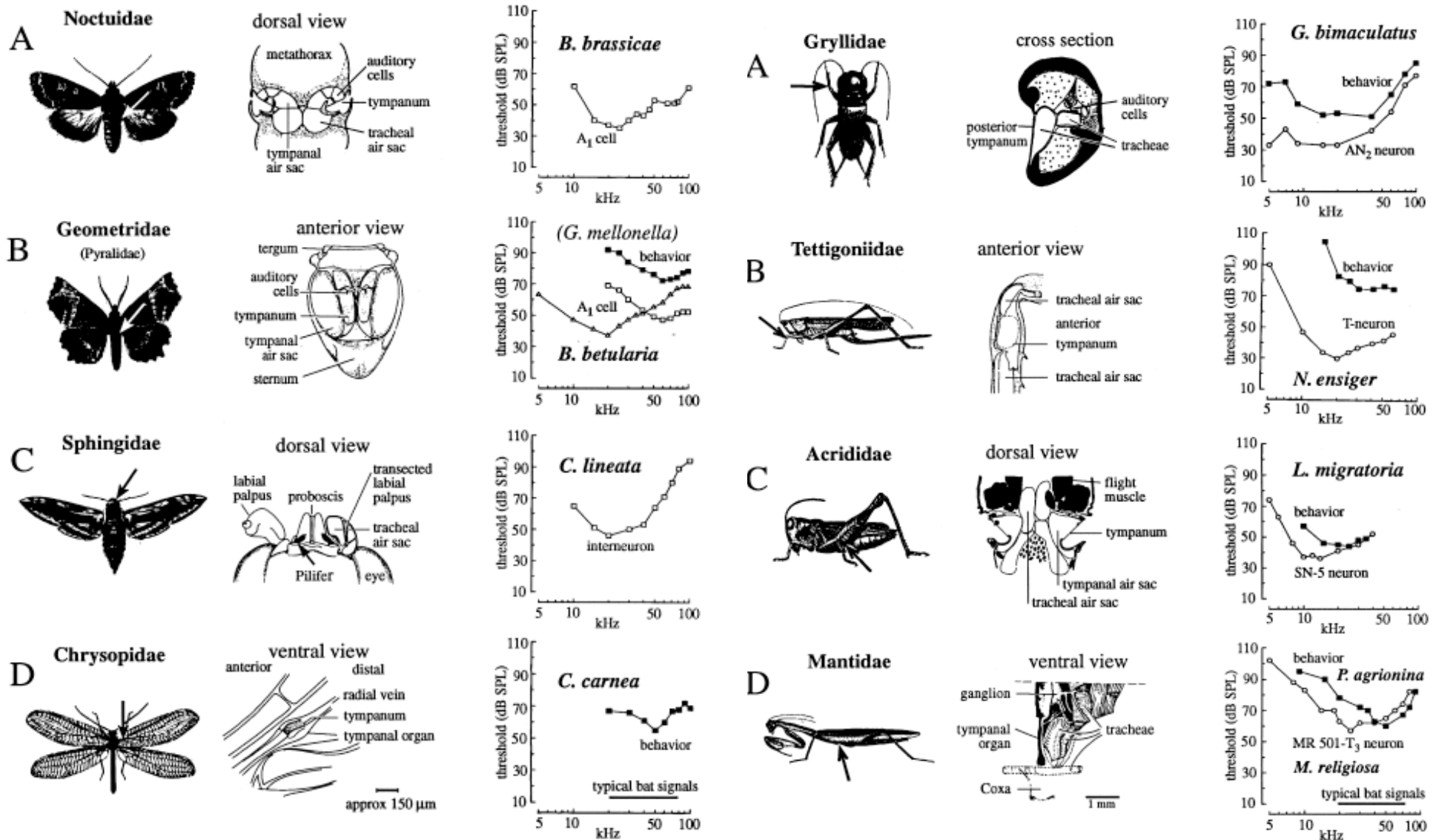


Fig. 14.15. (LEFT panels A-D) Insects with audition adapted specifically for hearing bats. Representative insects from the various families are shown in the left column, with the location of the ear indicated by arrow. Their general anatomy of each ear is shown in the middle column. The tuning curves for flight cessation (behavior), the A1 sensory cells, and an interneuron are shown in the right column. The frequency range for typical bat biosonar signals is shown on the abscissa (d, right). A cross section through the first abdominal segment of a geometrid moth viewed from the inside (modified after Kennel and Eggers 1933). A single tympanal air sac occupies the space behind the tympana (not seen in drawing). The pyralid ear (e.g., *Galleria mellonella*) is anteroabdominal like that of the geometrid (b, right). **(RIGHT panels A-D)** Insects with audition secondarily adapted for hearing bats. Representative insects from the various families are shown in the left column, with the location of the ear indicated by arrow. The general anatomy of each ear is shown in the middle column. The tuning curves for avoidance behavior (negative phonotaxis for orthopterans and nondirectional responses for mantid) and interneurons thought to be involved with the behavior are shown in the right column. (from Miller and Surlyke 2001).

The brain integrates the bat's impulses. Thus the impulses have long neuronal distances to travel and many circuits are crossed. The moth's neurons short-circuit the brain by looping from sensory neurons to ganglia to motor neurons.

Thus, the moth can produce evasive Maneuvers a little faster than the bat might be able to respond. The moth neural loop is a **reflex** action.

The ears of moths are highly specialized, so specialized that few moths end up in the stomachs of bats. A variety of mechanisms have evolved in the insects for evading bats. Many other insects have much simpler detection mechanisms. Crickets possess ultrasonic receptors in the forelegs that have a low intensity threshold to sounds in the 40 kHz range -- bat sound. They also possess another low intensity threshold in the 5 kHz range -- cricket song. If the legs detect 40 kHz, this causes sensory interneurons to relay the information to thoracic ganglia, which sends an impulse out to motor neurons of opposite rear leg. The muscles in the leg raise it into the wing, which causes the wing to beat with less energy on that side and the cricket turns away from the bat (avoidance behavior, Fig. 14.15). The reverse is true if it detects cricket song. It causes the rear leg on the same side to lift, and turn towards the song.

Cognition, perception, innate signals and frequency-dependent selection

Recall from chapter 5 on optimal foraging that cognition constitutes three steps (Roitblat 1987):

1. perception---units of information are collected and stored,
2. processing---this data, stored in memory, is analyzed with computational rules built into nervous systems,
3. environmental representations form from data processing---adaptive behaviors are based on these "pictures".

Though cognition promotes negative FDS (e.g., uncommon "picture" advantage), other noncognitive processes can influence FDS. Innate

recognition is a genetically codified signaler-receiver interaction. Habituation, sensitization, and input matching supply critical filtering systems in a messy world. For example, habituation of lizards to sinusoidal waveforms (blowing branches) favors mimicry to evolve in snake movement and morphology, thereby thwarting antipredator detection systems of lizards (Fleishman 1986). Learning builds correlations among many interrelated "pictures" of the environment. Cognition and innate neural processes thus contribute to correlations that build among the pictures or memotypes of neural systems (plastic: imprinted, habituated, sensitized, or learned signals; or genetic: innate), much like correlational selection on traits, but through positive and negative reinforcement or through signaler-receiver coevolution.

Learning mechanisms and frequency-dependent cycles

My goal in this section is to link correlative forces of perception and learning (i.e., cognitive representations of traits or memotypes) directly to CS and FDS on genotypes. Apostasis in predator-prey interactions (Cook & Kenyon 1991, Mallet & Joron 1999), analogous to mating system apostasies (e.g., rare male morph advantage, Chapter 9), promotes evolutionary cycles of highly variable forms.

Learning experiments on *Cyanocitata cristatta* in a virtual-reality environment, in which Bond & Kamil (1998, 2002) used many alternative cryptic forms generated by a computer, generate cycles in the frequency of computer-generated cryptic prey morphotypes. As *C. cristatta* switched between common type, learning preserved and cyclically generated new variation (Figure 14.16), experimentally confirming the role of prey learning in driving cycles of apostatic selection. Analogous effects with dorsal pattern manipulations have been demonstrated in nature (Forsman & Appelqvist 1998).

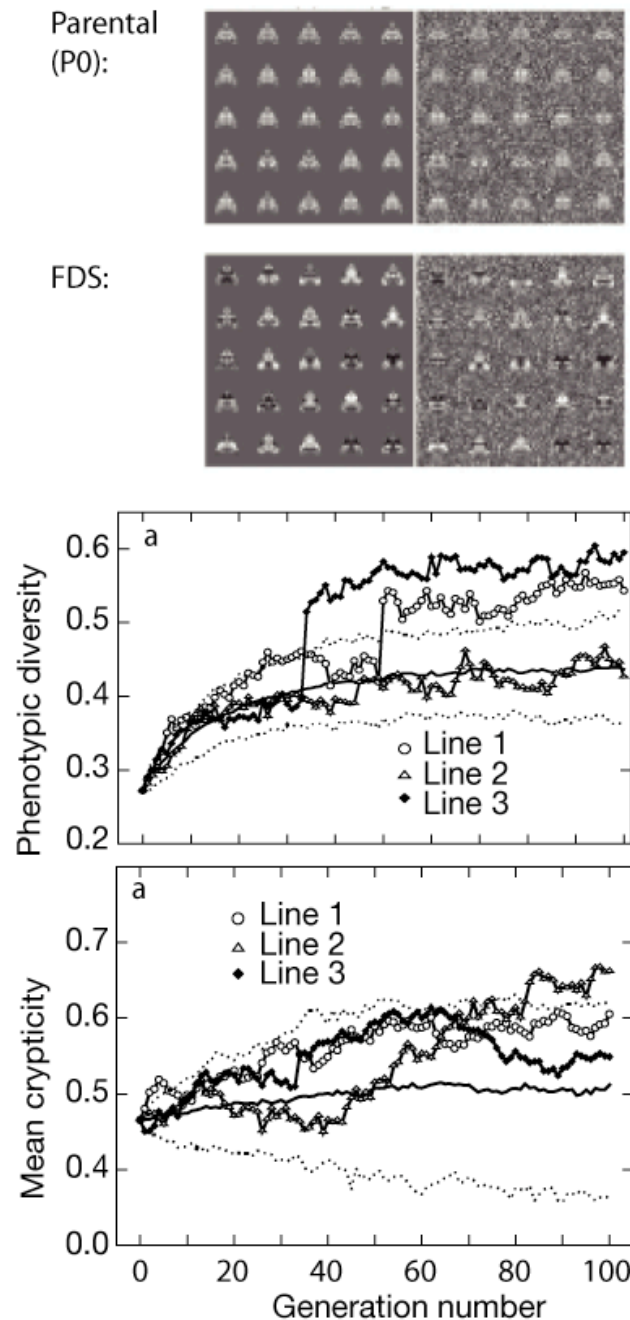


Figure 14.16 Top Panel: Samples of virtual prey (digital moths) for blue jays, *Cyanocitta cristata*, shown on uniform gray (*left*) and cryptically textured (*right*) backgrounds. Panels show prey items from parental prey population, P0 (a), and from computer simulation prey populations after 100 generations of frequency-dependent selection (FDS) by jays. Bottom panel: Moths from FDS lines were more cryptic than those in the nonselected lines, and more variable in appearance than those in the lines subjected to frequency-independent selection (not shown). Changes in mean crypticity and phenotypic variance across successive generations in three experimental lines (plotted with symbols), contrasted with distribution of values from two sets of control lines (from Bond & Kamil 2002)

Handedness

Handedness is a common form of FDS, which is hypothesized to become fixed owing to the advantages of a bias from bilateral symmetry that allows for rapid stereotyped actions to always commence within the same hemisphere of the brain and propagate through a dominant-handed motor pattern (Propper et al. 2005). Handedness is ancient in origin. Handed attack patterns appear on trilobite prey, owing to their handedly biased predators that hunted Cambrian ecosystems (Babcock 1993). Attack handedness of the scale-eating cichlid, *Perissodus microlepis*, which exhibits right- and left-jawed morphs, drives FD cycles via either learning or sensitization of their prey cichlid species (Hori 1993) (Figure 14.17). Handed feeding polymorphism in crossbills, *Loxia curvirostra*, generates FD advantages to rare chirality feeding forms (Benkman 1996, Benkman & Lindholm 1991) in opening cones that are either sinistral or dextral (e.g., chirality) with respect to spiral orientations of cone bracts.

Frequency Dependent Selection on Handedness

The Rift Lakes of Africa are an evolutionary playground. Within a very short period, perhaps as little as 10,000 years, a tremendous number of species of Cichlid fish have evolved by the process of speciation. The kinds of feeding behaviors found in the lake are stunning. Some cichlids feed in the pedestrian manner typical of fish, scraping algae off rocks or chasing after other fish. Other fish are egg robbers. The egg robbers do not eat eggs that other fish have laid in the lake; instead egg robbers have specialized on another cichlid that is called a mouth brooder. Mouth brooders swallow their own offspring but do not digest them, they keep them safe out of harms way in their mouths. Egg robbers get

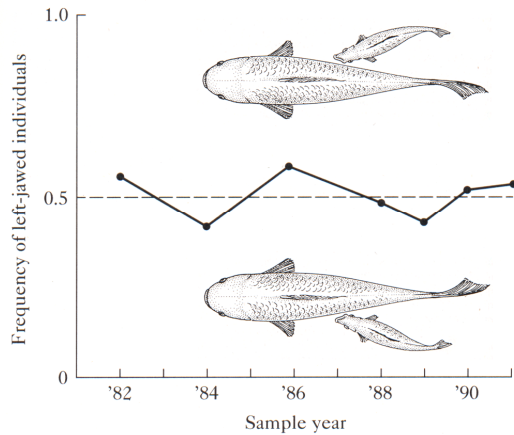


Figure 14.17. The frequency of the scale-eating cichlid, *Perissodus microlepis*, oscillates around 50%. Each year, the prey species learn to look over a particular “shoulder” to guard against predation by the scale-eaters. The rarer morph (e.g., Left-jawed in 1984) has an advantage and increases in frequency. The following season the other morph becomes rare (e.g., right-jawed in 85) in the following season (Hori 1993).

the mouth brooders to cough up their eggs. When they do, the egg robbers swoop in for the kill. There are over 250 fish in Lake Victoria, and most fish have a different way of making a living.

One of the strangest ways of making a living is found in the behavior of *Perissodus microlepis*, a cichlid fish that specializes in eating scales (Hori 1993). *Perissodus microlepis* will swoop in on its prey from the blind side and eat some scales. The scale-eater is a classic **partial predator** that feeds only on part of its prey, but

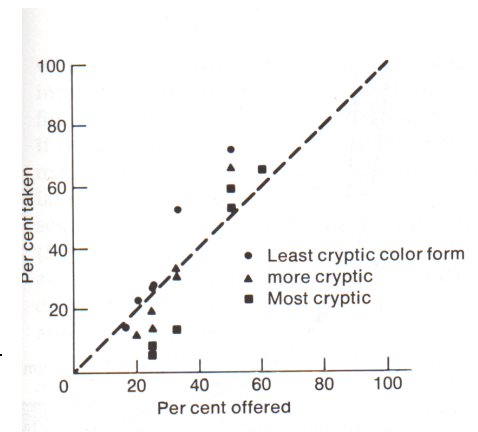
leaves the fish otherwise intact to learn something from the encounter. What is strange about this behavior is that it leads to a curious evolutionary cycle from an interplay between the predator’s genes, and the prey’s learning and reinforcement. At any point in time, there are two kinds of scale-eaters. One is always slightly more common than the other. In 1982, left-jawed scale-eaters were the most common. The prey are more often attacked on their right flank by a scale-eater with a jaw that curves to the left, so the prey learn to look to the right when being vigilant to attack. While the prey learn to look right, they leave their left flank exposed to the scale-eater with a jaw that curves to the right. This gives the rarer right-jawed morphology an advantage, and they do slightly better that year. The left-jawed morph does slightly worse, because the prey is vigilant to attack from the right flank attack, and the left-jawed morph declines in frequency.

A lopsided jaw makes it easy to eat scales on one side of the prey, but it is completely ineffective on the other side of the prey. The functional

constraints on a predator’s foraging behavior lead to an interesting evolutionary chase of sorts. Consider 1984 when left-jawed fish were below 50% in the population, and the right-jawed fish were above 50%. The prey learns to associate left side with attack, because right-jawed fish are common. Predators with a left-jawed form can successfully swoop in on the prey’s exposed right flank. These left-jawed fish have more resources, and thus produce more offspring. The next year, the proportion of left-jawed scale-eaters increases. They are so successful that prey now learn to look right. Now the right-jawed predators that attack from the left have an advantage. The population of predator and prey oscillate over very short evolutionary time because of strong frequency-dependent selection. Rapid learning and reinforcement for the side that is attacked most frequently drive the prey’s behavior. The predator’s behavior and genetics drive them to be more or less successful depending on whether they are common or rare. The rare form always has an advantage.

Classic evidence for such a switch in search image is found in an aquatic corixid bug, *Sigara distincta*, found in three cryptic color forms (Figure 14.18). The different species of fish that feed on the bugs tend to feed on the most common type when presented with a variety of color forms. **Polymorphisms** or alternative kinds of crypsis in the prey, can be maintained indefinitely because when a type becomes rare it gains an advantage in crypsis over the other common types and begins to slowly increase in frequency until it too becomes rare.

Figure 14.18. Prey selection by a predatory fish when feeding on three color morphs of cryptic corixid bugs, *Sigara distincta*. Each color morph suffers high predation when it is the most common cryptic color form. The one-to-one line is drawn for reference. If fish took prey in the frequency offered, then points should lie on the line (after (Clarke 1962 redrawn from (Futuyma, 1986)).



The frequency-dependent advantage of the rare prey item need not be restricted to this spectacular case of alternative feeding morphology. Frequency-dependent prey selection may be a common feature of many interactions between cryptic prey and their predators. Because many predators may form a search image (see Chapter 6), they will tend to form a search image for the most common prey encountered in the environment. When this occurs, they will begin to feed on that particular cryptic item, and not even notice the other cryptic prey. They continue depleting the common cryptic prey item until it too becomes rare. At this point, they may stumble on an alternative and more common cryptic

In humans, the advantage of handedness and other rare behaviors are common knowledge in sports (switch hitting, a form of ambidexterity; south paw in boxing; or regular versus goofy, a footedness advantage to surfing the rare left or right-hand wave depending on breaking surf). The advantage of left-handedness (Billiard et al. 2005), as judged by handedness frequencies in sports (Raymond et al. 1996), is most prominent in close contact sports (e.g., fencing or boxing compared to tennis). A rare left-handed advantage may have first arisen in close contact fighting (Faurie & Raymond 2005). Handedness in humans has a genetic basis (Klar 2005, McKeever 2004). However, learning is involved, because most training partners and contestants are right-handed. Defensive and offensive strategies will always be reinforced in real contests with right-handed opponents regardless of novel training regimes, such as sparring with south-paws.

Invasion of cheaters is also driven by rare advantage. For example, rewardless orchid species evolve conspicuous and colorful flowers but forgo provisioning them with nectar (Gigord et al. 2004). CS on floral morphology has been observed in rewardless orchids (O'Connell & Johnston 1998). As bumblebees emerge to feed in spring, they often visit rewardless orchids, which have evolved color mutations with rare advantage. Bumblebees visiting common floral types are negatively reinforced, and subsequently avoid that color (Smithson & Macnair 1997).

Aposematic Coloration and Mimicry Complexes

Aposematic or warning signals are bright colors or loud distinctive signals associated with prey. These signals alert the predator that it should not attack or there will be negative consequences. Many aposematic species form **Müllerian mimicry** complexes in which unrelated species come to resemble one another in form, all possessing some kind of toxin or deterrent. The predators do not have to learn to avoid a diversity of prey types, as the unrelated species all resemble one another.

Examples of aposematic signals include:

1. Monarchs ingest milkweed toxins (cardiac glycosides) as larvae and these compounds make birds vomit,
2. Coral snakes which are in the same family as cobras possess deadly toxins,
3. Rattlesnakes rattle and alert the predator of its toxic venom,
4. Bees and wasps have bright black and yellow or black and white banded abdomens and they buzz -- loudly,
5. Newts possess tetrodotoxin (TTX) that is deadly.

Each of the species listed above have a Batesian mimic associated with them. The **Batesian mimics** do not possess the noxious substances or dangerous venoms, but do benefit from the presence such deterrents in their toxic or deadly *Doppelgangers* (*German for twin*).

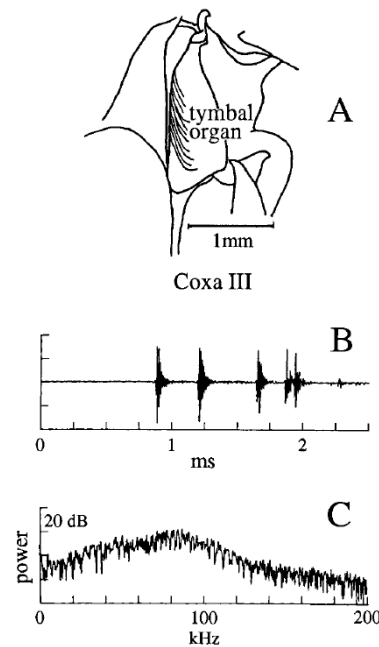
1. Monarch butterflies are indeed noxious, but there are many Monarch look-alikes, which are tasty and yet avoid being eaten.
2. Coral snakes are indeed deadly, but harmless milksnakes and kingsnakes possess the same red-white-black banding, which seems to provide some protection ("Red next to yellow can kill a fellow. Red next to black -- venom lacks).
3. Rattlesnakes are notorious for their bite, but fangless burrowing owls produce a similar vocalization and this sound deters ground squirrels from entering the burrows of owl burrows.
4. Bees and wasps buzz loudly and have the stingers to back it up, but Flicker chicks in tree hollows produce a similar kind of

vocalization that deters squirrels from entering and perhaps harming the chicks.

5. Newts flash their bright yellow eye and arch their back to show their bright red belly and a bird should avoid the newts because the tetrodotoxin is deadly (Chapter 3). The *Ensatina* salamanders of ring-species fame (Chapter 5) bat a similar yellow eye and expose a similar red belly which may allow them to escape from predators unharmed.

Warning signals can just include sound. Some moths that are toxic will vibrate in their roost sites (where they roost with bats) when they feel the bats approach (Fig. 14.19). It is thought that this vibration is a warning sound to the bats, which find the moths quite distasteful.

Figure 14.19. An example of a warning sound (power spectrum in B, C) that is produced by a moth that is distasteful to bats. A specialized sound production tymbal organ on a leg segment warns approaching bats that the Arctid moth, *Phragmatobia fuliginosa*, is toxic. (from Miller and Surlyke 2001).



How do predators come to avoid aposematic forms -- learning or innate responses?

Feeding trials of Monarchs to blue jays indicates that jays can rapidly learn to avoid vomit-inducing forms. Such aversive stimuli are rapidly learned and require only a single trial in most cases. Moreover, the jays also then tend to avoid Müllerian mimics such as Viceroy butterflies.

Innate Recognition of Coral Snake Mimicry

In other cases, the costs may be so high that innate recognition is beneficial. For example, motmots (a south american king fisher) do not appear to require any conditioned learning. Laboratory reared motmots (no experience in the wild) avoid rods painted with yellow and red rings, more so than they avoid yellow and red stripes or green- and blue-ringed rods. Butch Brodie III and his father Butch Brodie II (1981) tested whether milksnake batesian mimics are effective in nature against bird predators. Do Batesian milksnake dummies receive fewer pecks in the wild? In these experiments, milksnake models received far few pecks than non-mimetic models (e.g., banded by other colors).



Figure 14.20. Mountain king versus coral snake. Which would you touch?

The Evolution of Aposematic and Müllerian Mimicry

Why be bright and colorful and attract naïve predators when it will get you killed?

What is the benefit to the individual of aposematic coloration?

Sir Ronald Fisher (1930) observed that aposematic forms also tend to be quite gregarious and congregate in the same locale. Fisher speculated that kin selection may favor such aggregations. An individual may die during the learning required to teach a naïve predator that the color also results in a bad experience. However, because the predator leaves the

remaining kin alone, the inclusive fitness of the dead aposematling is positive because the costs of individual death is balanced by the surviving kin that are left alone. Gregariousness can easily result from kin groups (e.g., a localized clutch), and such kin groups greatly enhance the probability that aposematic coloration will spread even though brightly colored individuals attract attentions of naïve predators.

Fisher (1930) realized that a kin benefit in prey would favor evolution of aposematism if kin were aggregated, a form of positive FDS (Endler & Mappes 2004). Death of an individual that reinforced predator learning would benefit nearby kin. However, a constraint on studying origins of aposematism is a universal innate predator aversion to certain colors, which in avian systems are usually yellow or red (Brodie & Janzen 1995). Thus, extant bird species share innate aversion to feeding on certain colors, reinforced over eons of interactions with prey that have all converged on yellow or red aposematic signals.

It is difficult to address the origin of aposematic coloration and Müllerian mimicry because predators may not be evolutionarily naïve to signals (e.g., innate responses of motmots). Reconstructing the initial conditions during the origin of the trait is nearly impossible. However, Alatalo and Mappes (1997) used an artificially constructed world of prey types to test a fundamental factor involved in evolution of aposematism -- adaptive value of aggregation behavior. In creating their world they only used black and white markings to avoid any preexisting color biases in their naïve predators, the Great Tit, *Parus major*.

In the first series of trials they created hollow fat-filled rye straws -- Tit treats. They put wings on the straws and used symbols on the wings (pluses or squares) to make the treats stand out (e.g., warning signals) or be cryptic (the background matched the wing markings).

1. An aposematic individual was dipped in chloroquine (yuck) and had squares on its wings so as to stand out against the plus-covered background.
2. Other individuals were dipped in the same chloroquine, but as they had pluses on their wings, they blended in with the plus covered background.

3. A palatable individual just had pluses on its wings and it blended in with the plus covered background.

Finally, they created two treatments comprised of the three treat creatures with paper warning color wings (e.g., see Fig. 14.21):

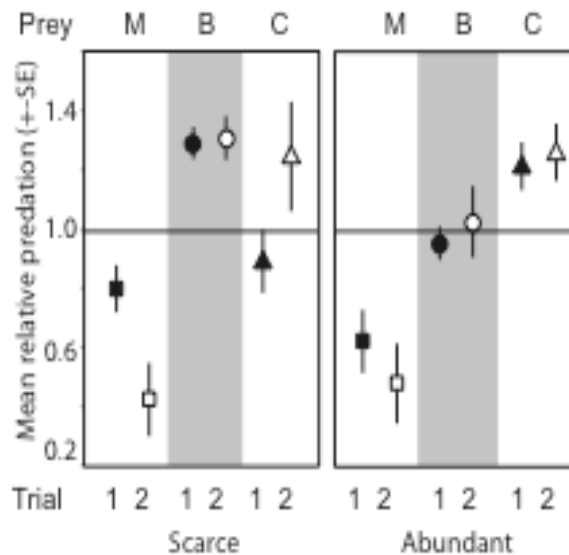
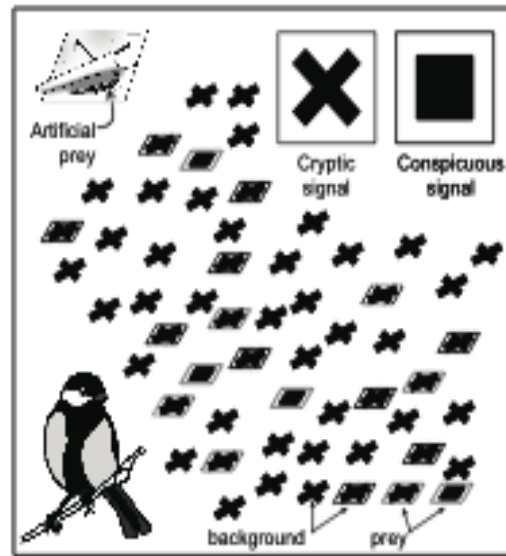
1. solitary creatures (mixed with 0.25 type 1, 0.25 type 2, and 0.5 type 3)
2. and clumped (again mixed with 0.25 type 1, 0.25 type 2, and 0.5 type 3).

They let the naïve great tits forage in amongst the treats and looked at the "death" rate of the three kinds of treat creatures.

The great tits took a lot longer to figure out that aposematic treats were unpalatable when aposematic treats were solitary compared to when they were aggregated. Thus, being aggregated is a definite advantage for aposematic forms compared to unpalatable cryptic and palatable cryptic forms. In fact, being aposematic and solitary attracted the great tit's attention and the Tit's would continue to pick up and attempt to eat solitary aposematic forms that stand out by virtue of their warning signals relative to the cryptic palatable and unpalatable treats. However, the tits learned that first aposematic treat in an aggregation were yucky in the first tasting and they avoided the remaining treats in the clump! Eventually, the great tits did learn that solitary aposematlings were nasty but it took much longer.

The second test used the same birds, but altered the creatures -- almond sliver bodies rather than rye straws filled with fat. They used a different body, but similar wings on the new creatures. They wanted to see if the new creatures were protected because the experiences of their Tit predators had conditioned the predators to avoid aposematlings. Again they used solitary and clumped almond sliver creatures. This experiment tests whether clumping is still important in the evolution of an Müllerian mimic. In Müllerian mimicry each of the two co-evolving prey species help to reinforce the signal in an evolutionary mutualism.

Figure 14.21. Predator learning, aposematic, and apostatic selection on prey. Top panel: A great tit inspects the floor of a novel world aviary during learning trials. Bottom panel: Data from novel worlds involving (I) an aposematic model (M), weakly Batesian mimics (B) and cryptic prey (C), which were presented at two frequencies, scarce and common (Lindstrom et al. 2004). Relative predation of models (*squares*), mimics (*circles*), and cryptic (*triangles*) prey in the two alternative prey treatments. Filled symbols indicate mean relative predation (with standard error bars) in the first trial, and open symbols in the second trial. A line indicates the expectation based on random predation. When alternative prey was scarce, imperfect Batesian mimics were selected against, but abundantly available alternative prey caused selection against imperfect mimics to be relaxed (*Top panel* with permission of M. Joron and *bottom panel* with permission of L. Lindstrom).



makes origin of warning signals contingent on prey behaviors or life history traits that aggregate signals. Aposematism is common in butterflies (Langham 2004), which often evolve to lay eggs in batches, thus establishing kin aggregations.

Extensions of the novel world approach (Mappes et al. 2005) demonstrated advantages of Müllerian forms that are conspicuous but not necessarily aggregated. Other studies demonstrated that aposematic forms are antiapostatic (Lindstrom et al. 2001), further underscoring impacts of rarity on origin of aposematism. Use of three morphs also confirmed the role of cryptic forms in maintaining imperfect Batesian mimicry (Figure 14.21). Batesian mimics evolve to resemble a noxious or toxic aposematic model and gain FD protection (rare advantage) from attack even though they lack defense, provided that cryptic forms are common.

Additional constraints and tradeoffs involved in perceptual systems of predators can drive CS and FDS on alternative antipredator prey traits such as escape behavior and dorsal patterns (Brodie 1992, Niskanen & Mappes 2005). For example, predators attacking a moving snake with stripes often miss because moving stripes appear stationary. The alternative tactic, freeze, becomes coupled to cryptic patterns (see Chapter 3). Though speed is often coupled to stripes, differential crypsis can arise through either pattern matching a background (e.g., spots on fine backgrounds, bars on bark), or disruptive patterns like large spots that break up the prey outline (Ruxton et al. 2004).

They found that the new creatures were protected even though they were quite novel in appearance. In addition clumping had no further advantage. Thus clumping and perhaps kin selection may be important in the early evolution of aposematic coloration. However, clumping is not essential for the refinement of Müllerian mimicry complexes. They also conclude that kin selection per se is not essential, but aggregation or clumping is the essential trait that reduces the risk of survival.

These early experiments (Mappes & Alatalo 1997) confirmed Fisher's idea that gregarious aposematic prey gain an advantage through single-trial learning of predators, in which clustered and obvious but noxious forms have a survival advantage over dispersed noxious forms. CS

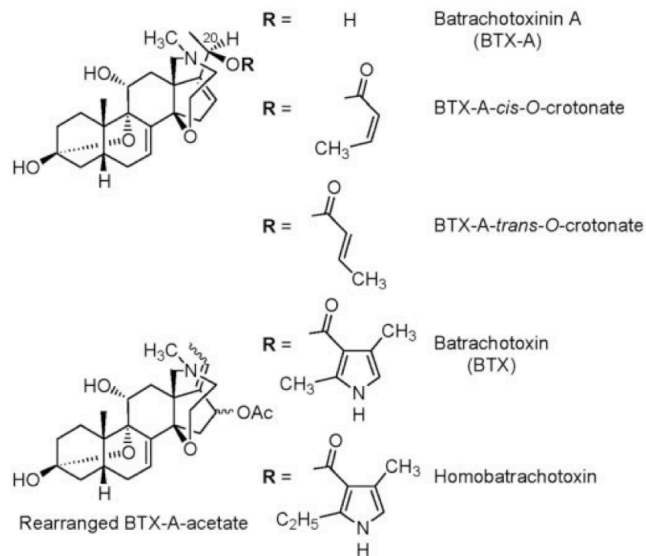


Figure 14.22. The Beetle genus that is ingested by both *Pitohui* birds and frogs in the genus *Phyllobates*, along with the most common Bratrachotoxins (BTX) extracted from the Beetle (*Choresine pulchra*) (Drumbacher et al. 2004).

Müllerian mimicry: convergence in animals worlds apart

The search for the source of toxin in aposematic species can involve interesting detective work. For example, birds in the genus *Pitohui* carry a batrachotoxin (BTX) (Fig. 14.22), which can cause death in mice (Dumbacher et al. 1992), therefore, the bright red body color and black head and wings of the *Pitohui* is thought to reflect aposematic warning coloration. New Guinean traditional village naturalist from Herowana identify a local beetle as “nanisani”. Nanisani is also the local name for the blue-capped Ifrita (*Ifrita kowaldi*), which is another bird that carries BTX and is aposematic. According to the village naturalist, the name “nanisami” refers to the unusual tingling and numbing sensation to the lips and face caused by contact with either the beetles or bird feathers.

Following up on these clues, Dumbacher et al. (2004) abandoned a decade long quest with high tech methods of radio-tracking *Pitohui* in their quest for the source of the BTX and found that beetles were indeed the source. Moreover, they examined gut contents and found traces of *Choresine pulchra* and a few intact *Choresine pulchra* in the museum *Pitohui* specimens.

Dumbacher et al. (2004) carried out a detailed phylogenetic analysis of the birds in the genus *Pitohui*, and focused on *Pitohui dichrous* and *P. kirhocephalus*. *Pitohui dichrous* is widely believed to be the aposematic model and *P. kirhocephalus*, has many members that resemble *P. dichrous* in coloration (and toxicity). Other members have very different plumage color (Fig. 14.23). Therefore, Dumbacher et al. (2004) tested whether any *P. kirhocephalus* were Müllerian mimics of *P. dichrous*.

To be considered Müllerian mimics the candidate must not have acquired the trait simply by shared ancestry, rather co-habiting a region resulted in a co-evolutionary force that caused correlational selection to acquire both the color signal and dietary toxin, which helps each species ‘educate’ any naïve visual predators. If the members of the *Pitohui* genus share a common ancestry, then the trait only evolved once as an aposematic mimic. The *Ifrita* is quite divergent in DNA sequence compared to the *Pitohui* (Dumbacher et al. 2000), therefore the *Ifrita* and *Pitohui* have likely acquired the BTX toxin and independently evolved bright warning coloration, reflecting the hallmark of Müllerian mimics. This co-evolution distributes the workload of education between two species a form of evolutionary cooperation (a mutualism).

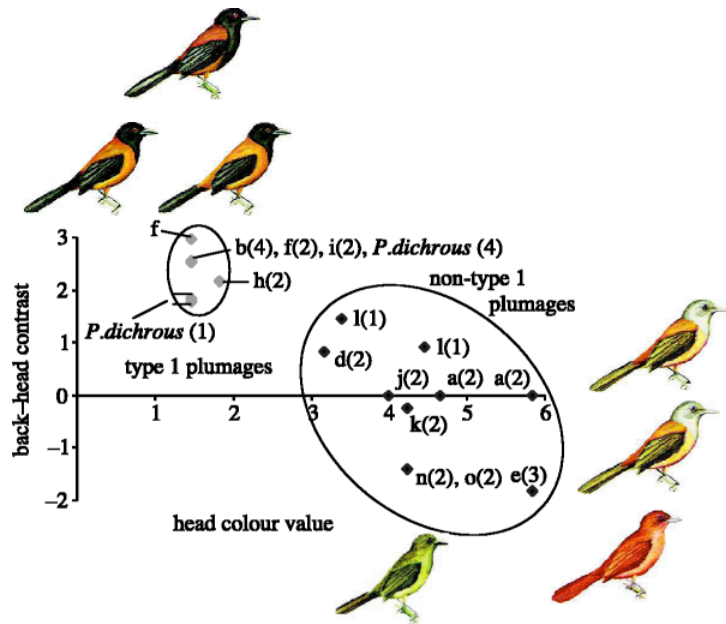
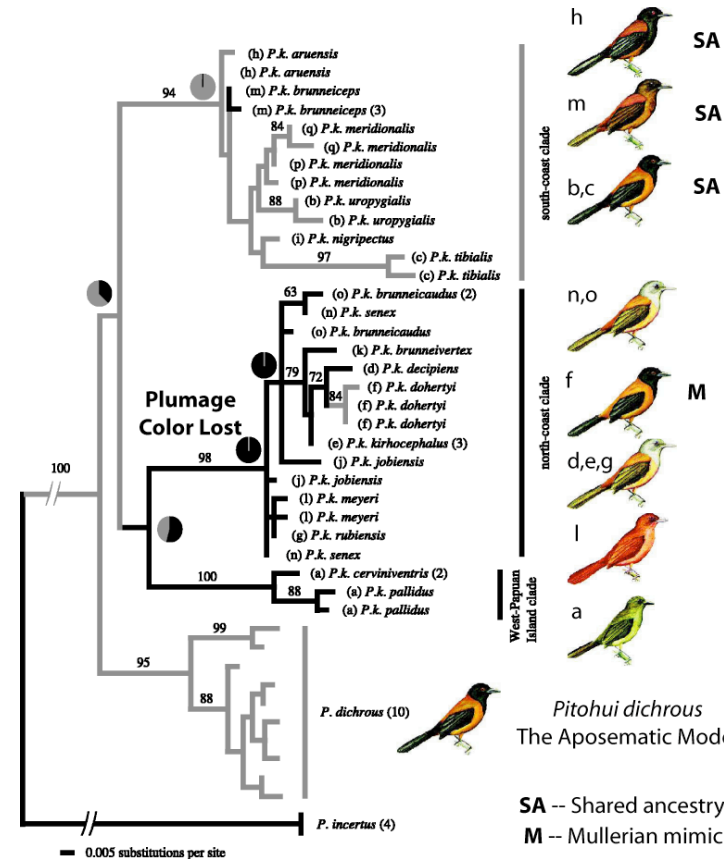
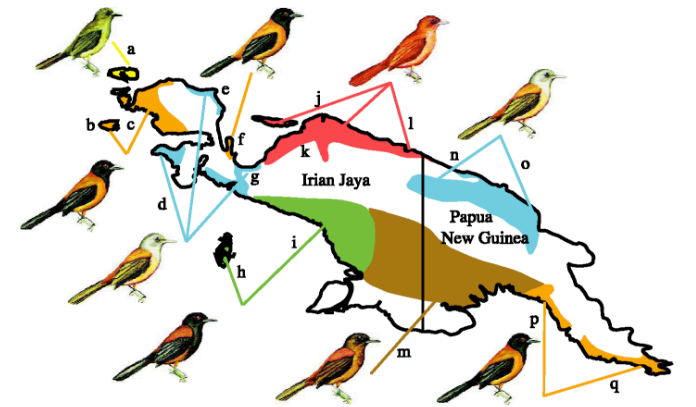


Figure 14.23. Birds in the genus Pitohui can possess a red body feathers and black wings and head, or an alternative set of non-aposematic colors. A cluster analysis reveals which species resemble one another (Drumbacher et al. 2004).

Dumbacher et al. (2004) found that most members of highly variable species group *P. kirhocephalus* shared aposematic color as an **ancestral trait** with *P. dichrous* (Fig. 14.24). A **common ancestor** to both species acquired both the bright warning color on the plumage and sequestration of dietary BTX, due to the process of correlational selection. This trait was then passed down to these members intact. However, a large set of species lost warning color in their plumage, except for *P. k. dohertyi* (clade f). The most likely reconstruction (maximum likelihood ancestral reconstructions, see Chapter 18) indicates that this subspecies reacquired both color and toxicity, thus it is the only true Müllerian mimic.

Figure 14.24. Phylogenetic analysis of pitohui color indicates that color arose once in a shared ancestor common to *P. dichrous* and *P. kirhocephalus*, however, color appears to be lost in a large clade and then reacquired in only one true Müllerian mimic, *P. k. dohertyi* (clade f). Phylogenetic methods (see Chapter 18) can be used to reconstruct the most likely ancestors at each node, which is indicated by a probability pie diagram. (Drumbacher et al. 2004).

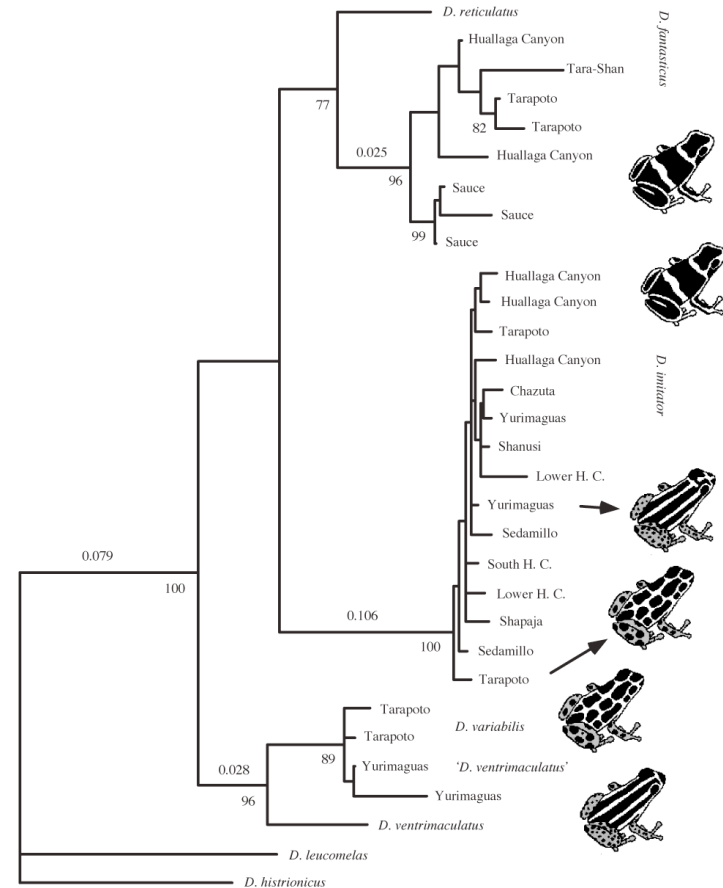
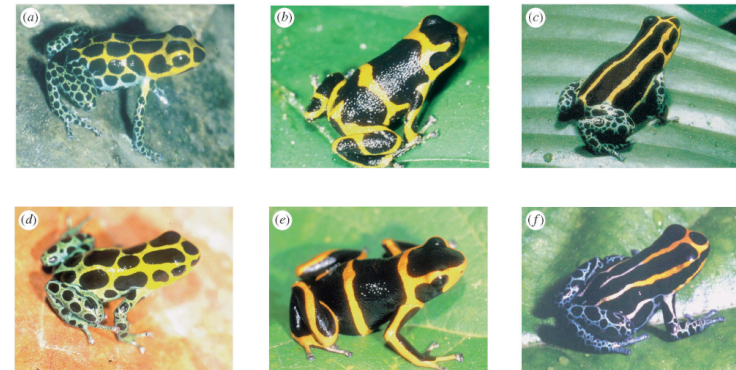


Poison Dart frogs One of the most compelling examples of Müllerian mimicry is found in the family of Dendrobatid frogs more commonly known as Dart Poison frogs. Hunters in many tribes in South America use the poison they extract from the skin of the frogs to tip their arrows. The toxin is potent that they hunters can take down a monkey (not strictly kill). The monkey takes a while to fall from the tree. Only a minute quantity of the toxin is actually transferred from the dart tip to the monkey, nevertheless it acts quite quickly to immobilize the monkey and cause it to go unconscious and fall from the tree.

The name for the unique steroidal alkaloids Batrachotoxin, BTX, was derived from the Greek “batrachos,” meaning frog. During the following 25 years, BTX was detected only in frogs of the dendrobatid genus *Phyllobates* and not in other species of poison frogs (Daly 1998). Only 3 species are toxic enough to be used by hunters for poisoning blow-dart tips: *Phyllobates terribilis*, *Phyllobates bicolor*, and *Phyllobates aurotaenia* (Meyers et al. 2004).

Similar to TTX described in the toxic Newt *Taricha torosa* (Chapter 3, see Side Box 3.3), BTXs bind with high affinity to voltage-gated sodium channels in nerve and muscle membranes, locking them in an open state. When raised in captivity poison dart-frogs lack BTX, confirming a dietary source of BTX. In other genera of Dendrobatid frogs besides *Phyllobates* other toxins are sequestered from ants into the skin. Skin extracts from *Dendrobates venrimaculatus*, *D. imitator*, and *D. variabilis* all contain potent alkaloid toxins (Daly et al. 1987, Shulte 2001), but these differ from BTX. Symula et al. (2001) demonstrated that the species *Dendrobates imitator* lives up to its Linnean binomial. It has independently evolved three completely different morphs, each of which mimics an independently derived model species (Fig. 14.25) that have ancient warning patterns.

Figure 14.25. (a-c) Three frog morphs are all putative members of a single species, *Dendrobates imitator*. Each of these different morphs is sympatric with a different species in a different geographical region. The species with which each morph is sympatric is shown directly below that morph. From left to right (d-f) the species are: *D. variabilis*, *D. fantasticus*, and *D. ventrimaculatus*. The corresponding phylogeny for the group does indeed reveal that all three morphs of *D. imitator* are true Müllerian mimics of the three unrelated model species (Symula et al. 2001).



Generalizing correlating mechanisms of cognition and perception

In preceding examples, neural processes are potent correlating agents by which cues or signals become coupled to preference or performance. Positive- or negative-reinforcement learning couples signals and conditioned response in a FD fashion, thereby coupling memotypes. Likewise, perceptual biases or innate behavior couples alternative attack behaviors in predators with alternative dorsal patterns and escape behavior of prey, thereby coupling genotypes. In other cases, signals attain universal meaning even among predator guilds via powerful aposematism. Even the *Choresine* beetle has black and red color, similar to black and red colors of *Pitohui* and *Ifrata* birds. Other birds cannot feed on *Choresine* beetles, due to the potent toxin, but *Pitohui* and *Ifrata* have evolved some mechanism that allows them to feed and sequester the BTX compounds from *Choresine* beetles into their feathers.

In other species novel Müllerian colors can be used, but they acquire powerful meaning, particular when many members of a genus, like *Phyllobates* or *Dendrobates*, colors and patterns achieve a fantastic level of conspicuousness, which appear to be quite distinct in small geographic areas. Within these areas Müllerian mimics like *D. imitator* converge on different model species in a co-evolutionary mutualism.

Three way interactions among species are a rock-paper-scissors

Rather than focusing on two-way interactions it will become necessary to shift our focus to three-way interactions of FDS, arising from interplay between positive and negative FDS and learning mechanisms (Fig. 14.26). Three players and RPS dynamics may be a common Red Queen dynamic in coevolutionary hotspots. Sinervo and Calsbeek (2006) suggest that a system with model, mimic, and cryptic forms is RPS if ($W_{rare,common}$):

$$W_{mimic,model} > W_{model,model};$$

$$W_{cryptic,mimic} > W_{mimic,mimic};$$

$$W_{model,cryptic} > W_{cryptic,cryptic}$$

Equation 14.1.

Such RPS conditions are entirely plausible given results of learning experiments in novel worlds (Fig. 14.21), and if the model pays costs of defense, which is likely in the case of chemical defense like TTX. Costs of defense, a tradeoff ignored in learning experiments, could reduce growth or delay maturation, thereby allowing mimics to invade, particularly at low frequency and when alternative cryptic prey are common. At high frequency, Batesian mimics should lose against rare cryptic forms, particularly because crypsis is under apostatic selection. To invade, models with weak defense should be aggregated, and common cryptic and edible prey must also be present. In the case of a model, a mimic, and generalist predator (Kokko et al. 2003), it is difficult to equate fitness of predator and alternative prey. We propose a modification to standard game theoretic approaches (e.g., Equation 3) and introduce the idea of rare versus common cognitive representations developed in predators. A common aposematic form in a predator's search image depresses a predator's fitness, which would otherwise be able to feed on mimetic forms. Conversely, predator fitness is elevated when Batesian mimics are common in its search image. Thus, this system is an RPS in which: (a) mimic beats model and applies selection to model---mimic pays no costs of defense but gains signal benefits, (b) predators pay costs of mistakes and learn quickly to recognize and eat imperfect mimics or evolve refined discrimination or learning, (c) ongoing predator mistakes with models cause models to chase away from mimics and refine the signal or add greater defense. RPS cycles repeat endlessly (Side Box 14.3), refining each player via powerful correlational selection in a runaway cycle, or when the Batesian mimic itself evolves defense and is converted in a more mutualistic Müllerian form. We substitute a cognitive representation of frequency (i.e., memotype), predator{mimic} versus predator{model}, for genotype frequency, model versus mimic, to define ESS conditions under which the three-player dynamic is RPS:

$$W_{mimic,model} > W_{model,model};$$

$$W_{predator\{mimic\},mimic} > W_{mimic,mimic};$$

$$W_{mimic,predator\{model\}} > W_{model,predator\{model\}}$$

Equation 14.2.

Box 14.3. Why is the RPS common in the world?

Figure 14.26. Summary of 2-way, 3-way, and multi-way interactions discussed in this book. Arrows with straight lines indicate negative frequency-dependent selection (FDS), whereas circular arrows indicate positive FDS or analogues for positive FDS in learning, innate behaviors, or immune system memory in the MHC.

(A) The simple coevolutionary dynamic involving a host's immune system (e.g., MHC) and a foreign pathogen. The immune system, which retains immunity from cross reactivity, a form of memory, is susceptible to invasion by rare mutant pathogens that beat the MHC.

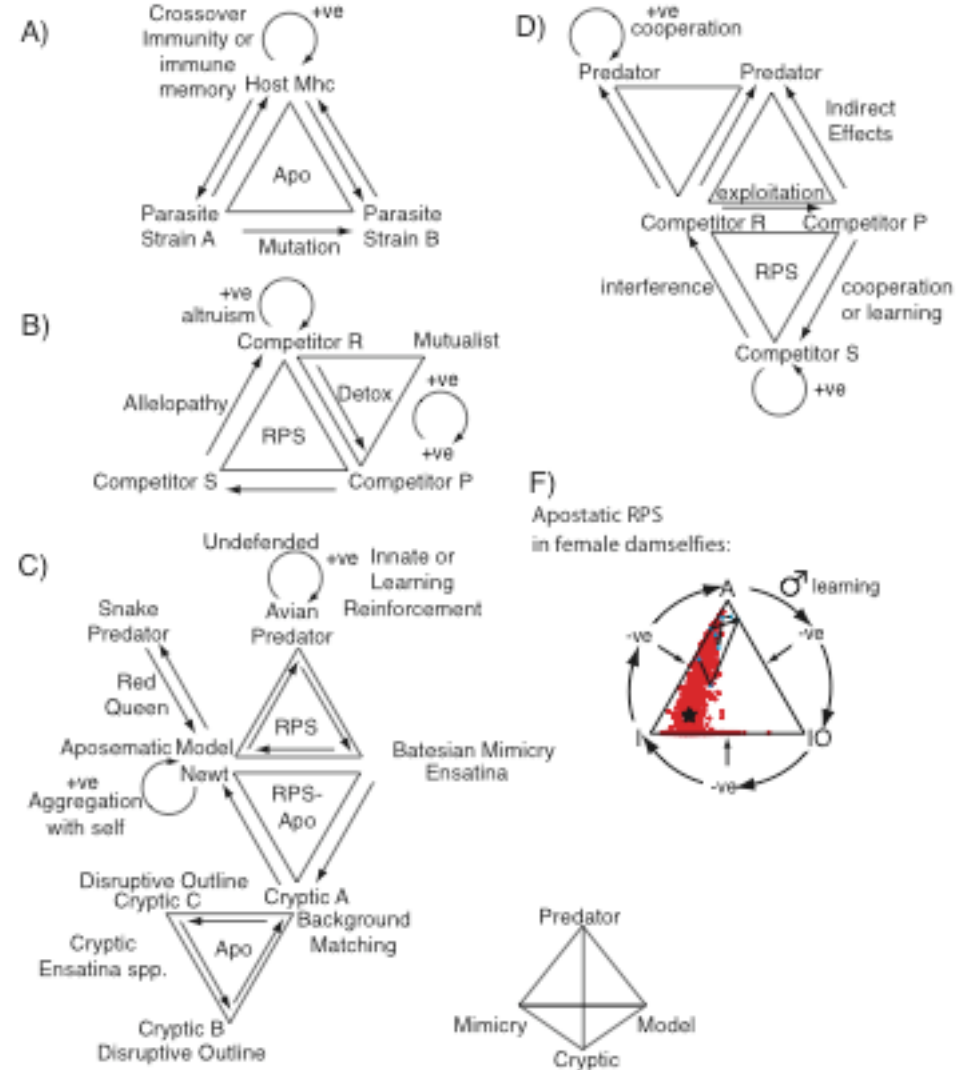
(B) The bacterial rock-paper-scissor (RPS) is hypothesized (Kerr et al. 2002) to generalize to allelopathy in higher ecosystem interactions. If so, additional frequency-dependent FD detoxification interactions or cheater dynamics might involve coevolutionary interactions and positive and negative FDS between plants and fungal mutualists or parasites (Bruns et al. 2000, Taylor et al. 2004).

(C) Coevolutionary arms race between a toxic newt, *Taricha torosa*, and a snake predator, *Thamnophis elegans* (Brodie et al. 2005), generates a coevolutionary hotspot in Northern California that coincides with a Batesian mimic, *Ensatina eschscholtzii xanthoptica* (Kuchta 2005) (See Chapter 3). In addition, alternative cryptic prey found in the ring species of *Ensatina* (Wake 1997) are hypothesized to be maintained by either background matching or two alternative forms of disruptive coloration (Chapter 5). This complex of mimicry and crypsis may serve to exert reinforcement learning on avian predators (discussed above) in an RPS dynamic. The complete predator-prey dynamic is actually best visualized as a tetrahedron, rather than two RPS triangles (C, lower right). The predator resides at the apex, aposematic model (and Müllerian forms) at one vertex, Batesian mimics at the other vertex, and cryptic forms at the third vertex.

(D) Indirect effects are hypothesized to govern three-way interactions between a predator and two-prey species (Bolker et al. 2003). An RPS may arise from competition among three competitors, which is set up by tradeoffs among exploitative and interference competition, and additional tradeoffs from either cooperative competitors or competitors under other forms of positive FDS such as learning. Alternative predator behaviors such as individual vs. group foragers (Chapter 7) may generate tradeoffs, and negative and positive FDS respectively.

(E) An RPS generated by male damselflies foraging for females, which was discussed in the section on alternative strategies, is driven by learning processes in which a rare female form has an advantage over the standard female form, and a male mimic has an advantage over a the rare female form, which once common is beaten by the now rare standard female form. Several

RPS dynamics are given in a schematic on the following page. Milo et al. (2001) discuss other network diagrams besides the rock-paper-scissors circuit. These other ecosystem networks, along with the RPS network circuits discussed in this chapter, contribute to the stability of ecosystem dynamics.



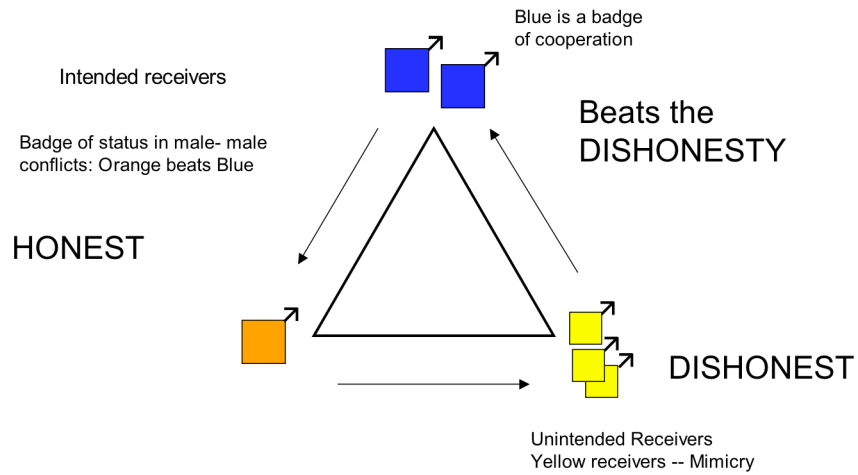
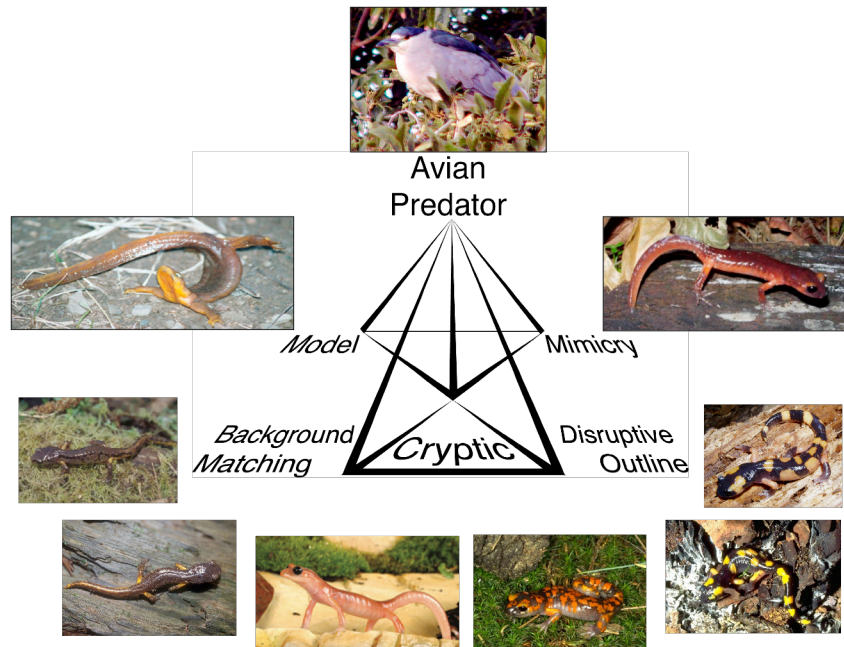


Figure 14.27. The previously discussed relationship between honesty (in two players) and the invasion of dishonesty. The same relationship underlies an RPS dynamic in other mimicry systems like the *Ensatina*-Newt Avian predator system (below, which also harbors alternative cryptic prey (see Side Box 14.3), the honest signaling relation of parents and offspring is invadable by dishonest egg dumpers, in this case Viduine finches (right top).



Brood parasitism as an RPS

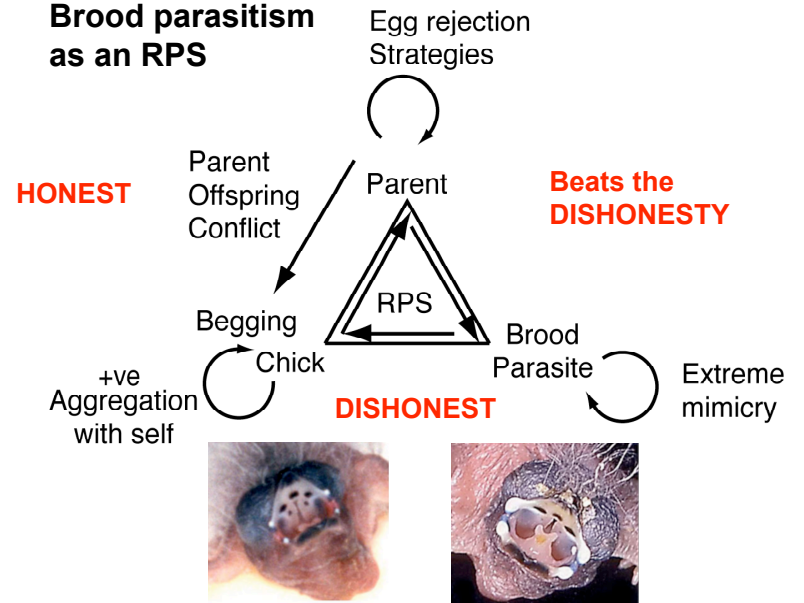
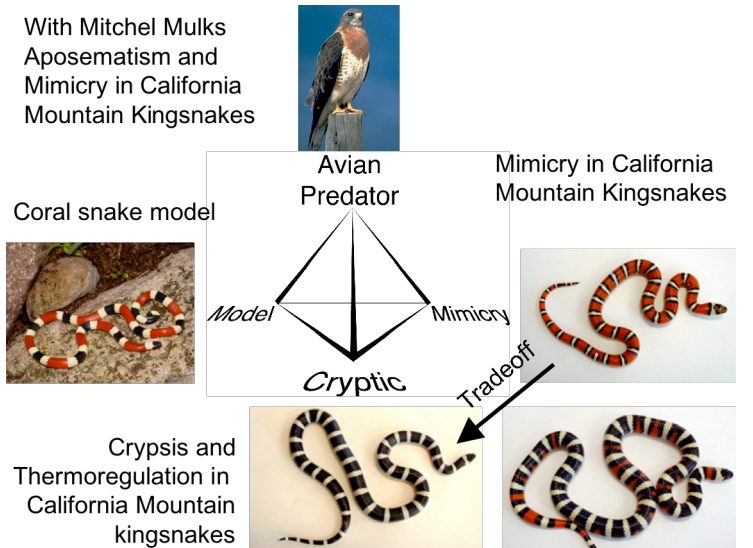


Figure 14.28. Finally the coral-snake-bird system likely forms an RPS, with the caveat that in cold high alpine environments, crypsis trade-offs against an largely black color valuable in thermoregulation. In these alpine environments in the Sierras Nevadas, migratory raptors are rare.



Study Questions for Predator and Prey

1. Describe stimulus filtering in predator vision. What is stimulus filtering useful for?
2. Describe habituation mechanisms in a prey's vision system. What is habituation useful for? If it is useful, then why has evolution led to a situation where the prey can be exploited by a predator?
3. Describe sensory exploitation from the viewpoint of the female-male relationship, and from the point of view of the predatory prey relationship using the example of tungara frogs.
4. Describe the step-by step neural bases of echolocation and predator evasion in bats versus insect.
5. What habitats favor FM vs. CF bats? Why (discuss the two kinds of interference or masking)? Is this sensory drive?
6. How are time delays built in the bat's nervous system? Why are time delays built into the bats nervous system?
7. How is the bats nervous system modified relative to a basic vertebrate acoustic processing system.
8. Describe Fisher's theory for the evolution of aposematic signals in terms of Hamilton's equations for kin selection and inclusive fitness.
9. Describe the evolutionary scenario that leads from palatable to unpalatable aposematic forms in terms of a learning experiments on great Tits in a novel world.
10. Describe the analogies between the mating system RPS and the hypothesized RPS in mimicry systems of predation.
11. Outline the major players in aposematic mimicry and the FDS that acts on the prey.
12. Outline the kind of FDS that operates on cryptic forms.