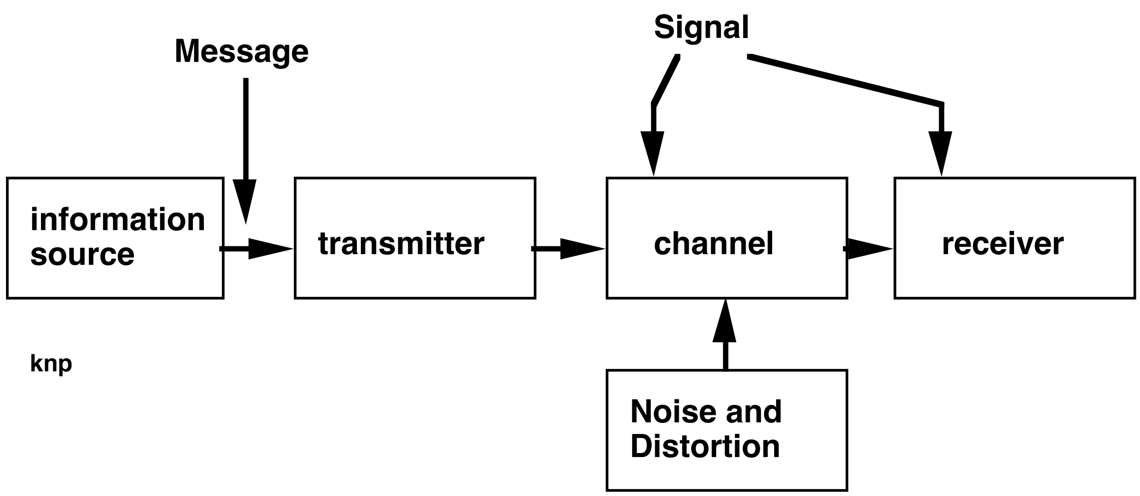
Class Notes: Communication
Ethology & Behavioral Ecology

I. Definition and General:

A. The ability of one animal to predict or influence the behavior of another is easily seen as adaptive. Krebs and Dawkins (1984) call the ability to guess another's future behavior ***mind reading***. Harper (1991) points out that communication will evolve whenever mind reading is mutually beneficial. He sees the <u>most common</u> (but not only) first step of the evolution of a communication system as always being cooperative -- both parties benefit.

B. <u>**Operating definition of communication**</u>: the most common means of ascertaining whether or not communication has taken place is behavioral -- if one animal's action can be <u>shown to alter the behavior of another</u>, it is assumed that communication has taken place.

C. <u>Components of a communication system</u> -- an engineer's view that we've seen before:



1. In some ways the most important element of the system is the **RECEIVER** since it's capabilities are what allow information to be identified as such. <u>Receivers filter through the vast amount of potential information and focus on relatively specific manifestations</u>.

a. The <u>presence of a suitable receiver is required for information to have any real meaning</u> -- without it, we can talk about potential information at best.

b. In order <u>for information to be transmitted</u>:

i. There must be <u>at least two different states produced in the channel</u>.

ii. <u>**Difference is, in part, a property of the receiver**</u>.

2. The I**NFORMATION SOURCE** and **TRANSMITTER (XMITTER)** are often the same or are certainly closely connected entities. If they are the same, they are simply something that produces at least two discernibly different (to a receiver) states.
More formally:

a. The **SOURCE** creates the information as something we refer to as a **MESSAGE** (information that can potentially be received and acted upon) and passes it on (internally) to the xmitter.

b. The **TRANSMITTER** takes the message and **TRANSDUCES** (changes) it to a different form and then "broadcasts" the information into some portion of the surrounding environment.

3. At this point, the message is now refereed to as a **SIGNAL**, with the difference being that the message can be thought of as information located in some place while the signal is a representation of that information that moves.

4. The particular physical or chemical means by which the message propagates is referred to as its **CHANNEL**. For instance, messages that are converted into vibrations of air molecules are signals utilizing the **ACOUSTIC** channel; broadcasted pheromones are said to be signals that use the **CHEMICAL** or **CONVECTIVE-DIFFUSIVE CHANNEL**, displays that consist of moving of various body parts (ex: waving arms or wings, etc.) are examples of signals using the **VISUAL CHANNEL** as are bioluminescent and chromatophore signals. We'll see an explicit table of channels below.

5. Notice that the signal may be **DEGRADED** -- that is, the information contained in it can be lessened or even changed. There are two general ways this can happen:

a. **NOISE** -- random, unpredictable signals that mask the signal of interest to sender or receiver.

b. **DISTORTION**: specific operations that in a potentially knowable manner alter the signal.

c. The process of removing or minimizing noise and distortion by the receiver is termed **FILTERING** This is a very important process and one that generally needs to be minimized within an organism if possible -- it is far better (i.e., more **reliable**) to generate signals for internal use that are reliably passed than to try to reconstruct them at the receiver.

Example of Noise and Distortion: Using the chemical channel, a noise would be other chemicals that would potentially interfere with the signals detection by a receiver; an example of distortion would be a situation where a signal consisted of a mix of two chemicals but one traveled better than the other -- over distance one would be predictably lost.

D. **General Types of Information that is passed on**:

1. **About environment** -- could be biotic or abiotic -- example -- alarm calls.

? How do such calls evolve and why are they so similar in different species? Is it interspecific cooperation or likely to be something more complex?

Hint: think about a mechanism that involves convergence and another involving homology. How would you tell them apart? Explain how the evolution would work within a species. What would be the role, if any, or kinship?

2. **<u>About Individual Identity</u>**

(a) Species Isolation or SMRS (specific mate recognition system)
(b) Kinship
(c) Pairs
(d) Individual

3. **<u>About individual ability</u>**

(a) **<u>Contests</u>** -- all out fight, limited fight, or signal. Notice that all of these are communication although in two cases it involves actual physical conflict. When to signal as compared to fight can be modeled with games theory -- ex: Hawk and Dove

(b) **<u>Signals to Predators</u>**: example is **<u>stotting</u>** in Tommies -- African wild dogs go after those that stott at the lowest rates

(c) Signals **<u>to potential mates</u>**: information about condition, resources, etc. beyond simple location and species recognition.

4. **<u>Information about intentions</u>**

5. **<u>Information About Nothing</u>**

II. Evolution of Signaling

A. First, signals (messages) can have one of two <u>general function types</u>

(i) **Signal (beacon)** -- simply, here I am -- **presence** and **location**
(ii) **Iconic** -- additional information beyond the presence or location.

Types of **<u>messages</u>** defined by their benefits and costs. Independent of the two previous functions we can classify signals into four general types based on the fitness consequences of the messages to the sender and receiver:

Type / actor -->	**Sender**	**Receiver**
Cooperative (honest)	**+**	**+**
Uncooperative (dishonest)	**+**	**-**
Spiteful	**-**	**-**
Unintended	**0 or - (rarely +)**	**0 or + (rarely -)**

B. **<u>A series of constraints operate on the ways that signals can evolve</u>**. Some of these are imposed by the nature of the message itself -- for instance, complicated iconic messages are hard to send via some channels (e.g., chemical) while others come from the sender, receiver, or the environment

1. General constraints from the environment (note that these are approximate and measured relative to the best):

Feature	Type of signal Chem.	Tactile	Auditory	Visual	Electrical
Range	long	short	long	medium	short
Rate of change	slow	fast	fast	fast	fast
Pass obstacles?	good	poor	good	poor	yes
Locatability	variable	high	medium	high	high
Energetic cost	low	low	high	low	low

2. **General constraints acting on the sende**r -- morphology, structure, energy, predation

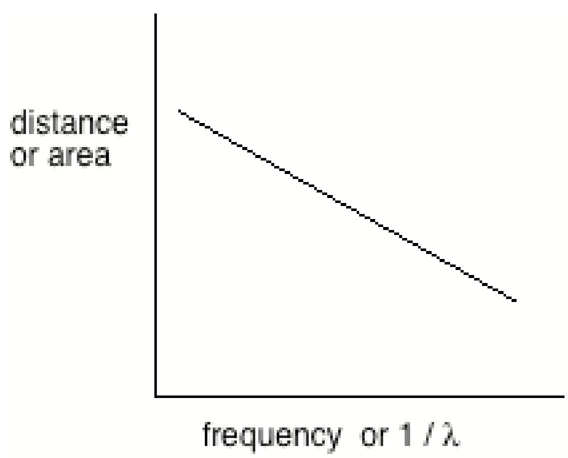
a. **Energy cost -- minimize if possible**

b. **Unintended receivers -- minimize -- white lipped bats, Ormia** and mole crickets

c. Strict **morphological limitations** imposed by the need to optimize with respect to other functions. Here's an example dealing with **body size and sound production:**

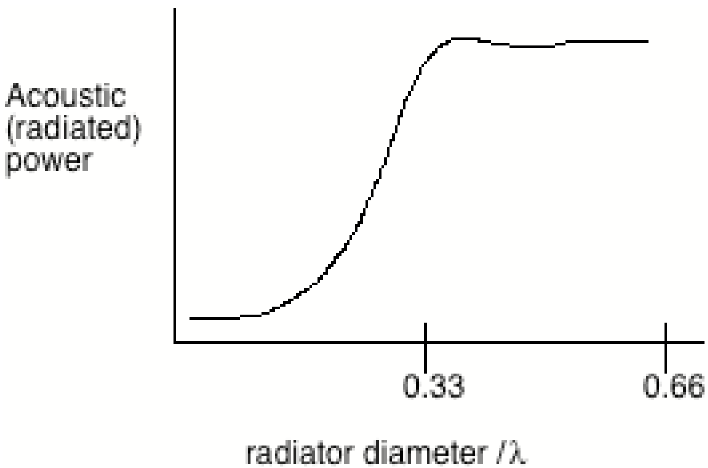
Let's assume that animals need to communicate over as wide of an area as possible. One way to increase the area is to increase the amount of energy used to produce the signal. In the case of acoustic signals, this is quite expensive. Evolution may well act to make signals more conspicuous by increasing the energy used to produce the call but there is a maximum amount of energy that is available. So what other things could be done? Let's assume that energy input to make the sound is not on the table -- we'll assume that individuals all average the same energy input.

One thing is to decrease the frequency of the signal. In most environments, low frequency signals are transmitted over longer distances than high frequency. Moreover, greater distance traveled also means greater area over which the signal can be heard:



Now sound is produced as the result of muscle action causing some part of the body to vibrate. Not all of the energy used to make the body part (the **radiator**) vibrate actually turns into sound.

A lot of it is lost as heat. Moreover, there is a relationship between the frequency (and wavelength) of a sound and how efficiently the sound is radiated (*i.e.*, there is a relationship between the size of the radiator, wavelength of the sound, and the amount of energy inputted to the radiator that will actually turn into sound). It is common to look at this relationship by seeing how much sound (power output as vs. the power input to the muscles that started the vibration -- remember, power input is constant in this example) is produced as a function of a ratio of the size of the radiator to the wavelength. Thus, when the radiator is larger than the wavelength, this ratio is greater than one; when the radiator is relatively small, this value is less than one and may in fact be much, much less than 1. Here is a typical relationship:



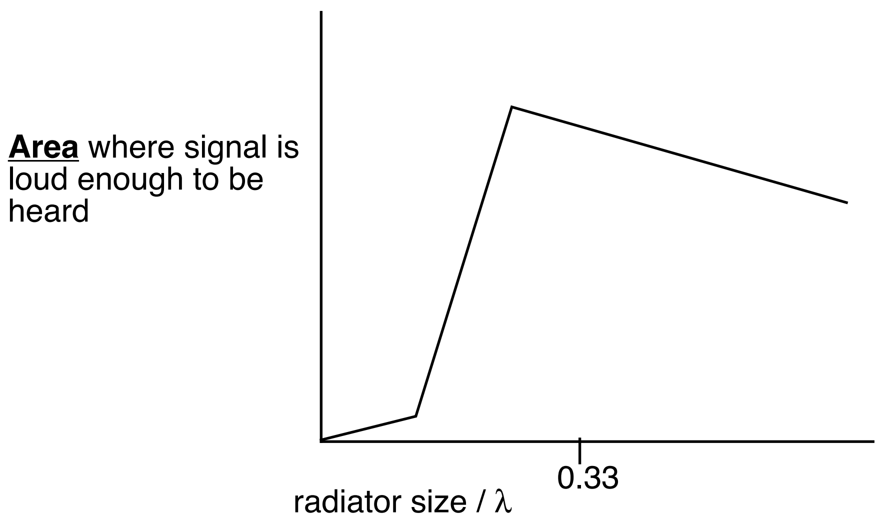
This graph shows that <u>for a constant energy input to the muscles</u>, anytime the diameter of radiating surface (for example, vibrating wing, vocal cord, opening of mouth, etc) is <u>less than 1/3 the wavelength of the sound being produced, the amount of energy radiated decreases,</u> eventually to close to zero. Put another way, the efficiency with which inputted energy is turned into sound decreases. Notice that at any ratio of radiator to wavelength that is greater than 0.33 the efficiency is constant.

To help understand this graph a bit more, lets say I have a sound at 340 Hz. A human could easily produce such a sound. Such a sound has a wavelength of 1 meter. Thus, to achieve maximum efficiency of radiation, the radiator would need to be 1/3 * 1 = 0.33 meters in diameter. Since the radiator surface for humans is the opening of the mouth, I don't care how much of a "big mouth" someone is, they will not radiate sound at peak efficiency. Likewise, if an animal produces a sound at 3.4 kHz, the wavelength is 0.1m and the radiator would need to have a diameter of at least 0.033 m to achieve maximum efficiency.

OK, so what is the problem? It is simply that small animals will never be able to produce sound efficiently at low frequencies. In most cases their radiators can be no larger than their bodies and in most cases they will be far smaller. So the production of sound will be highly inefficient at wavelengths that are long compared to their bodies (*i.e.*, at low frequencies). This is a constraint acting on the sender.

Let's combine the information for the two graphs given above into a graph that will show us what happens to the area over which an animal's call is above a certain loudness as a function of the ratio of the radiator diameter to the wavelength. As before, we assume that the energy inputted is constant in all situations.

Let's reason through this and then see the graph. Let's assume that we have an animal of a certain size. If it uses a lower frequency, the call carries better and therefore in principal should be audible over a greater area. However, the lower the frequency it uses, the less efficient it is at being able to produce sound. So the sound is weaker at low frequencies and even though it carries well, it simply is too weak to be heard over a large area. What if the animal selects a very short wavelength relative to its size -- a high frequency? Now, lots of sound is produced (the second graph above) but the sound dies out rapidly (graph #1) and therefore the coverage area is less. The best frequencies tend to be intermediate -- a bit lower than the best wavelength to get highly efficient sound production:



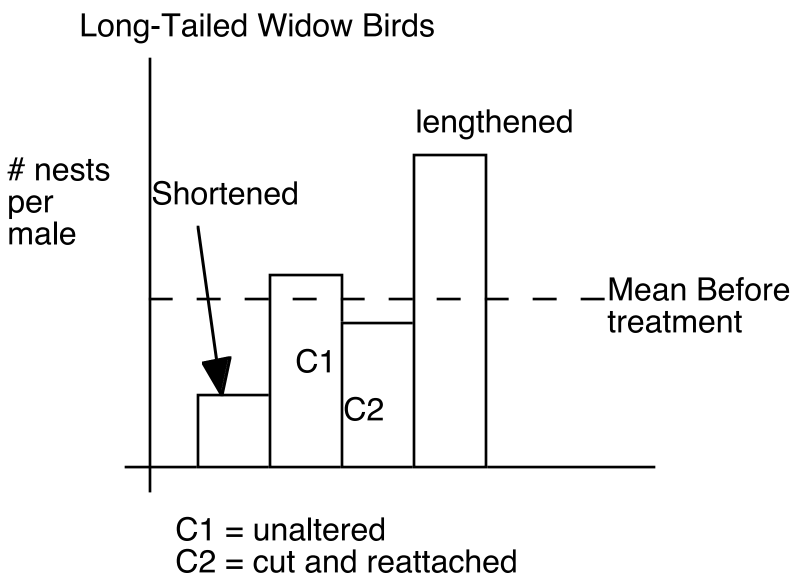
Thus, notice that if senders are trying to maximize the area over which they are heard, they face a number of constraints. This last figure shows one way to optimize this particular performance.

Sometimes animals develop ways around these constraints. These bizarre acoustic tricks include using natural or specially constructed cavities to essentially amplify the sounds they make; they are beyond the scope of this course.

3. Constraints from the receiver.

Signals are not signals unless there is a receiver. In fact, it is quite likely that the receiver drives much of the evolution of signals. One important idea in this regard comes from John Endler and Mike Ryan who speak about signals evolving in response to **sensory biases** on the part of the receiver. This idea can also be called **sensory exploitation** because the sender can be seen to create its signals to take advantage of the sensory system of the receiver. Note however that "take advantage of" and "exploitation" do not mean that the communication needs to be manipulative (non-cooperative). It might be, but it is far more likely that the signal is honest and simply takes advantage of the receiver's biases to make a good signal.

Some of the most exaggerated of signals are those used in **sexual selection** and so this is a good time to discuss these since these signals generally appear to be the result of selection on the sender that results from receiver biases.
Recall that sexual selection is a process that achieves differential reproduction through greater access to mates or to resources controlled by mates. Sexual selection produces differential reproduction, not by causing an animal to live a longer or shorter time, as is typically the case in natural selection, but instead by making an individual somehow more attractive to mates or to somehow give greater access to mates. Some of the most outlandish of all signals in the animal kingdom have evolved in response to sexual selection. These include ornaments, highly conspicuous displays and obnoxiously loud and repeated calls. An example of these types of signals is the long tail feathers commonly found in the males of many bird species. A number of experiments have shown that the length of the tail feathers is an important feature of male fitness. For instance, if the feathers are experimentally lengthened or shortened, there are great consequences on the males' ability to get a mate. Here's an example using an old world species -- the long-tailed widowbird:



Conclusion -- long tails are better. Is it runaway selection or is it selection for good genes?
ref. Anderson

This sort of thing is seen over and over. For some reason, receivers (usually females) seem to find that "bigger is better". Why is this?

There are two ideas about this. One is that the exaggerated signals are the result of an arms race where signalers have evolved signals that try to match the expectations of the receiver **but** where the signals mean nothing themselves except that they are preferred by the receiver. In the other case, it is believed that the exaggerated signals are used to tell the receiver something about the general fitness and condition of the sender.

R. Fisher put the first idea forward in the 1930s. In this case the signals are often called **Fisherian signals** and they are seen as the result of an "arms race" or runaway selection. They do not signal anything about the general fitness of the possessor anymore than owning a nice watch signals really proves that the owner is rich.

Here's how Fisherian signals are believed to evolve:

a. A predisposition exists in the receiver to prefer a particular signal. The reason for this predisposition is essentially related to the construction of the receiver's nervous system -- certain signals just seem easy for it to pick out. These sensory biases on the part of the receiver do not reveal whether or not the sender is generally in good condition -- they are simply preferred as a by product of the way the receiver's nervous system operates.

b. The senders produce different versions of the signal preferred by the receiver (including no signal at all). The receivers choose those individuals that produce a signal that at least approximates what the receiver wants to see.

c. As a result, the offspring now have genes that both allow the expression of the signal and the preference for the signal. Therefore, they will either produce the signal (in the case of one sex) or prefer this same signal (the other sex). The ability to produce and prefer the signal are now said to be CORRELATED.

d. The assumption is that initially the signal is rather weak compared to what the sensory systems of the receiver would actually like. The receivers will tend to select those who make the best (most extreme) versions of the signal. So, over time and via sexual selection, the signals become more and more extreme. Thus, a period of runaway selection occurs

e. How far does it go? As sexual selection results in a more and more extreme signal (for example, longer tails on birds), natural selection starts to work against the signal getting more extreme. Clearly, the more outlandish the signal, the more likely it is to cause trouble to the sender. Evolution eventually stops when the advantage gained via sexual selection is equaled by the disadvantage of fitness lost via natural selection

Once again, notice that in this system the signal is arbitrary.

<u>Signaling Good Genes: the Handicap Hypothesis of Zahavi</u>: The alternative to the signals being arbitrary as in the case of Fisherian selection is to assume that signals evolve to pass on honest information about something. In the case of sexual selection, this sort of information would most likely convey the condition of the sender to the receiver. Condition should correlate with "good genes" and therefore the alternative hypothesis about sexual selection can be termed the **"good genes"** hypothesis. This traces largely to the work of Amos **<u>Zahavi</u>**.

Zahavi stated that females or other receivers chose certain signals because they are difficult for the sender to produce -- they are **<u>handicaps</u>**. Thus, these signals are costly to the actor and to some degree hurt the actor. Receivers prefer signals that hurt senders, not because they are sadistic, but because these signals reveal the condition of the sender. Good condition should generally correlate with "good genes". In later formulations of this idea, Zahavi and others emphasized that senders produced the trait to the extent that they could do so without actually hurting themselves. For example, if a frog were in good condition it would call for a long period of time every night. If it were in poorer condition it would call for a shorter period -- it would do the best it could. The reason it could not do better was because the signal was so costly to produce.

Notice that individuals who are in poorer condition do not necessarily totally fail. They still produce the signal to the extent they are able. The receivers most likely do not have perfect knowledge as to how well all senders can produce the signal, thus there is a chance that some receivers will respond to individuals who produce less than ideal signals. Moreover, notice that the sender only produces the signal to the extent that it is capable of doing so - often it will not "go for broke" and produce a signal that literally runs it into the ground.

Zahavi formulated these ideas in the mid to late 1970s. In the later 1980s WD Hamilton and his graduate student at the time, Marlene Zuk, postulated that most "honest" signals used in sexual selection were signaling good genes in terms of resistance to parasites (micro to macro types). They pointed out that most individuals of a species probably do not differ greatly in terms of their ability to get food, etc. Or at least, these differences were not as important a selective factor as the ability to resist various forms of parasitic attack. They pointed out the widespread nature of disease would be cause for continuous evolution.

Hamilton and Zuk's hypothesis has been tested a number of times in recent years. One of the most famous tests was that of Möeller using barn swallows. The males have elongated scissors-like tails; females lack these.

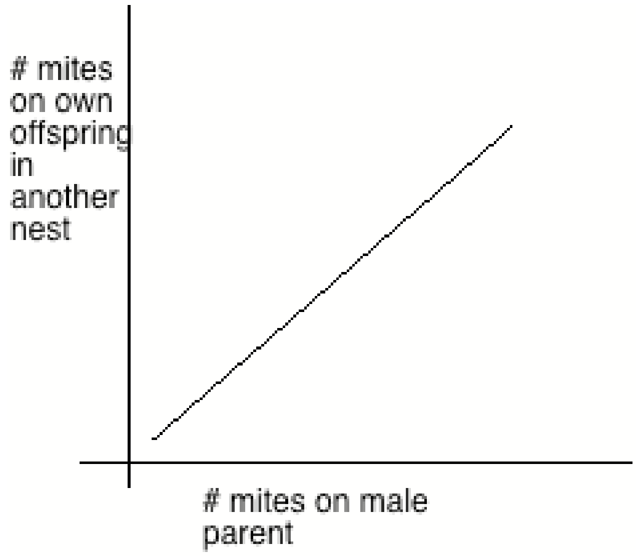
Möeller argued that to support the Hamilton-Zuk hypothesis he needed to show that:

1. Parasites reduced host fitness. In this case the parasites are mites.
2. Resistance to parasites is genetically based.
3. Resistance is signaled by ornaments (long tails in this case -- a visual signal).
4. The females must prefer the most extreme version of the signal (longest tail feathers).

SO, he did the following

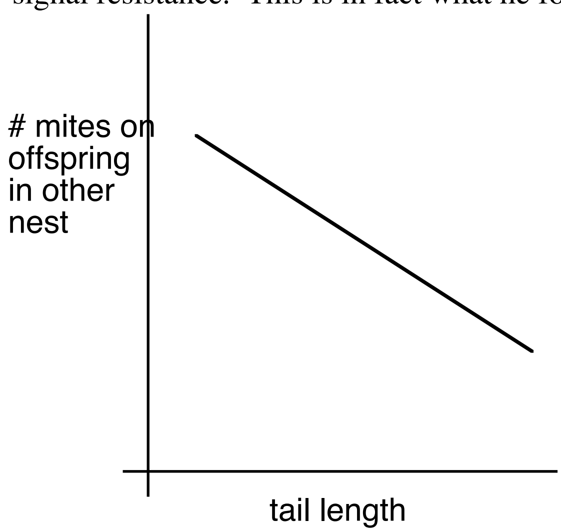
1. <u>Parasites reduced host fitness</u>: If mites are removed from nests (by fumigation) the result is faster growth, larger weight and more fledglings. So, clearly the presence of parasites does reduce host fitness.

2. <u>Resistance is genetic</u>. For this, he used cross-fostering experiments where birds were taken from one nest where the parents had a certain parasite load and introduced into another nest with a different load. If resistance was genetically based, the cross-fostered young should have parasite loads like their true sibs, not like those of their "adopted" sibs.

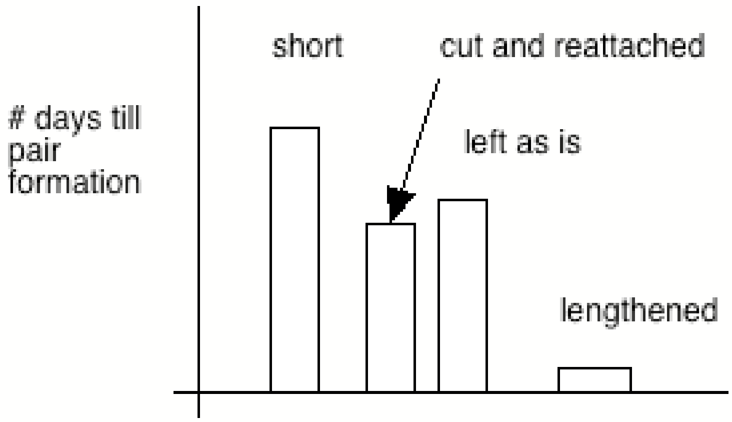


The data above show that in fact parasite resistance does seem to be genetically based.

3. <u>Resistance is signaled by ornaments</u>. Here, the tail length should correlate with the parasite load of an individual's offspring that were foster reared in another nest. Thus, males with high genetic resistance to mites (low numbers of mites) are expected to offspring with low numbers of mites (regardless of where they were raised) and this should correlate negatively with tail length since long tails supposedly signal resistance. This is in fact what he found:



4. Females prefer signal: here the experiment was just like the one we saw previously with the long tailed widowbirds



So, this experiment is a nice support to the Hamilton and Zuk version of Zahavi's hypothesis.

Beyond sexual selection, it is now generally believed that one of the main factors affecting the evolution of signals is the preference of receivers for signals that are likely to be honest because they cannot be faked (once again, this selection does not require consciousness).For instance, stotting (which we considered earlier) is believed to be only "do-able" by a gazelle in top condition. Lions are selected to ignore individuals that give this signal because they truly are in top condition and, from the lions point of view, will be hard to catch. Both sender and receiver benefit but notice that the onus was on the gazelles to come up with a signal that would be honest -- else selection would tend to cause the lions to attack all gazelles -- perhaps especially those that made signals.

C. An introduction to Deceitful Communication: It should be obvious that deceitful communication cannot evolve on its own. In other words, selection would never allow the de novo appearance of a signal that hurts the sender. Dishonest communication always evolves to exploit an honest system that already exists. Here are a number of examples:

1. **Aggressive Mimicry**: usually interspecific

(a) Firefly Femme Fatales: Firefly males normally cruise around and advertise themselves; conspecific females wait on vegetation and give an answering signal when interested. In some species, females are able to give the answering calls of other species; unwary males approach and are eaten!

(b) Bolus spiders. These spiders synthesize the pheromones used by females of certain species of moths to attract male conspecifics. The spiders put these pheromones on a ball of silk attached to a silken line. They move it about to volatilize the pheromones and it attracts males; when they get close, the spiders aim the ball and the moths. It is sticky and catches them; they are then devoured by the spider instead of being consumed by lovemaking!