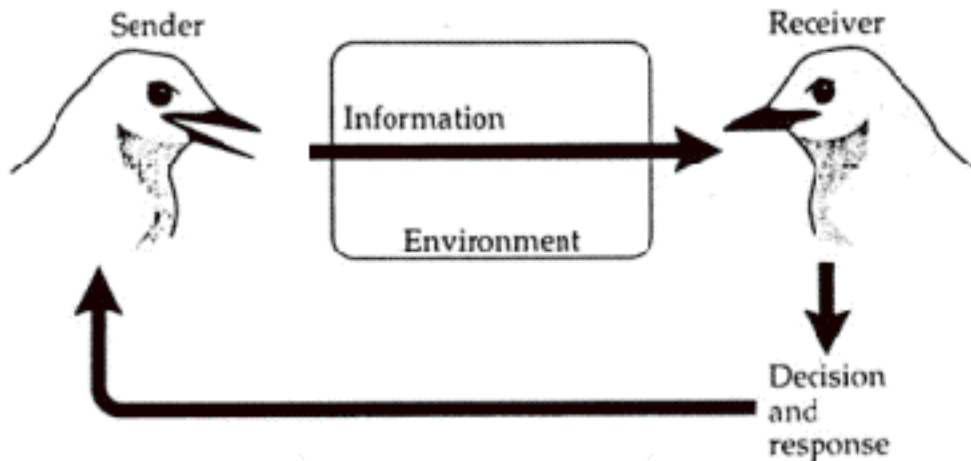


# What is communication?

- Signaling: The process in which a sender/signaler uses a specially evolved “signal” to modify the behavior of the receiver
  - Response, on average, benefits sender
  - Neutrality with respect to receiver’s fitness
- “Cue”: modifies the behavior of the receiver, but is not an evolved adaptation of sender/emitter



# Who benefits?



Change in  
receiver's fitness

Change  
in  
sender's  
fitness

	+	- / neutral
+	mutually beneficial	manipulation, deceit
- / neutral	localization, eavesdropping	

# Who benefits?



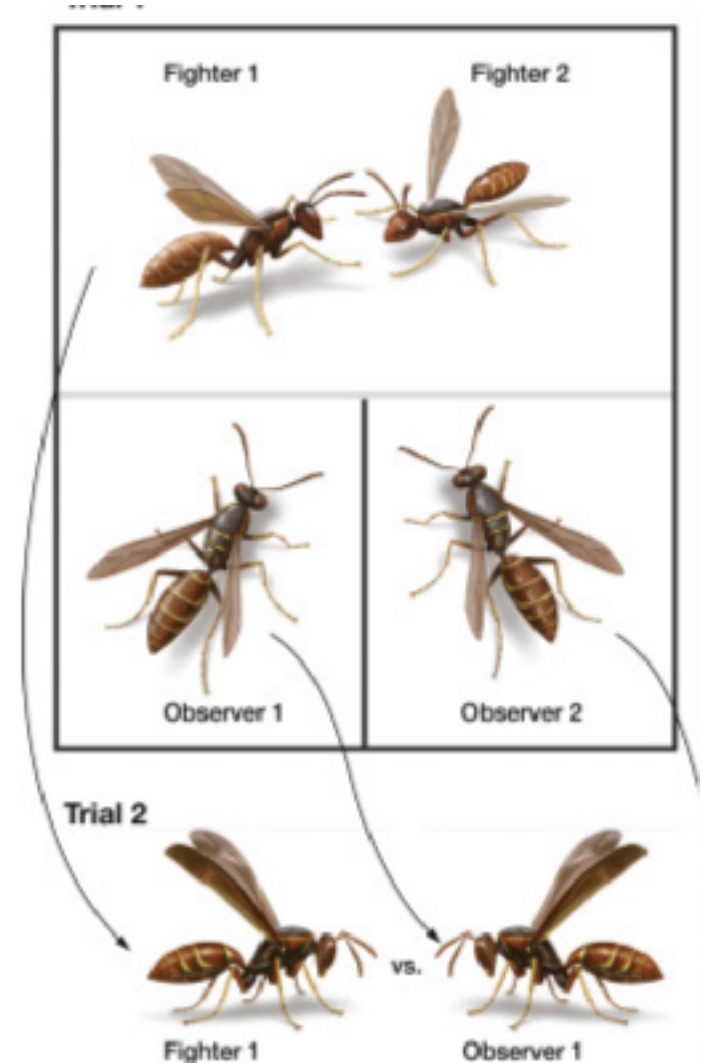
Change in  
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	+	-/neutral
+	mutually beneficial <sup>Signal</sup>	manipulation, deceit <sup>Signal</sup>
-/neutral	localization, eavesdropping <sup>Cue</sup>	

# Eavesdropping

- Eavesdropping: “illegitimate receivers” pick up on cues
  - ex. wasp learns of fighting ability by watching subject fight.



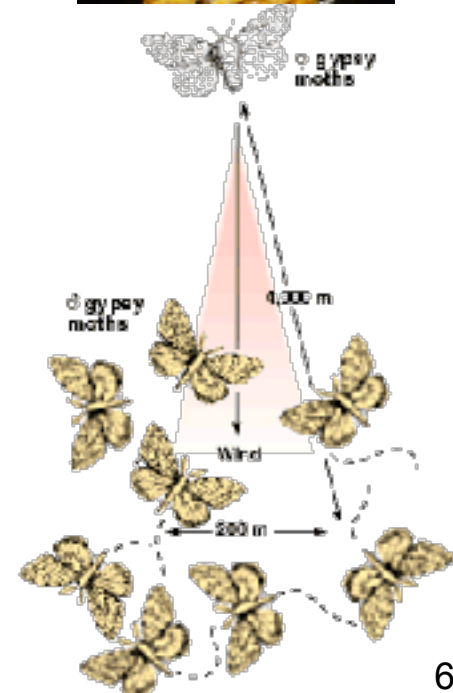
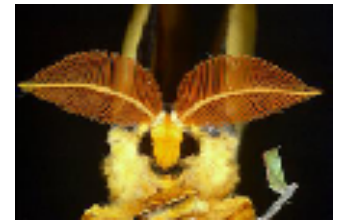
# How do animals communicate?

- Five primary types of signal modalities
  - Chemical
  - Auditory
  - Visual
  - Tactile/Vibrational
  - Electrical



# How do animals communicate?

- Chemical (probably oldest form of communication)
  - 1) Pheromones (Intraspecific chemical signals)
    - RELEASER = immediate response
      - » female moths attract males downwind
    - PRIMER = gradual response
      - » inhibition of reproduction in termites

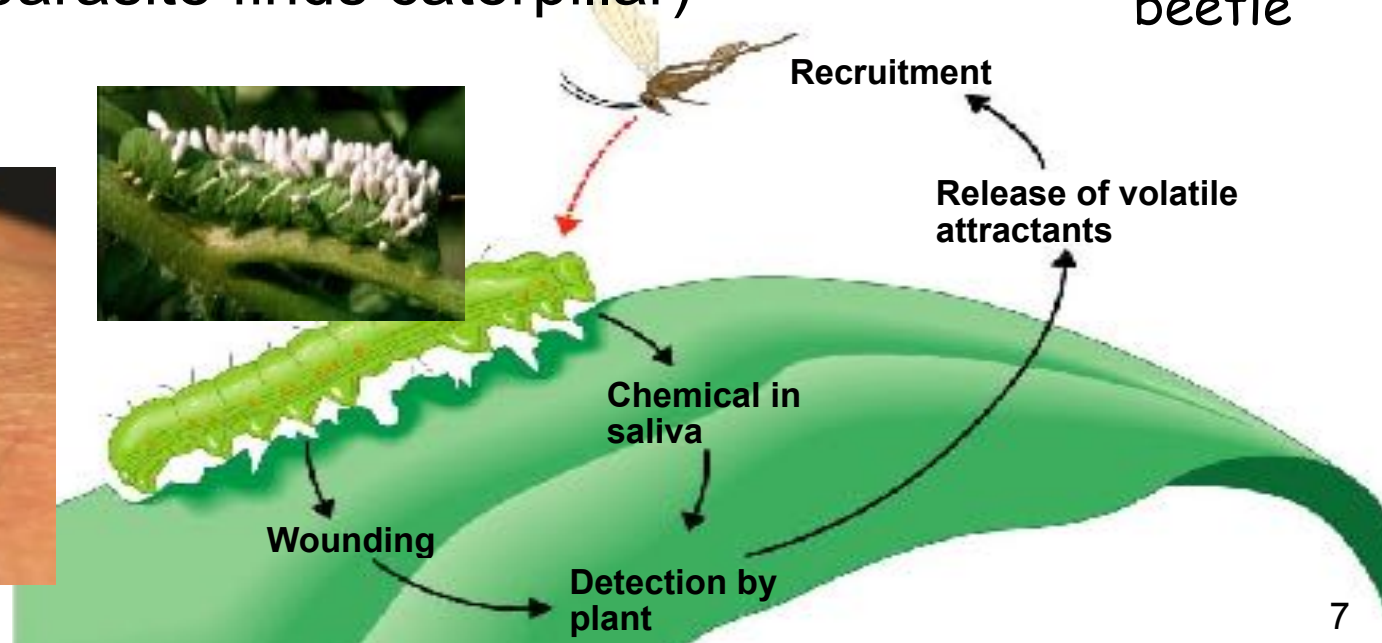


# How do animals communicate?

- Chemical (probably oldest form of communication)
  - 2) Allomones (interspecific chemical **signals**)
    - favorable to signaler (ex. chemically toxic beetle)
  - 3) Kairomones (interspecific chemical **cues**)
    - favorable to receiver (ex. mosquito find host; parasite finds caterpillar)



Aposematic beetle



# How do animals communicate?

- Acoustic
  - Least constrained by environment--night or day, air or water, can travel long distances
  - Potential for complexity and temporal modulation
  - Degraded by distance and environmental factors





# How do animals communicate?

- Visual
  - Requires ambient light, or bioluminescence
  - Blocked by environmental obstacles
  - High potential for complexity, information coding



# How do animals communicate?

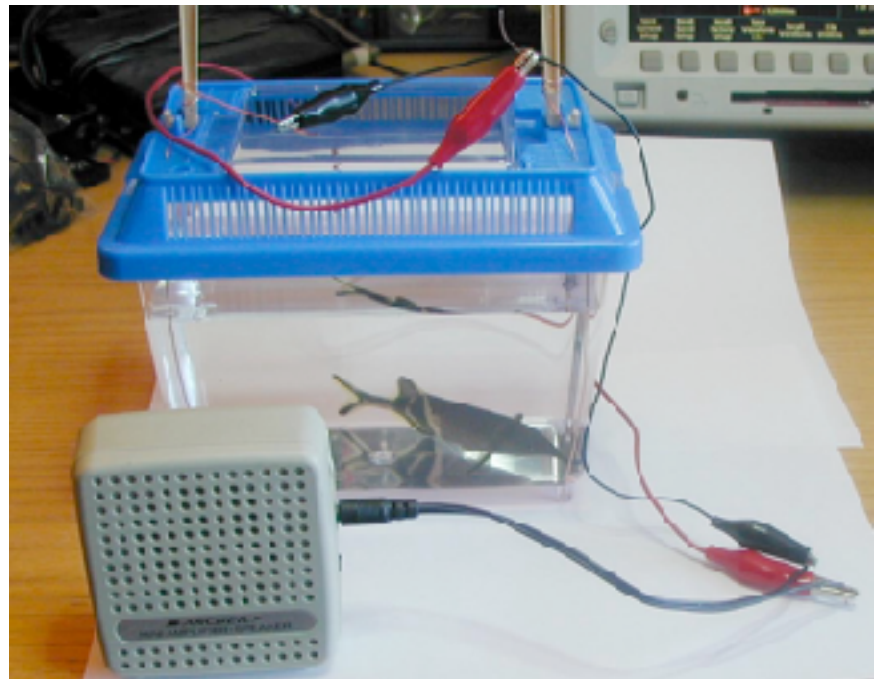
- Vibrational/Tactile
  - Little morphological specialization needed
  - Low transmission range



# How do animals communicate?

- Electrical
  - Only aquatic vertebrates (several fish lineages)
  - Short duration, rapid modulation
  - Low complexity, short range

<http://www.youtube.com/watch?v=9bk35q5z3ug>



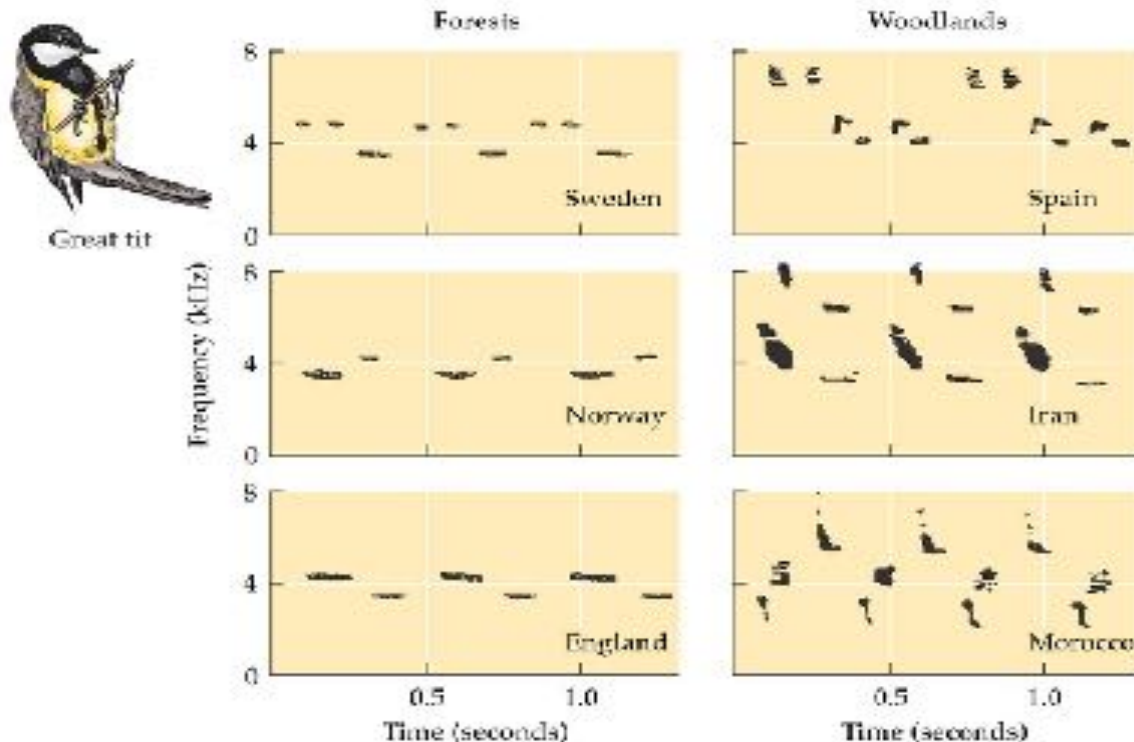
# Transmission of signals in different modalities

FEATURE	TYPE OF SIGNAL				
	VISUAL	AUDITORY	CHEMICAL	TACTILE	ELECTRIC
Effective distance	Medium	Long	Long	Short	Short
Localization	High	Medium	Variable	High	High
Ability to go around obstacles	Poor	Good	Good	Good	Good
Rapid exchange	Fast	Fast	Slow	Fast	Fast
Complexity	High	High	Low	Medium	Low



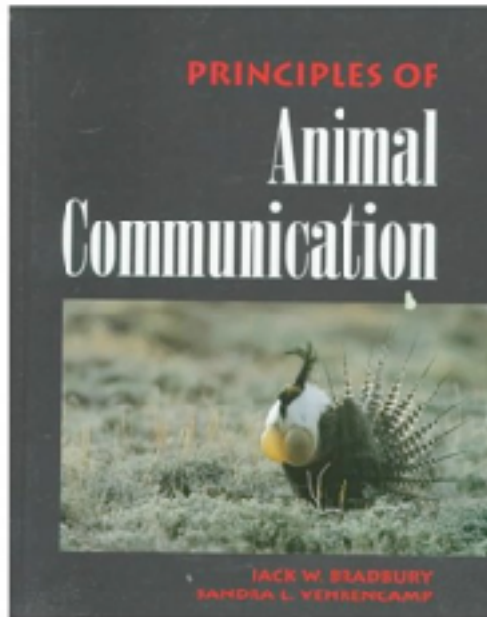
# Signal design

- Regardless of modality, design often reflects need
  - Birds modulate calls in different environments to deal with constraints
    - ex. high frequency sound does not pass well through dense vegetation, so used only in woodlands



# When are signals honest?

- Animal communication is generally not a cooperative interaction
  - Receivers 'demand' (through selection) honest signals



# When are signals honest?

- Unforced honest communication
  - Interest of sender and receiver are congruent (mutual benefits for both parties)
    - Sender is closely related to receiver, or has overlapping interests with receiver



# When are signals honest?

- Forced honest communication
  - Interest of sender and receiver are incongruent
    - Courtship: females often want best male, males want any/more matings
    - Predator-prey: prey wants to live, predator wants to eat
    - Dominance/Fighting: intimidate rivals without getting hurt









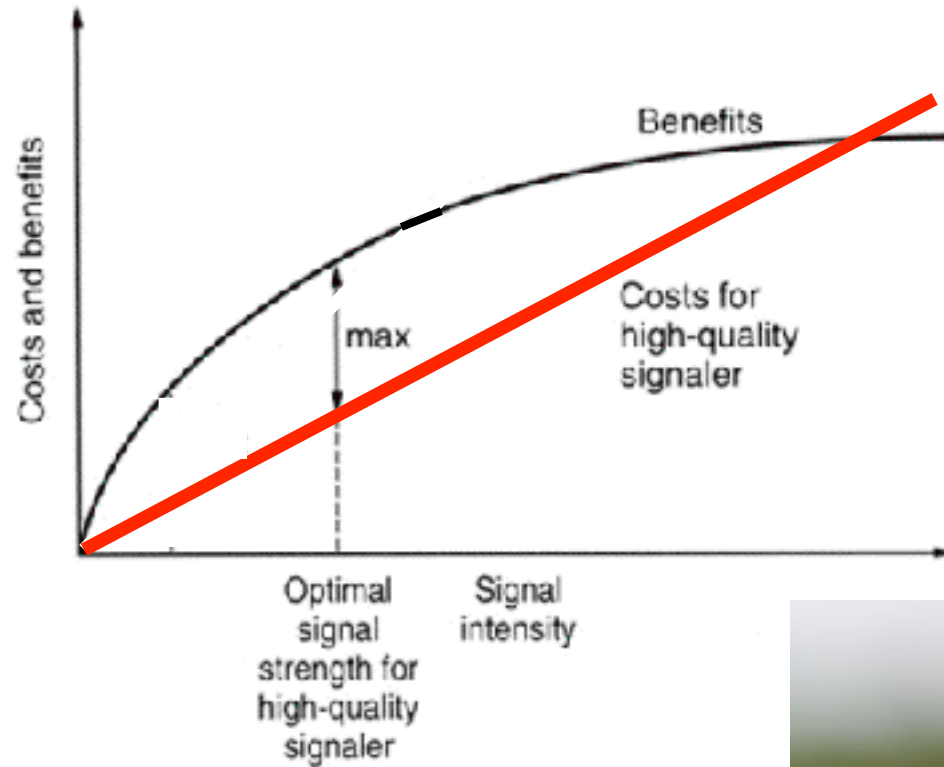
# When are signals honest?

- How is honesty maintained?
  - 1) Handicap (condition dependent) signal
    - Signal production is condition dependent
      - Lower marginal costs for high quality individuals (i.e., higher quality individuals pay a **relatively** lower cost for a given trait)



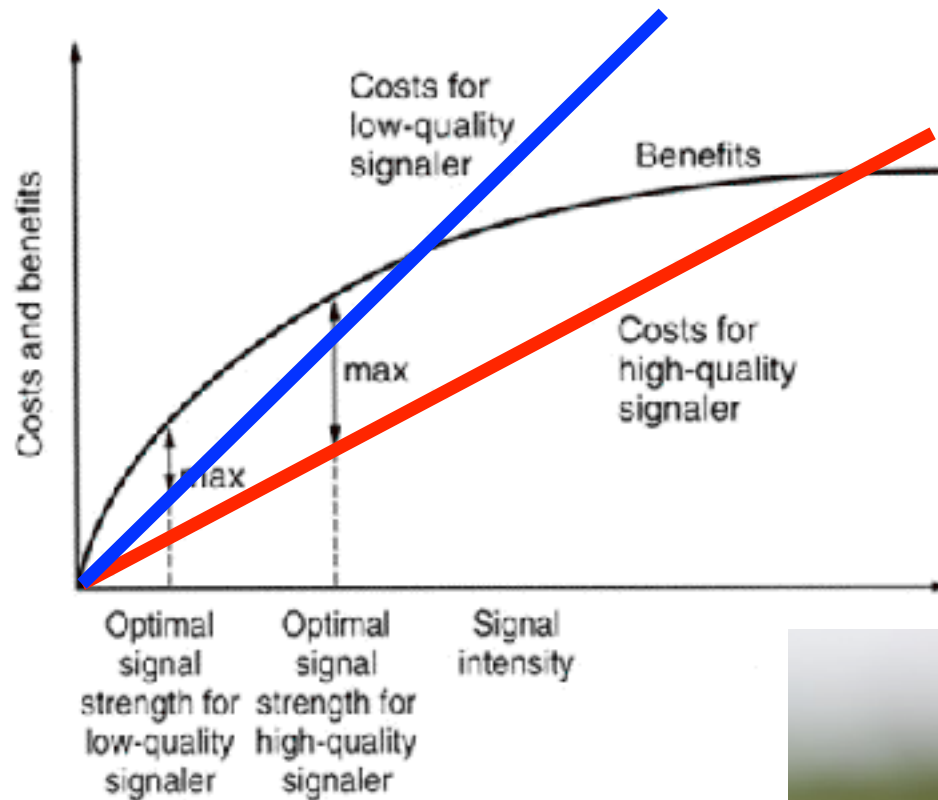
# When are signals honest?

## Condition-dependent signal costs



# When are signals honest?

## Condition-dependent signal costs



# When are signals honest?

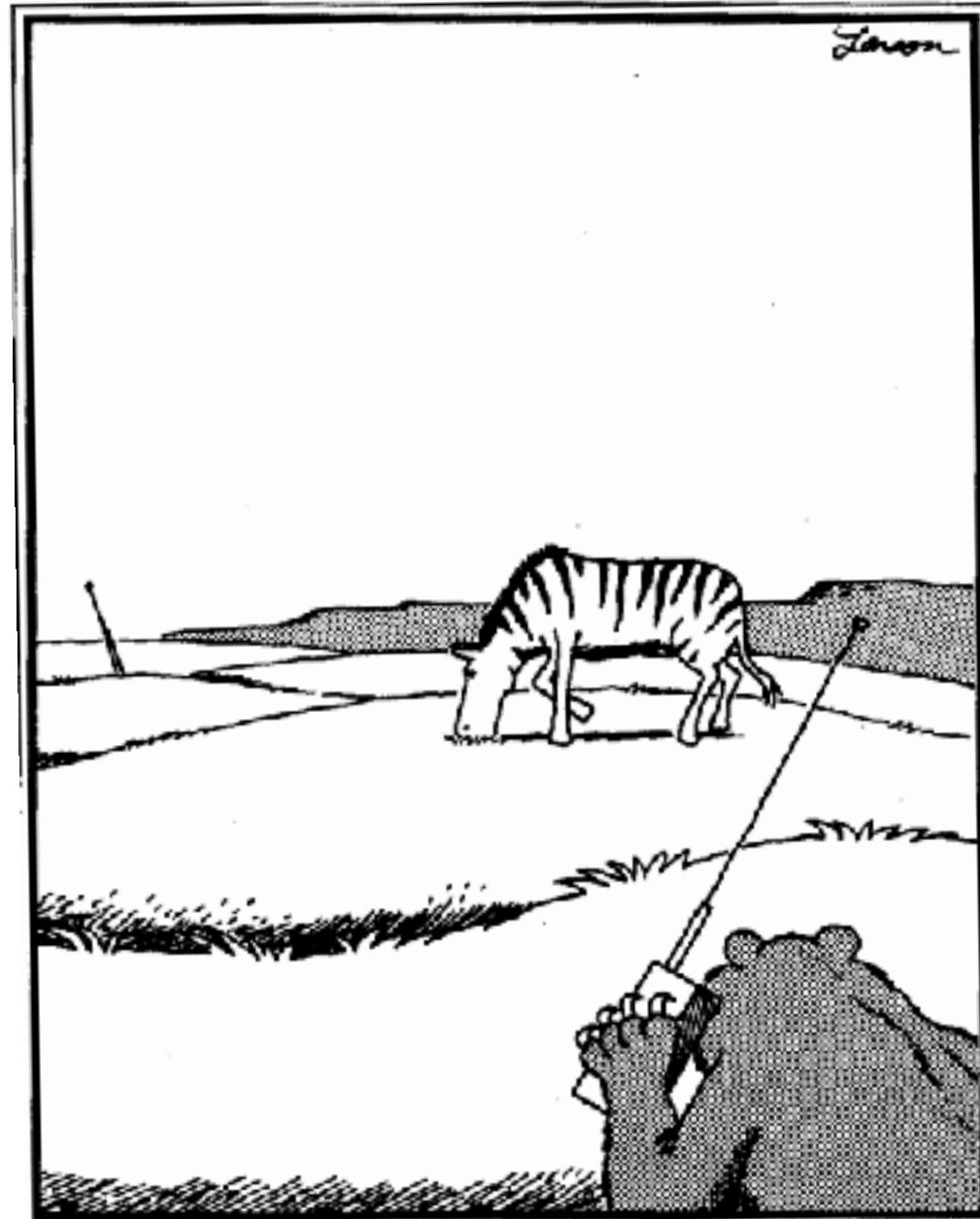
- A human handicap example
  - Two males of varying quality (measured in \$\$) attempt to attract mates by signaling their quality with a status symbol such as a car
    - What kind of car would a really rich guy buy?
    - What kind of car would a not-so-rich guy buy?
      - ASSUME both are maximizing benefits

# When are signals honest?

- A human handicap example
  - Two males of varying quality (measured in \$\$) attempt to attract mates by signaling their quality with a status symbol such as a car
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# Animal communication



The modern lion



# When are signals honest?

- How is honesty maintained?
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      - Lower marginal costs for high quality individuals (i.e., higher quality individuals pay a ***relatively*** lower cost for a given trait)



# When are signals honest?

- How is honesty maintained?
  - 2) Index signal
    - Signal production is physically constrained so that lying is not physically/physiologically possible
      - Frog call frequency is inversely proportional to body size
      - Bear scrapings indicate height



# When are signals honest?

- How is honesty maintained?
  - 3) Socially enforced signal  
The honesty of a **status signal** that conveys information about dominance can be maintained by the threat of receiver retaliation (i.e. if you bluff you get attacked).

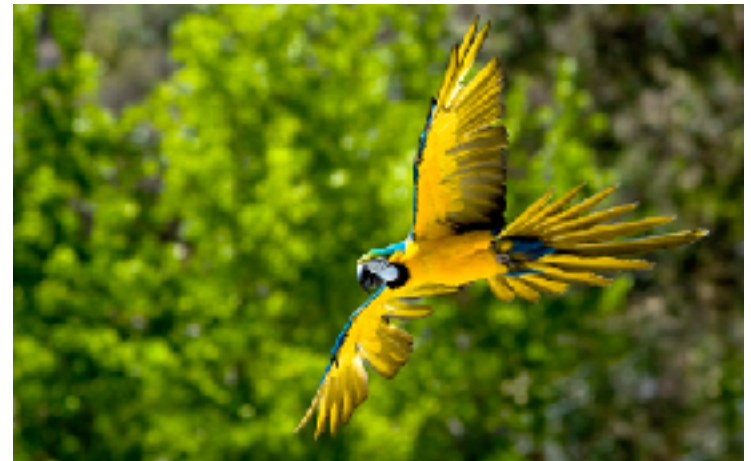


house sparrows

--ex. Black badge size indicates dominance

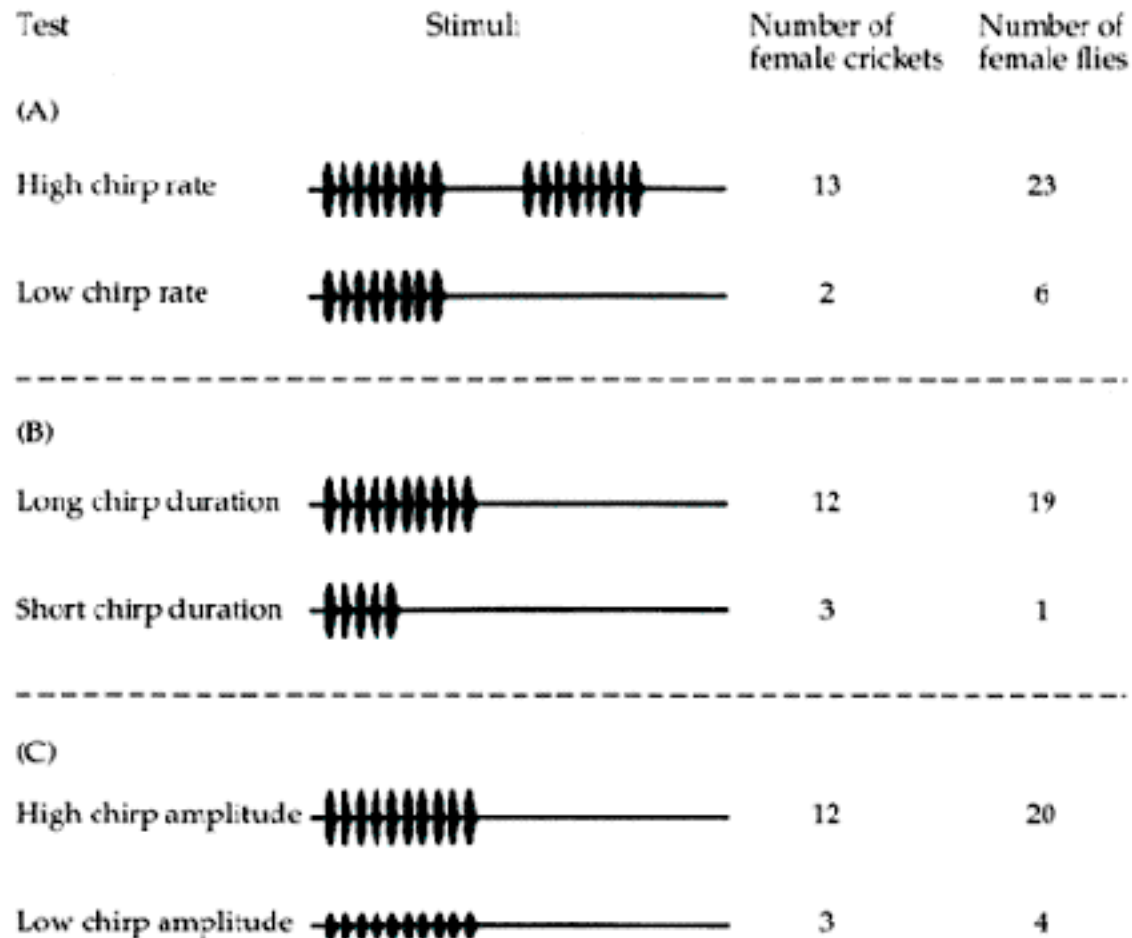
# Signaler costs

- Production costs (costs when signal used/displayed)
  - Conspicuousness to predators & parasites
  - Energetic costs
  - Opportunity costs (lost time)
- Development costs
  - Energetic costs  
(growth of antlers, long tails, neural circuitry)
- Maintenance costs
  - (flying with long tail, preening)



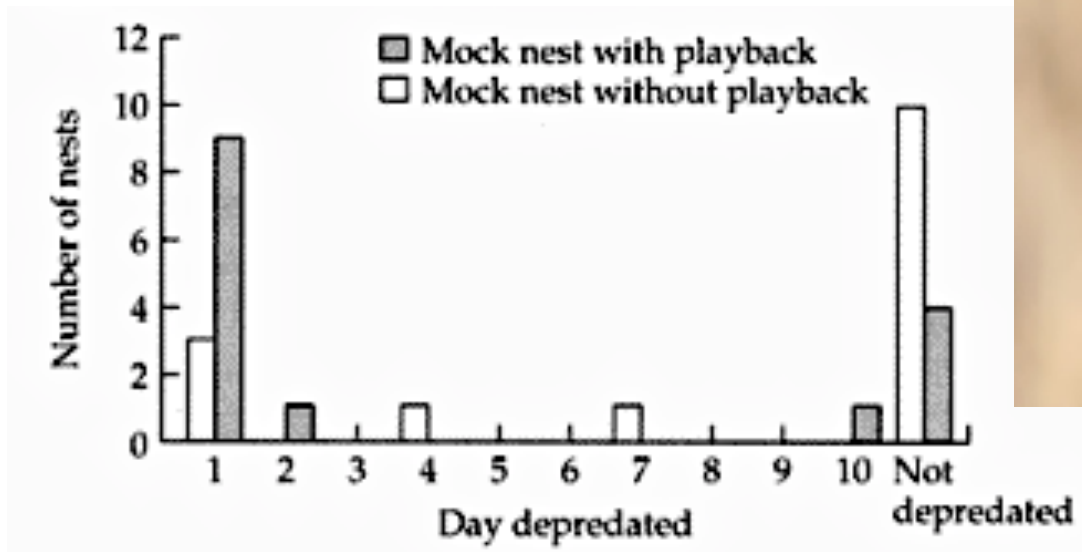
# Signaler costs

- Production costs
  - Male cricket chirps attract parasitic *Ormia* flies (and females)



# Signaler costs

- Production costs
  - Red-winged blackbird calls attract predators



# Signaler costs

- Production costs
  - Sage grouse displays are energetically costly

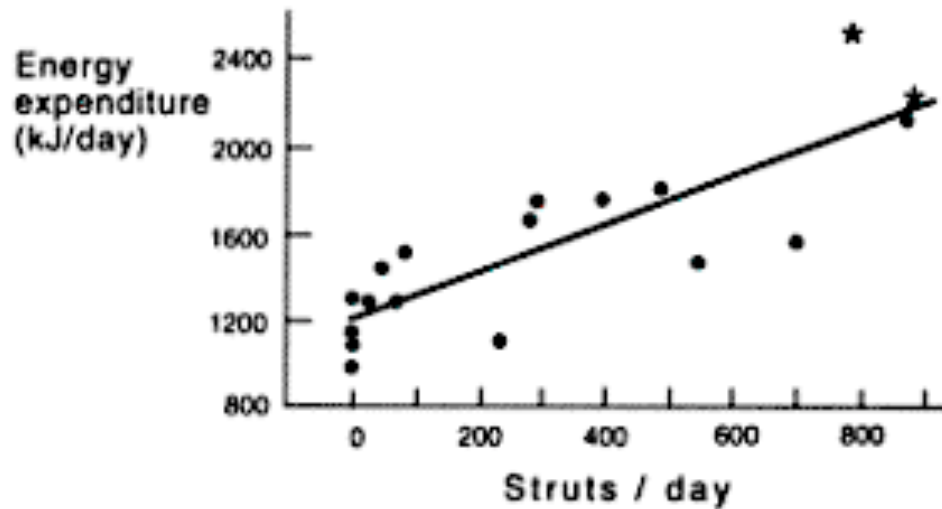
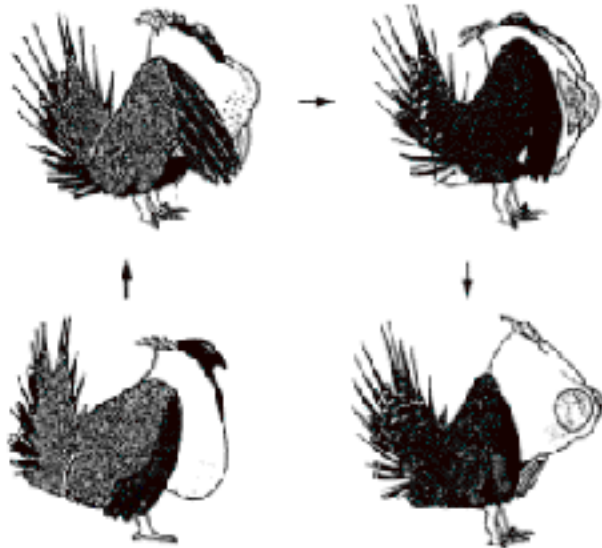


# Signaler costs

- Production costs
  - Sage grouse displays are energetically costly



<http://www.youtube.com/watch?v=m0M8pZnNlnI>





# Signaler costs

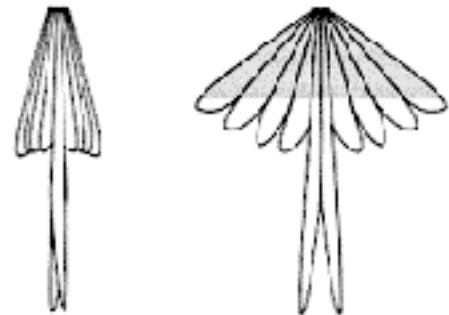
- Maintenance costs
  - Drag of elongated tails



(A) Shallow fork



(B) Pintail



IS

(C) Deep fork



(D) Graduated



Gray - generate lift

White - produces drag

# Signaler costs

- Maintenance costs
  - Preening, signal maintenance



# Signaler costs



- Developmental costs
  - Cost of learning
    - Neural tissue required for learning and memory is energetically costly to maintain
    - Learning often time-consuming and mistake prone
  - Cost of growth (e.g., long tail feathers)
  - Cost of allocation (e.g., carotenoids put into feathers are taken away from immune system)

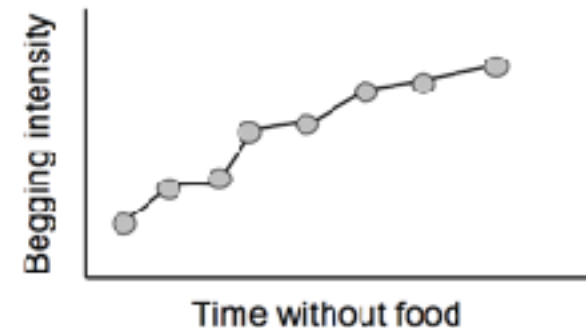
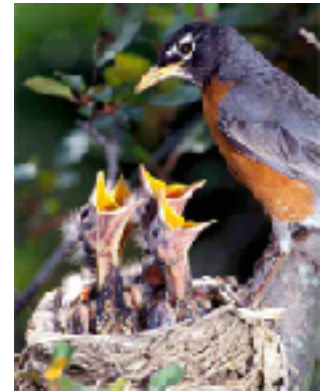


# When are signals honest: Differential benefits



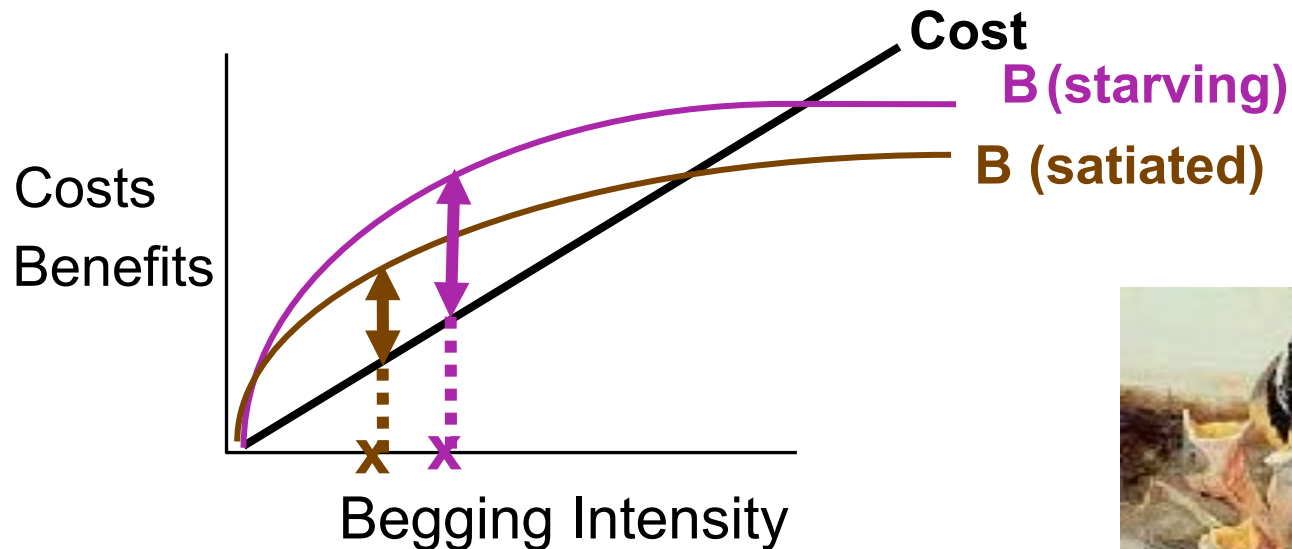
# When are signals honest: Differential benefits

- Begging signals
  - Interests of parent and offspring do not completely overlap
    - thus, expect forced honesty
  - Energetic cost of begging appears low, but begging often increases attraction of nest predators (this is cost that keeps system honest)
  - Evidence signaling system is honest:
    - Begging intensity increases when nestlings are hungry



# When are signals honest: Differential benefits

## Condition-dependent benefits



# Who benefits?



Change in  
receiver's fitness

Change  
in  
sender's  
fitness

	+	-/neutral
+	mutually beneficial <sup>Signal</sup>	manipulation, deceit <sup>Signal</sup>
-/neutral	localization, eavesdropping <sup>Cue</sup>	



# Deceit

- Sender benefits, receiver is harmed
  - What could receivers do when sent a dishonest signal?
    - Ignore
  - Why would receivers pay attention to a dishonest signal?
    - Still a net benefit to paying attention to signal if frequency of deceit is low or cost of responding is low





# Deceit



## letters to nature

*Nature* 319, 143 - 145 (09 January 1986); doi:10.1038/319143a0

## Birds that 'cry wolf'

CHARLES A. MUNN

Wildlife Conservation International, New York Zoological Society, The Bronx Zoo, Bronx, New York 10460, USA

**Reports of animals using alarm calls deceptively are rare (refs 1–3 and R. Cheney and D. Seyfarth, personal communication in ref. 4). Here I have studied two species of flycatching birds in Amazonia, *Lanio versicolor* and *Thamnomanes schistogynus*, which lead flocks of mixed species in the canopy and understorey of the forest, respectively, and act as sentinels, giving alarm calls at the approach of bird-eating hawks. These two species feed to a large extent on the insects flushed out by the foraging of the rest of the flock. My observations suggest that *L. versicolor* and *T. schistogynus* use the predator alarm call deceptively to distract other birds, thereby increasing their own chances of capturing arthropods. This result suggests that deception among animals may be more widespread than is generally assumed.**