Behavioral Ecology of Vertebrates

Unit 13. Communication

Module 5 Cooperation

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Learning, Discovering and Sharing Knowledge

Last Unit we talked about interactions where both actor and recipient benefit. In this unit, we extend that idea to communication, where the actor sends signals and the receiver has specialized traits to decode that information. In the previous editions of our textbook, the effects of both the physical and social environment were covered. However, in this most recent edition, considerations of the physical environment has been cut out of the storyline. The emphasis is primarily on use of game theory models to examine effects of the social environment. Remember that the joint effects of the physical and social environments has been a theme running throughout the textbook.

Learning Objectives (Davies et al. 2012:422)

Co-evolution: sender and receiver genotypes:

1. **Mutual benefits:** game theory, sender/ receiver, information/influence, language, reward/punishment
2. **Honest indices:** signal conveys accurate information about the sender; edits "non-discriminating" receiver genotypes out of the gene pool
3. **Fake handicaps**: discriminating receivers edit the fake signals out of the gene-pool, benefits exceed the costs for honest costly displays (elaborate handicaps)

In studying communication, we are brought face to face with what it means to be human. Our unique abilities to use spoken language shapes our perspectives on the communication systems of other animals. In our human society, there is a preoccupation with honest and deceptive communication, so naturally these are the game theory models that shape analysis of animal communication. As Konrad Lorenz stated, what we see in the communication of other animals is a reflection of our own folk psychology.

Davies et al. 2012, Fig 12.6

Pay-offs for sender/receiver of the same species

1. MUTUAL BENEFITS

Lets start with the theme that carries over the best from the previous unit on cooperation: communication that has mutual benefits for sender and receiver. As humans, we are socially conditioned by the rewarding payoffs of a mutual glance of admiration. In these two images, which is the sender and which is the receiver? What is the information that passes between them? How might this influence their behavior? Lets see what happens when we apply this folk psychology to other species.

1.1 Game theory (Maynard –Smith & Harper 2003)

Payoff Matrix		RECEIVER: honest	RECEIVER: dishonest
SENDER	honest	Mutual benefit (+/+)	Sucker (-/+)
SENDER	dishonest	Deception (+/-)	Unstable (-/-)

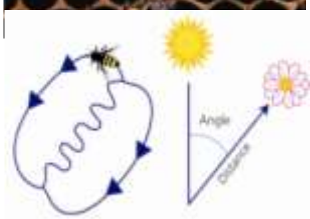
Applied to human language, are payoffs proximate or ultimate?

The underlying concept map for communication in this chapter is based on game theory. So we are looking at the exchange of information between sender and receiver. We only know when this information has been received when we detect the influence on the response of the receiver. Where the payoffs are mutually beneficial, what would we expect to be the influence of the sender on the receiver? Would sender or receiver be expected to break off the interaction when the payoff is “sucker”? When the payoff is “deception”? Why would the interaction be unstable when both sender and receiver are dishonest? Remember that in studying human language , the payoffs are proximate, not ultimate. Language is learned.

1.2 Language (Davies et al. 2012:120, Fig. 14.14)

- Sender/receiver
  - Signal- Information
  - Response- Influence
- Mechanism differs
  - Bees- inherited instinct
  - Humans- learned words
- Payoff matrix
  - Bees- ultimate fitness
  - Humans- proximate reward/punishment

See Bradbury & Vehrencamp 2011!



There is a lot more to the study of communication than game theory! For example, Davies et al. recommend the textbook on animal communication by Bradbury and Vehrencamp. I highly recommend their textbook if you are really interested in communication and how environmental factors have shaped animal signals. Lets use the example of the dance language of bees to compare and contrast language in humans and other animals.

1.3 Inter-species (Davies et al. 2012, Fig. 14.18)

- “Sucker” payoff category (+/-)
- Predator/prey
  - Anglerfish lure (+)
  - Instinctive response to lure (-)
- Prediction
  - Dishonest signal persists
  - Instinctive response would be edited out of the gene pool

Under what conditions would the maladaptive response persist?

Lets look at the application of game theory models to a famous example, the predatory behavior of the anglerfish. This is an example of information passed between sender and receiver. However, the payoffs to the receiver, the prey fish that gets eaten are clearly negative “sucker punch”! The only way this could have persisted over evolutionary time is if there is a counterselection maintaining the genotype of the receiver to respond instinctively to stimuli with the property “small wiggly object”. The next step for the researchers is to show that fish that respond to this stimulus got more to eat in previous generations, thereby fixing the genotype for the instinctive response in the gene pool.

1.4 Poll- lets see if you understand

About which topics would you like to chat more?

a) Game Theory computer simulations
b) Differences between human language (proximate payoffs) and animal signals (ultimate payoffs)
c) Differences between communication within one species (one gene pool) and between species (two gene pools)
d) I'm good, lets move on

Davies et al. 2012, Fig 14.22

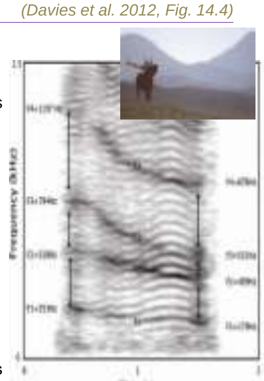
Senders as editors of receiver genotypes

2. HONEST INDICES

If the payoffs for communication within a species convey mutual benefits, then game theory would lead us to predict that the information in a signal honestly predicts whatever the receiver "needs to know". In this photo, the stag on the right needs to know the relative power of the stag on the left that is escalating. If a signal, like a roar, honestly indicates the power of the stag on the left, then the one on the right may learn to avoid that individual before a conflict escalates to potential injury. Stags that learn to associate the roar with the risk are more likely to have higher lifetime reproductive success than those that do not. In this sense, the sender of the signal is editing the receiver genotypes in the gene pool of his species. Those receivers that did not learn, would have been more likely to have been injured and sire fewer offspring.

2.1 Information- roars *(Davies et al. 2012, Fig. 14.4)*

- Roars from red deer stags may serve to draw attention to themselves (Reby and Charlton, 2012) and "harsh roars" may serve to alert females to location and personal characteristics
- Spectrogram of red deer "common roar" represents the distribution of energy (in grey) across time (x-axis) and frequency (y-axis)
- Red deer stags have a descended, mobile larynx that allows vocal tract to be lengthened during a roar (Reby & McComb, 2003)
    - Observed drop at the end of the spectrogram reflects fully extended vocal tract Is this a dishonest index?
    - Does roar communicate body size?
    - Tested whether or not "formant frequencies and dispersion…provide a reliable index of body size" (Davies et al. 2012:402)



credit: M. Green (edited by J. Packard)

Thanks to Milan for bringing to our attention a hot new article about the information value and influence of roars in red deer! The authors showed that females are more likely to pay attention to the "harsh roars" of stags. They are not just responding instinctively like the prey fish attracted to the false anglerfish lure. They are collecting a lot of information about the context of the roars and the individuals that roar.

Reby, D. and Charlton, B.D. 2012. Attention grabbing in red deer sexual calls. Journal of Animal Cognition. 15:265-270

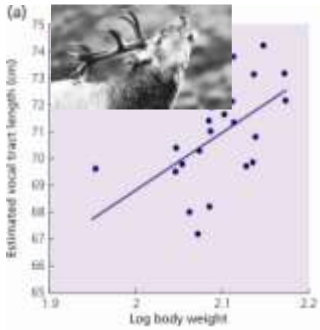
Lets look in more detail about the information contained in a common roar.

2.2 Honest index *(Davies et al. 2012: 402-404, Fig. 14.5)*

- Large amount of research done on red deer population on the island of Rum (Inner Hebrides, UK)
- Test done by Reby and McComb (2003) to compare roars of stags
  - Fundamental frequency not correlated with body size
  - Formant frequency can determine length of vocal tract
- Found vocal tract length to be greater in larger stags that produced lower formant frequencies

What is a formant frequency?

Does this prove influence?



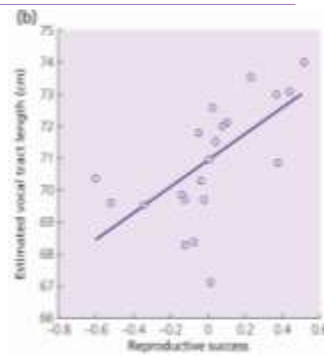
credit by F. Cartaya

Reby and McComb were able to tease apart exactly what information is conveyed in the signal. As stags mature, their body size increases and vocal tract length increases. Longer vocal tract, lower fundamental frequency. However, fundamental frequency no longer is a good predictor of body size, because stags can cheat, they can drop the vocal tract and exaggerate, making the sound seem lower. This put "selective pressure" on receivers that could distinguish between those with truly longer vocal tracts and those with apparently longer vocal tracts due to dropping. The formants convey honest information about body size. But does this really prove communication is mutually beneficial? Don't we need to know whether there are genetic benefits to providing an honest signal?

2.3 Honest payoffs *(Davies et al. 2012: 402-404, Fig. 14.5)*

- Longterm results by Reby and McComb showed stags with lower formant frequency had better reproductive success
- Showed by number of offspring
- Take Home: More research needed to see if deer vocalizations are used as signals to other individuals in harem

Photo credit by Anthony Miners



credit by F. Cartaya

To test the hypothesis about genetic benefits of an honest signal, they predicted that reproductive success would be correlated with body size. In this figure, is reproductive success measured per season or per lifetime? Are the payoffs due to influence on female or male receivers?

2.4 Poll- lets see if you understand

About which topics would you like to chat?

a) Information contained in animal signals
b) Signals as honest indices
c) Payoffs for honest indices
d) Senders as editors of receiver genotypes
e) I'm good, let's move on

Lets dialogue more about this using the elearning discussion tool

Davies et al. 2012 Fig. 14.8

Receivers as editors of signaler genotypes

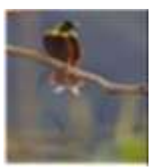
3. FAKE HANDICAPS

We just got through talking about senders as editors of receiver genotypes. Red deer that were better able to discriminate formants produced more copies of their smart genotype. However, in our chat, we noted that receivers also function as editors of sender genotypes. First there was the fundamental frequency as an honest index. Then the cheaters who dropped the larynx were selected and their genotypes came to outnumber the honest ones. This is a series of coevolutionary steps where a change in the sender genotype influences the receiver genotype and vice versa. Now let's look at the receivers as editors of the sender genotypes. The lyrebird in this photo is amazing in the number of ways that its signals have become exaggerated. How could this evolve? Wouldn't elaborate signals draw the attention of predators? Wouldn't the receivers evolve ways of detecting the fake signals in cheaters?

3.1 Handicaps *(Davies et al. 2012: 405, Fig. 14.8)*

- Extravagant and very costly displays
  - Such displays are handicaps --> Handicap Principle (Zahavi, 1975)
- Why are handicaps favored by natural selection?
  - Favored BECAUSE they are costly
  - They signal that the male is "high quality"
  - FP: Low quality males cannot "afford" to produce extravagant displays (Grafen 1990a, 1990b)

In what way were receivers "editors" of these sender genotypes?



credit: C. Wilcox (edited by J. Packard)

The key here is to understand that the traits of the receiver are "under genetic control". So once an instinctive response becomes fixed in a gene pool, then individuals are no longer detecting what is real and what is fake. These photos of two species of birds of paradise are actually teasers. To see the amazing behavior displays associated with this distinctive plumage, go to the Cornell Lab of Ornithology. Search for the website of the Birds-of-Paradise Project. Watch their collection of videos of these amazing displays.

What do we mean by "the male is high quality"?

3.2 Handicap Principle *(Davies et al. 2012: 407, Fig. 14.10)*

- Amotz Zahavi proposed that extravagant displays are favored in natural selection because they are costly, thus, making them reliable
- This principle requires a direct correlation between high-quality individuals and the display versus an index trait that includes a less direct correlation.
- Stalk-eyed flies experiment (Cotton, et. al. 2004)
  - Varied the amount of pureed corn fed to larvae
  - Eye-span decreased in lower food condition
  - Decrease was greater with male individuals
  - Statistically controlled variation in body size: small body size also had smaller eye spans.

Why was the handicap principle controversial? What problems do you see with it?

credit: J. Cantwell (edited by J. Packard)

Jenna wrote: I think it would be good critical thinking for the class to discuss why this principle was controversial, and how they would estimate this hypothesis without the results of the study. I think they are good enough critical thinkers to identify that extravagant displays are a sign of better body condition, and make males more desirable to females, but why?

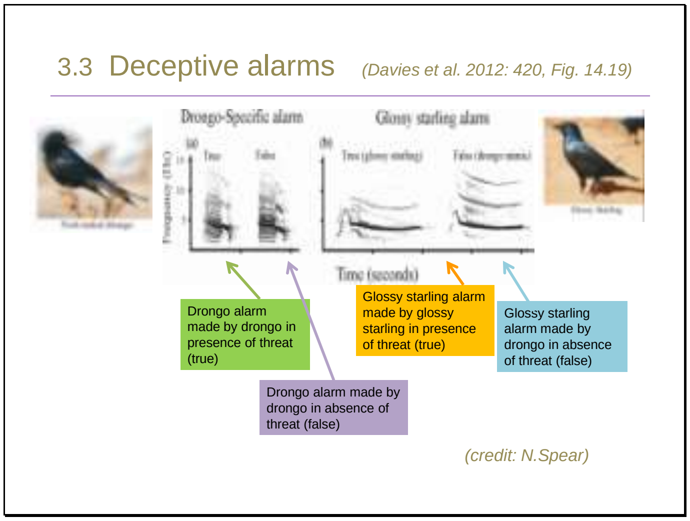
Jane adds:

Q1. If this is due to a proximate treatment, is it even relevant to evolutionary change, since there is no variation in genetic quality?

A1. It showed that the eye stalk was costly, because poorly nourished individuals did not produce as big a signal (eye span)

Q2. Why is this evidence for a "costly handicap", not an "honest index"?

A1. Honest index of genetic quality would not vary with the environmental conditions (diet)

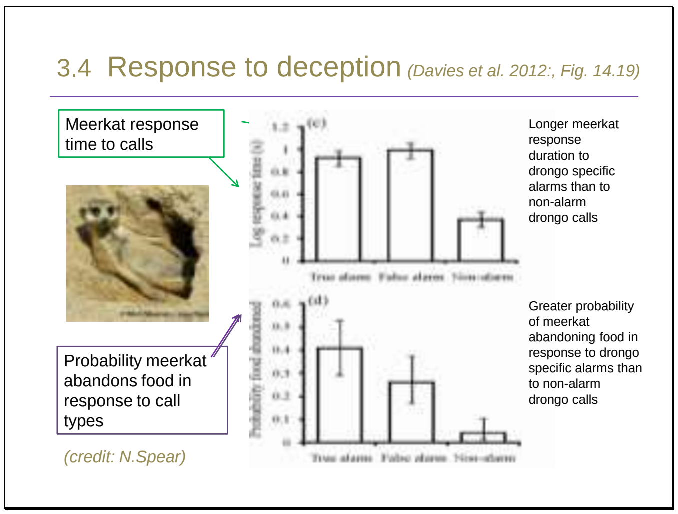


Fork-tailed drongos in Kalahari usually forage alone (insects in the air, lizzards and crickets on the ground). However, they

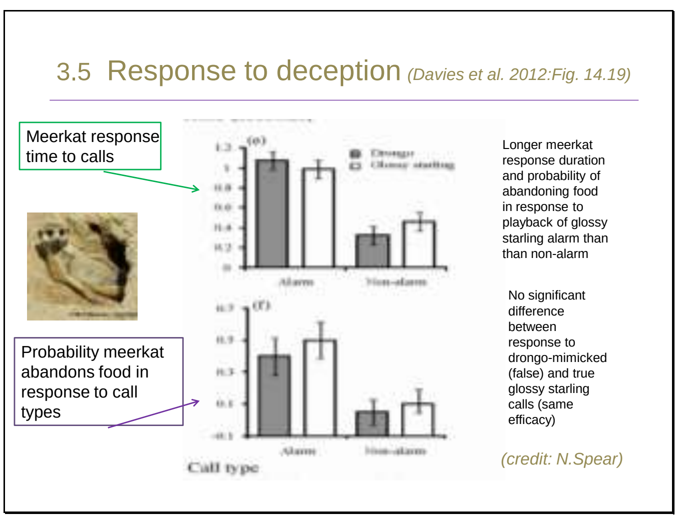
- May follow cooperative hunting groups of pied babblers and meerkats to forage on what has been flushed by these predators before them.
- Also may steal food caught by these other species (10% of drongo diet).

To steal food, drongos either

- Take food directly from forager or
- Take food forager has abandoned



Fork-tailed drongos make false alarm calls, mimicing the glossy starling when there is no predator. Meerkats heed the warning of glossy starlings. A study by Flower (2011) looks at the influence of drongo calls on meerkat responses. Study used recorded calls made by drongos and glossy starlings.



A study by Flower (2011) looks at the influence of drongo calls on meerkat responses (time & food abandonment). Study used recorded calls made by drongos and glossy starlings. Do you think the drongo mimicry of starlings is instinct or learned? Is the response by meerkats instinct or learned?

3.6 Badges of Status *(Davies et al. 2012: 410, Fig.14.12)*

- Signals of status or quality, can sometimes be used falsely. What is the cost of this?
- Individuals who falsely signal ability pay a social cost-increased aggression or punishment. (Dawkins and Krebs, 1978)
- Tibbbets and Dale, (2004) used paper wasps to demonstrate the social cost of false status signals.
  - More dominant individuals have more black spots on their faces.
  - Wasps that signaled above their status received more aggression (Tibbets and Dale, 2004)
  - Social cost maintains the honesty of signals of status.

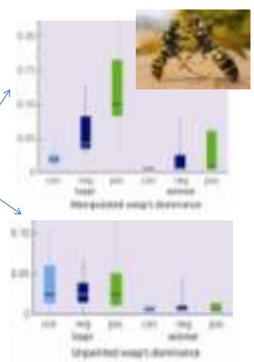
(credit: J. Travis)

(photo: Pete La Quaglia)

(photo: Elizabeth Tibbets)

3.7 Dishonest badge (Davies et al. 2012 Fig. 14.13)

- Social cost: are "cheaters" punished?
- Influence
  - a) unpainted wasps mount rate
  - b) painted wasp's mount rate
- Results
  - treatment did not influence behavior of sender
  - Losers with "dishonest spots" received 6X more aggression



The treatment was complex. First they "fought" the wasps and decided which was the winner or loser. Then they added (pos) or subtracted spots (con). Then they paired them up in fights again. Mount rate was measured as the index of winning a fight.

3.8 Poll- lets see if you understand

About which topic would you like to chat more?

a) Handicap Principle
b) Deceptive alarms
c) Badges of status
d) Receivers as editors of sender genotypes
e) I'm good, let's move on

Lets dialogue more about this using the elearning discussion tool

Summary (Davies et al. 2012:422)

Co-evolution: sender and receiver genotypes:

1. **Mutual benefits:** game theory, sender/ receiver, information/influence, language, reward/punishment
2. **Honest indices:** signal conveys accurate information about the sender; edits “non-discriminating” receiver genotypes out of the gene pool
3. **Fake handicaps**: discriminating receivers edit the fake signals out of the gene-pool, benefits exceed the costs for honest costly displays (elaborate handicaps)