UNIT 14. THE DESIGN OF SIGNALS: ECOLOGY AND EVOLUTION

SOURCES *(for powerpoint format: http://wfsc.tamu.edu/jpackard/behavior/wfsc622/powerpoints.zip)*

required: Chapter 14 in Krebs & Davies (1993:318-374) TIP: we skipped Ch 13 because it is about invertebrates

remedial: "Rearing the Young" in Halliday 1994; "Talking to Strangers" in the Trials of Life video series
supplement: Chapter 8 in Blumstein, D.T. and Fernandez-Juricic, E. (2010) "A Primer of Conservation Behavior"

PARTS OF THIS LECTURE OUTLINE

1. Ecological Constraints on channels
2. Response of Receivers
3. Information Content of Variable Signs

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1. ECOLOGICAL CONSTRAINTS ON CHANNELS

1.1. **Comparative approach- functions of sensory channels** ***(Krebs and Davies 1993:350 Table 14.1)***

1. range: chemical = auditory > visual > tactile
2. long-lasting: heavy molecular weight chemical>auditory = visual = tactile
3. pass obstacles: chemical = auditory > visual = tactile
4. locatability: chemical = auditory < visual = tactile energetic cost: chemical < auditory > visual = tactile

1.2. **Signal design: degradation in forest vs. grassland** ***(Krebs and Davies 1993:353 Table 14.2)***

1. comparison of bird species in Panama *(Morton 1975 cited in Krebs and Davies 1993:352)*
   a. forest species used low frequency, pure tones, narrow frequency range
   b. sound more likely to go around vegetation than buzzy trills in grassland
2. rufous-collared sparrow: forest *(Krebs and Davies 1993:354 Fig. 14.2a)*
   a. sing slower trills than grassland sparrow species
3. great tit: compared birds in open woodland with dense forest *(Krebs and Davies 1993: 354Fig. 14.2b)*
   a. open habitat: higher frequency, rapidly repeated notes, wider frequency range

1.3. **Primates: forest species**

1. grey cheeked mangabey *(Krebs and Davies 1993:357 Fig. 14.3; Table 14.3)*
   a. whoop-gobble: spacing between troops
      i. low frequency => can be heard at a long distance (1000 m)
   b. scream: fights within troop
      i. high frequency => carries a short distance (300 m) less likely to attract predator

1.4. **Take-home message: ecological constraints of signal design**

1. signal features (channel, dominant frequency, frequency range) adapted to habitat
2. e.g. rufous-collared sparrow, great tit, grey-cheeked mangabey

Part 1	**Study Questions for Chat & Quiz 14 "The Design of Signals: Ecology and Evolution"**
1.1.1	Comparing different sensory channels, which are most suitable for long-range and long-lasting communication signals? (TIP: Table 14.1)
1.1.2	Comparing sensory channels, which signals are most effective (a) in environments with much vegetation (obstacles), and (b) in communicating location of the signaler? (TIP: Table 14.1; rank the channels separately for the functions of "passing obstacles" and "locatability")
1.2	Compare design of signals used by grassland and forest birds? (TIP: Fig. 14.2)
1.3	For mammal species, explain how signal design is related to function for two signals? (TIP: e.g. mangabeys)
1.4	What are some ecological constraints on signal design?

2. RESPONSE OF RECEIVERS: FIXED SIGNALS

TIP1. Last unit was about the co-evolution of "helping" and "parenting". This unit is about the co-evolution of "receivers" and "signalers". When the genotype for the "receiver" has become fixed, then typically the genotype for the "signaler" also evolves as a fixed strategy. Similar to what you learned in the unit on mate choice, the presence of choosy recipients in the population may "exert selection pressure" on the genotypes that code for the signals.

2.1. **Origin of signals (DIM)- ancestral form was functional** ***(Hinde 1970 cited in Krebs and Davies 1993:360 Table 14.4)***

1. H1: **Displacement** activity (e.g. redirected grass-pulling in gulls; preening in ducks)
2. H2: **Intention** movements (e.g. forward threat posture of gulls)
3. H3: **Motivational** conflict (e.g. urination in wolves)

2.2. **Ritualization (HAM): derived form became symbolic during evolution** ***(Krebs and Davies 1993:362,364 Fig. 14.4, 14.5)***

1. H1: **Honesty** (predictors of good quality mate)
2. signals are reliable, maintained by cost, link between signal design and meaning
3. H2: **Ambiguity** reduced (classical view)
   a. more stereotyped, exaggerated, repetitive (e.g. species-specific courtship)
   b. meaning is unlikely to be confused or ignored by a stranger
4. H3: **Manipulation** (co-evolutionary arms race)
   a. Step 1: receiver not responsive (sales resistance)
   b. Step 2: actor increased the signal to get same response

2.3. **Co-evolution: signal receivers and signal generators**

1. a feature of the sensory system of the receiver may precede evolution of the signal Tungara frogs *(Ryan et al. 1990 cited in Krebs and Davies 1993:268)*
   a. females in two species are most sensitive to sounds of 2.1 kHz
   b. male "chuck" call (2.1 kHz) evolved in one species, not the other
2. swordtail fish and platyfish *(Basolo 1990 cited in Krebs and Davies 1993:369)*
   a. females of both species prefer males with long tails
   b. swordtail males have long tail, platyfish do not

2.4 **Signals with a function of species recognition** (Fig. 14.5 in Krebs and Davies 1993:364)

1. lizard head-bobs (Scleroporus)
2. fiddler crab claw waving,
3. tree frog calls (Hyla)

2.5. **Take-home message: predictable response of receivers to fixed signals**

1. Co-evolution of unambiguous symbolic displays and sensory system of receiver
2. e.g. Tungara frogs, swordtail and platyfish

Part 2	**Study Questions for Chat & Quiz 14 "The Design of Signals: Ecology and Evolution"**
2.1	Using the comparative method, what are three hypotheses about the functional precursors of fixed signals that are now symbolic derived traits? (TIP: DIM)
2.2	What are 3 examples of ritualized display signals? (TIP: Fig. 14.4)
2.3	Why does evolution of a symbolic display imply co-evolution of feature detectors in the receiver of the signal? (TIP: tungara frogs, swordtails)
2.4	What is your favorite example of signals that aid in species recognition? (TIP: Fig. 14.5)
2.5	How has coevolution resulted in predictable responses of receivers to fixed signals? (TIP: take-home message)

3. INFORMATION CONTENT OF VARIABLE SIGNS

TIP2. Notice here in Part 3, that the assumption of "variable signs" is that the heritable strategy is conditional , meaning that the genotype codes for individuals learning signs, like tactics, from their social companions. In contrast to part 2, "fixed signals" referred to variation that is highly heritable, due to the variation in genotypes, not the social environment. Keep it clear in your mind that "signals" are more like genotype strategies and "signs" are more like learned tactics. Signs are a behavioral adaptation to a fluctuating social environment. Signals are adaptations to what has been predictable in the past history of each species. Similar to what you learned previously about fixed and conditional, only here it is applied to the function of "transfer of information".

3.1 **Variation within individuals: motivational level**

1. fulmar: graded continuum of attack displays (cost and effectiveness are correlated)
   a. low intensity: wing-raise => retreat (12%) or attack (1.7%)
   b. high intensity: rushing from behind => retreat (28%) or attack (28%)
   c. more likely to escalate if bird is more hungry
2. arctic skuas: 11 types of display *(Paton & Caryl 1986 cited in Krebs and Davies 1993:371)*
   a. display was a poor predictor of actor's subsequent behavior or receiver's response
   b. need to control for: resource value, internal state of actor and of receiver

3.2. **Context: variation in meaning of sign is learned *(Krebs and Davies: 1993:372 Box 14.1)***

1. vervet monkey predator calls vary with context *(Cheney & Seyfarth 1990 cited in Krebs and Davies 1993:372)*
   a. "leopard call": ground predator
   b. "snake call": tree predator
   c. "eagle call": aerial predator
2. receivers respond appropriately: climb tree, jump out of tree, seek cover
3. ontogeny: young vervets call out of context; learn consistency with experience

3.3. **Window on animal minds *(Cheney & Seyfarth 1990 cited in Krebs and Davies, 1993:372)***

1. learned expectations (e.g. vervets climb trees in response to leopard call)
   a. in stable social groups, individuals learn what to expect from partners
2. goal-directed intentionality (e.g. avoid injurious interaction with dominant)
   a. individuals change their own actions in a manner that achieves a goal
3. deceptive manipulation (e.g. give leopard call when dominant is threatening)
   a. a sign used out of context, in a way that benefits actor, not the receiver

3.4. **Take-home message: information content of variable signs**

1. the meaning of variable signs may be learned in a group context=> variable response
2. e.g. fulmars, vervet monkeys

Part 3	Study Questions for Chat & Quiz 14 "The Design of Signals: Ecology and Evolution"
3.1.1	What is your favorite example of how motivational intensity is expressed by a signs that vary along a graded continuum? (TIP: e.g. fulmar)
3.1.2	Comparing fixed signals and variable signs (conditional strategy), what are the differences in design and function? (TIP: compare Part 2 & Part 3)
3.2.1	What are 3 examples of predator calls by vervet monkeys, which convey different information appropriate to the context in which the call is given? (TIP: pg. 372)
3.2.2	What is the technical and colloquial meaning of "information" in the context of communication theory? (TIP: Box 14.1)
3.3	How does the study of communication serve as a "window on animal minds"? (TIP: pp 372-373)

4. SUMMARY

4.1 Ecological constraints of signal design

1. signal features (channel, dominant frequency, frequency range) adapted to habitat
2. e.g. rufous-collared sparrow, great tit, grey-cheeked mangabey

4.2 Predictable response of receivers to fixed signals (DIM and HAM hypotheses)

1. coevolution of unambiguous symbolic displays and sensory system of receiver
2. e.g. Tungara frogs; swordtail and platyfish

4.3 Information content of variable signs

1. the meaning of variable signs may be learned in a group context=> variable response
2. e.g. fulmars, vervet monkeys

Summary	Study Questions for Chat & Quiz 14 "The Design of Signals: Ecology and Evolution"
4.1	What are 3 take home messages from this unit on communication? (TIP: summary)
4.2	In animal communication, how has the physical and social environment shaped the design of variable signs and fixed signals?

TIP3. The hypotheses about behavioral adaptations with the function of communication have changed over the years. This history provides insight as to the different approaches summarized in Parts 1 & 2 compared to Part 3. At first, the classical ethologists were interested in the study of communication channels and displays (fixed signals) because these behaviors were considered to be evidence of the genetic control of behavior. Remember, that was back in the era before we had the technology to investigate genetic markers. So much of the information in Parts 1 &2 was examined under the theory that all communication was adaptive, cooperative, for the "benefit of the species". Krebs and Davies challenged this perspective in their edited volumes published before and after this introductory textbook. They introduced the perspectives of "mind reading" and "manipulation". These ideas really captured the imagination of comparative psychologists and behavioral ecologists, and a whole new subfield of "cognitive ethology" emerged (i.e. windows on animal minds). These ideas have practical application to animal behavior management. You can manipulate your animals by using fixed signals to which you know they will respond in a predictable manner. However, be aware of their abilities to learn your flexible signs and manipulate you! When you sense this is occurring, use standard behavioral modification techniques to teach your animals the flexible signs that you want them to learn, and to which you want them to respond such that you are manipulating them, not vice versa!