Chapter 18: Signal Design

Why that particular signal?

Signal design features

- **Signal range**: context and sender/receiver distance
- **Locatability**: cryptic vs conspicuous
- **Duty cycle**: % on
- **Identification level**: information content - species, sex, individual
- **Modulation potential**: stereotyped vs graded
- **Form-content linkage**: arbitrary or linked due to source or other constraint

e.g. mate attraction vs courtship

- Range:
  - – Attraction: long distance
  - – Court: close up
- Locatability:
  - – Attraction: no point otherwise
  - – Courtship: not needed (already there)

Mate attraction signal rules

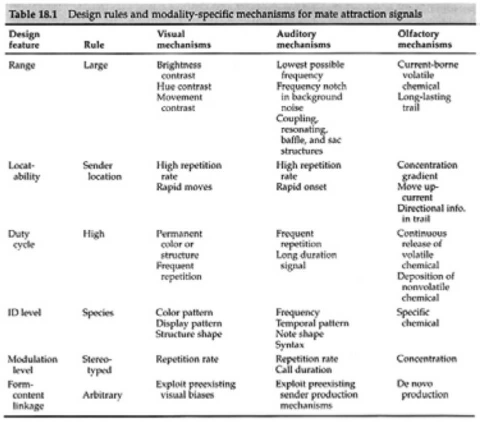


Table 18.1 Design rules and modality-specific mechanisms for mate attraction signals

Design feature	Rule	Visual mechanisms	Auditory mechanisms	Olfactory mechanisms
Range	Large	Brightness contrast Hue contrast Movement contrast	Lowest possible frequency Frequency notch in background noise Coupling, resonating, baffle, and sac structures	Current-borne volatile chemical Long-lasting trail
Locatability	Sender location	High repetition rate Rapid moves	High repetition rate Rapid onset	Concentration gradient Move up-current Directional info. in trail
Duty cycle	High	Permanent color or structure Frequent repetition	Frequent repetition Long duration signal	Continuous release of volatile chemical Deposition of nonvolatile chemical
ID level	Species	Color pattern Display pattern Structure shape	Frequency Temporal pattern Note shape Syntax	Specific chemical
Modulation level	Stereotyped	Repetition rate	Repetition rate Call duration	Concentration
Form-content linkage	Arbitrary	Exploit preexisting visual biases	Exploit preexisting sender production mechanisms	De novo production

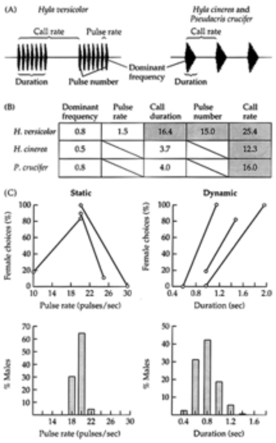
Form-content Linkage

- Recall that signals may convey more than one type of information
- Different parameters may reflect different design rules
- e.g. Arbitrary vs linked
  - Stereotyped recognition signals: arbitrary
  - But often competitive: linked (converge on best designs for competitive signalling)

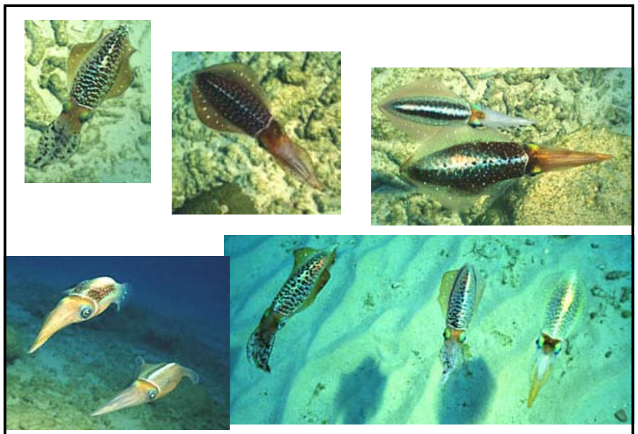
Static vs dynamic calling displays

Static components:
Convey information about species differences.
Females prefer mode.

Dynamic components:
Convey information about individual differences.
Females prefer extremes.



	Dominant frequency	Pulse rate	Call duration	Pulse number	Call rate
H. versicolor	0.8	1.5	16.4	15.0	25.4
H. cinerea	0.5		3.7		12.3
P. crucifer	0.8		4.0		16.0



Chapter 19: Game Theory

Just when you thought the math
was over.

Up until now…

- Payoffs for alternative strategies depend on context
- Optimal strategy depends on correct identification of the current condition
- Signals used to carry information regarding current condition

But…

- What about interactions with other individuals
  - They can do more than one thing
  - Current condition is defined by what they do
  - Payoff depends on what opponent does
  - **Conflicts of interest**
- **Game Theory**
  - **Finding the best strategy when the payoffs are affected by the strategies of others**
  - Frequency-dependent payoffs
  - Derived from economics

Game theory

- Economic vs evolutionary game theory
  - Economic games use money as currency, evolutionary games use fitness.
  - Economic games are zero-sum, i.e. increasing the payoff to one player decreases the payoff to others. Evolutionary games need not be zero-sum.
- Game solution is the best strategy
  - Social scientists require rational behavior, evolution requires natural selection

Game Theory

- List all alternative strategies that each of 2 or more contestants might adopt in a “game”
- Each contestant plays one of the possible strategies
- Compute fitness payoffs for each possible match-up of strategies, and find best response to each possible opposing strategy

Games

- At least 2 “players”
- Roles
  - Different players may have different strategies available, e.g. male/female, small/large, etc.
- Strategies
  - Alternative behaviours available to a player in a particular role

Evolutionary Stable Strategy (ESS)

- Strategy that, when adopted by all members of a population, cannot be invaded by any alternative strategy (higher payoffs than any other strategy).
- Note: not all situations (games) have an ESS.

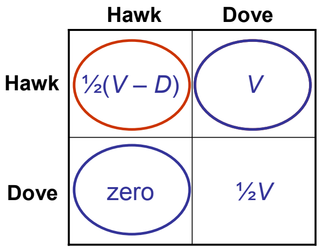
e.g. The Hawk/Dove Game

- Two opponents contesting a resource
- Roles
  - Hawk
  - Dove
- Strategies
  - Fight
  - Non-violent display
- What is the ESS?

Payoffs

- If 2 hawks
  - They fight, both equally likely to win
  - Winner gets *V*, loser gets -*D*
- If 2 doves
  - They flip a coin, both equally likely to win
  - Winner gets *V*, loser gets zero
- If hawk meets dove
  - Hawk attacks, dove retreats
  - Hawk gets *V*, dove gets zero

Payoff Matrix



	Hawk	**Dove**
Hawk	$\frac{1}{2}(V - D)$	V
Dove	zero	$\frac{1}{2}V$

If *V* > *D*, then it always pays to be a hawk: *pure ESS*

But if *V* < *D*, then no single best strategy: *mixed ESS*

Pure vs Mixed ESS

- Pure ESS
  - Best response is always the same, regardless of opponent's strategy
- Mixed ESS
  - No single best response, depends on opponent's strategy
  - How does this work?

Mixed ESS

- If *f* is frequency of hawks in population
- Equilibrium occurs at:

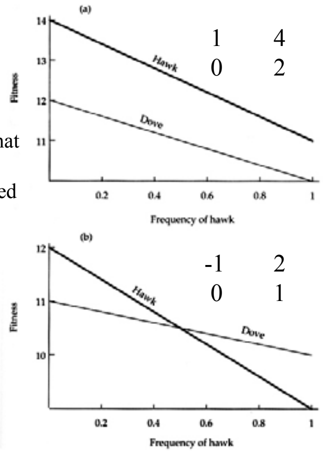
f_h = (V – ½V)/(V – ½V)+[0- ½(V – D)]
= V/D

V/D of the population should be hawks and (1-V/D) should be doves. As the cost of fighting (D) increases relative to benefit of winning (V), more should be doves. Or, each individual could be hawk V/D of the time, dove (1-V/D) of the time.

Frequency dependence

Frequency dependence means that fitness depends on strategy frequency. This can be illustrated By plotting fitness against freq.

$W_H = W_o + 1/2(V\text{-}C)p + V(1\text{-}p)$
$W_D = W_o + 1/2(1\text{-}p)$



$$\begin{matrix}1 & 4\\0 & 2\end{matrix}$$

$$\begin{matrix}-1 & 2\\0 & 1\end{matrix}$$

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e.g. Take Game

- Gulls are fishing
  - Some (*passive*) concentrate on fishing, catch *P* fish/day
  - Others (*cheat)* spend part of their time looking for chances to steal fish from other birds, they catch *P – C* fish/day and steal *B*
- Payoffs
  - 2 passives: *P*
  - 2 cheats: *P – C*
  - passive & cheat: *P – B* & *P + B – C*

Payoff Matrix

	Passive	**Cheat**
Passive	*P*	*P - B*
Cheat	*P + B - C*	*P – C*

As long as B > C, cheat is a pure ESS, even though all payoffs would be higher (P) if all were passive.

ESS is not necessarily the global optimum (or global optimum not necessarily stable). Cheaters really can ruin it for everyone. Note: there is also a Give Game (see text).

- **Pareto optimum**
  - Global maximum, no player can improve without decreasing payoff to other players
  - Not necessarily stable
- **Nash Equilibrium**
  - Best reply to a best reply
  - An ESS

Game classification

- Both previous examples are ***discrete symmetric*** games
  - Discrete: alternative strategies are discrete
  - Symmetric: all players have the same strategies and payoffs available
- Other classes of games are possible

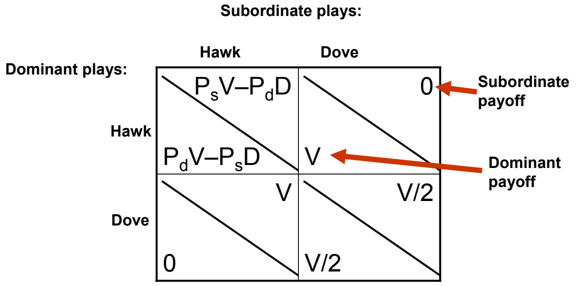
Game classification

- Strategy set
  - Discrete or continuous
- Role symmetry
  - Symmetric vs asymmetric
- Opponent number
  - 2-person contests vs n-person scrambles
- Sequential dependence
  - if outcomes of early decisions constrain later decisions, then the entire sequence is the game and each decision is a bout within the game. These are dynamic games.

e.g. Dominant/Subordinate

- Discrete, asymmetric
- Similar to Hawk/Dove, but roles are asymmetric
  - Dominant and subordinate have different payoffs for each strategy
  - Either one can be hawk or dove, but dominant hawks have higher probability of winning an escalated contest ($P_d > 0.5$) than a subordinate hawk ($P_s = (1-P_d) < 0.5$)

Payoff Matrix



Subordinate plays:

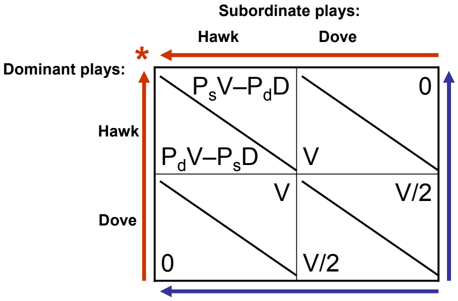
Dominant plays:

	Hawk	**Dove**
Hawk	$P_sV–P_dD$ $P_dV–P_sD$	0 V
Dove	V 0	V/2 V/2

Subordinate payoff

Dominant payoff

Arrow Method



Subordinate plays:

Dominant plays:

	Hawk	**Dove**
Hawk	$P_sV–P_dD$ $P_dV–P_sD$	0 V
Dove	V 0	V/2 V/2

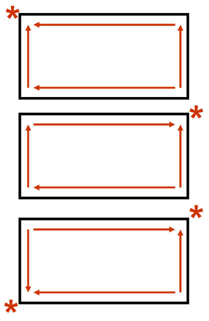
If V < 0, hawk is best response to dove by either opponent.

Best response to hawk depends on values of P_s, P_d & D. If:

$P_d>P_s>D/(V+D)$

Hawk is pure ESS.

Three possibilities



- $P_d > P_s > D/(V+D)$
  - Hawk is pure ESS
- $P_d > D/(V+D) > P_s$
  - Dominant hawk, subordinate dove
- $D/(V+D) > P_d > P_s$
  - Either can be hawk or dove
  - Resource of little value,

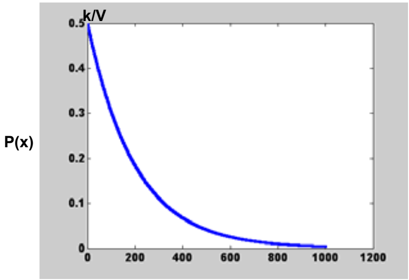
e.g. War of Attrition

- Continuous game
  - Symmetric or asymmetric versions
- Two opponents, each devotes some effort to the contest (eg bears a cost of aggressive display in proportion to effort), winner is the one who tries hardest (or hangs in there the longest)
  - Contest of how much cost you can take
- Is there an ESS?

Symmetric War of Attrition

- All players suffer same cost of display, *k*, and get same payoff for winning, *V*
  - Amount of signalling is *x*, so cost of contest is *kx*
- If all play same *x*, winning is random and all get *V/2 – kx*
  - Then a mutant who plays any *x'* > *x* would always win, therefore mutants would invade the population
  - Once *x'* > *V/2k* payoffs are negative, and a mutant who plays x = 0 could invade
  - But there is an ESS

Probabilistic strategy



P(x) = k/V*exp(-kx/V)

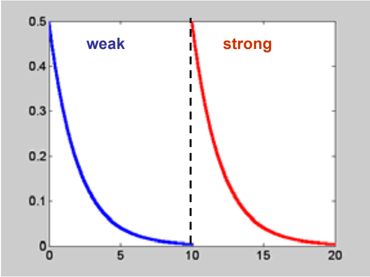
Play all values of x with varying probability – lower values more probable.

Asymmetric War of Attrition

- Usually costs are not the same for everyone
  - Assume different levels of cost and resource value for each player
  - Maximum investment for a player is the break-even point: *V – kx = 0, x = V/k*
  - Player with larger V/k ratio can always win, so if they *know* then there's no need for contest. But they usually don't know perfectly. Therefore must play the game.

Asymmetric War of Attrition

- Assume two classes of player (strong & weak)
- Maximum effort for the weak *S = V/k*
  - They should choose display level 0 < *x* < S
- This should be *minimum* effort for the strong
  - Choose display level *S < x < infinity*
- If both think they have the same role, then this is the symmetrical game



This will be relevant to honest signalling (next lecture).