Signal Origin and Evolution

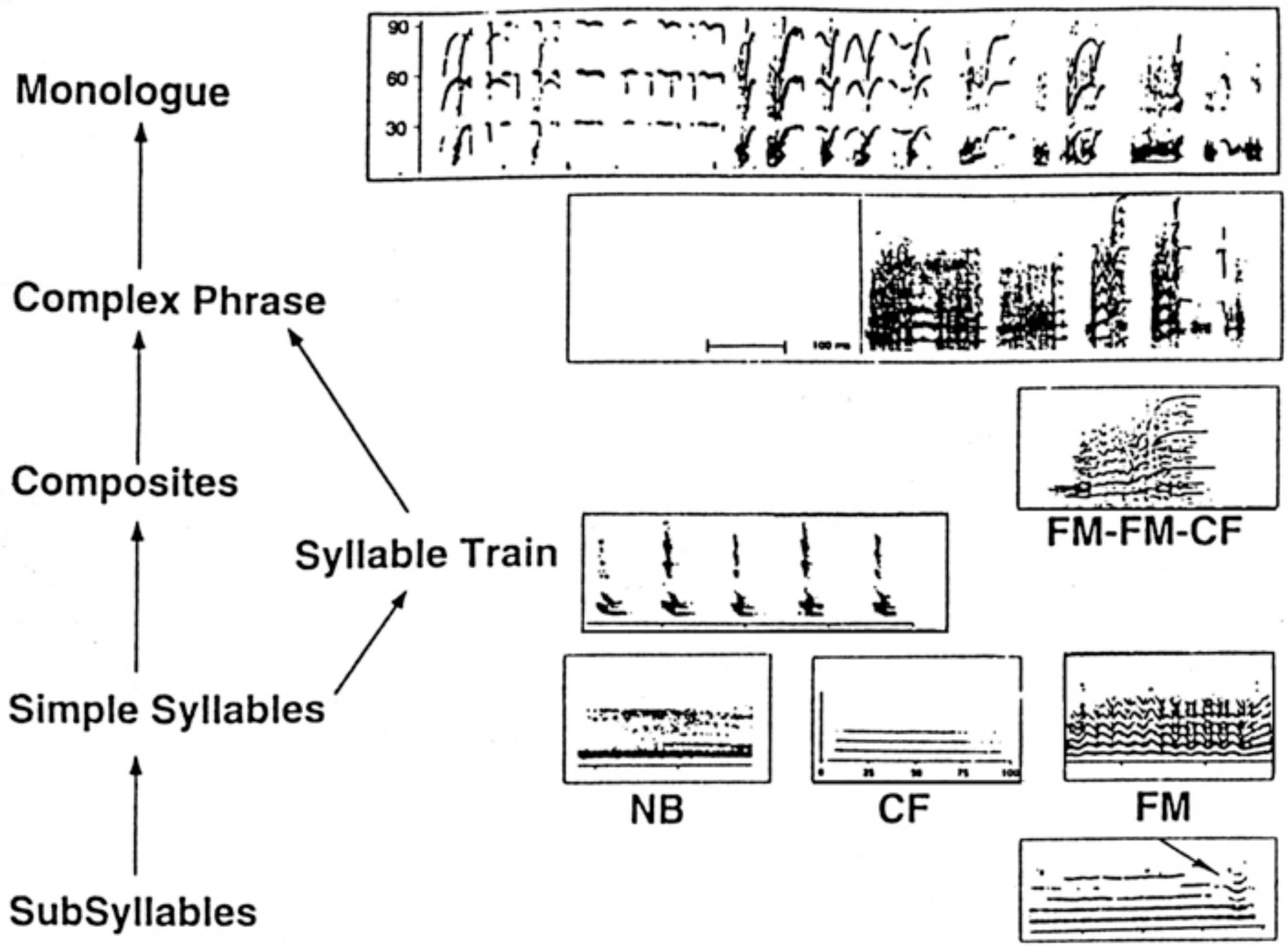
- Signal coding schemes
- The process of signal evolution
- Sender preadaptations
  - Visual, auditory, olfaction
- Receiver preadaptations
- Reading: Ch. 15: 460-474, 483-494; Ch. 16: 497-535

Coding schemes

- Codes require signal diversity
- Variation can be created by
  - Modifying signal elements (lexicon)
    - Sound: amplitude, frequency, duration
    - Light: color, size, location
  - Combining signal elements in series (syntax)
  - Can lead to hierarchical structure
- Signal elements must be perceptually distinct
  - Certain clusters of signal element combinations retained, intermediate regions avoided
  - Can lead to stereotypy

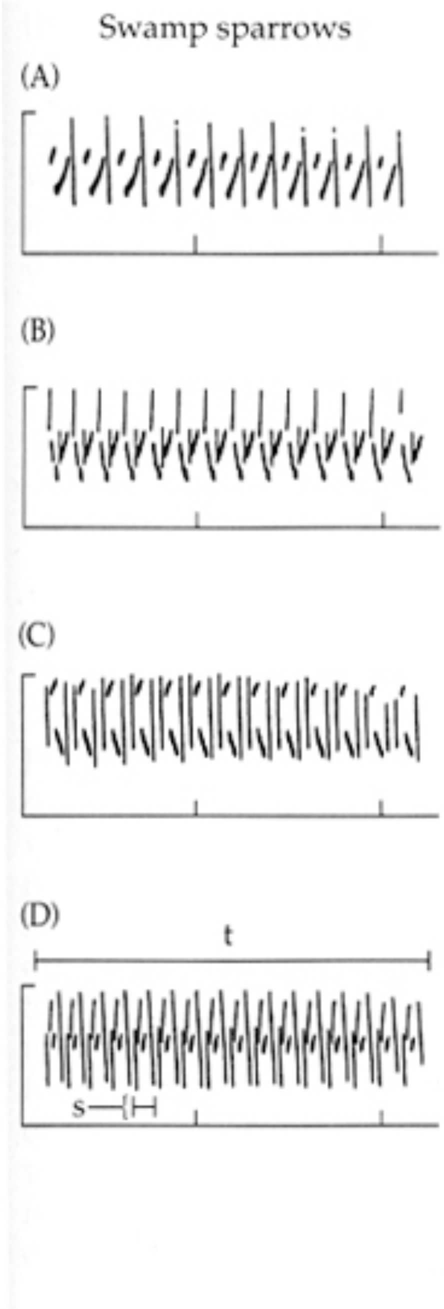
Syntax Formation

Pteronotus parnelli



19 simple, 33 composite syllables; Kanwal et al, 1994

Hierarchical syntax



Hierarchical syntax

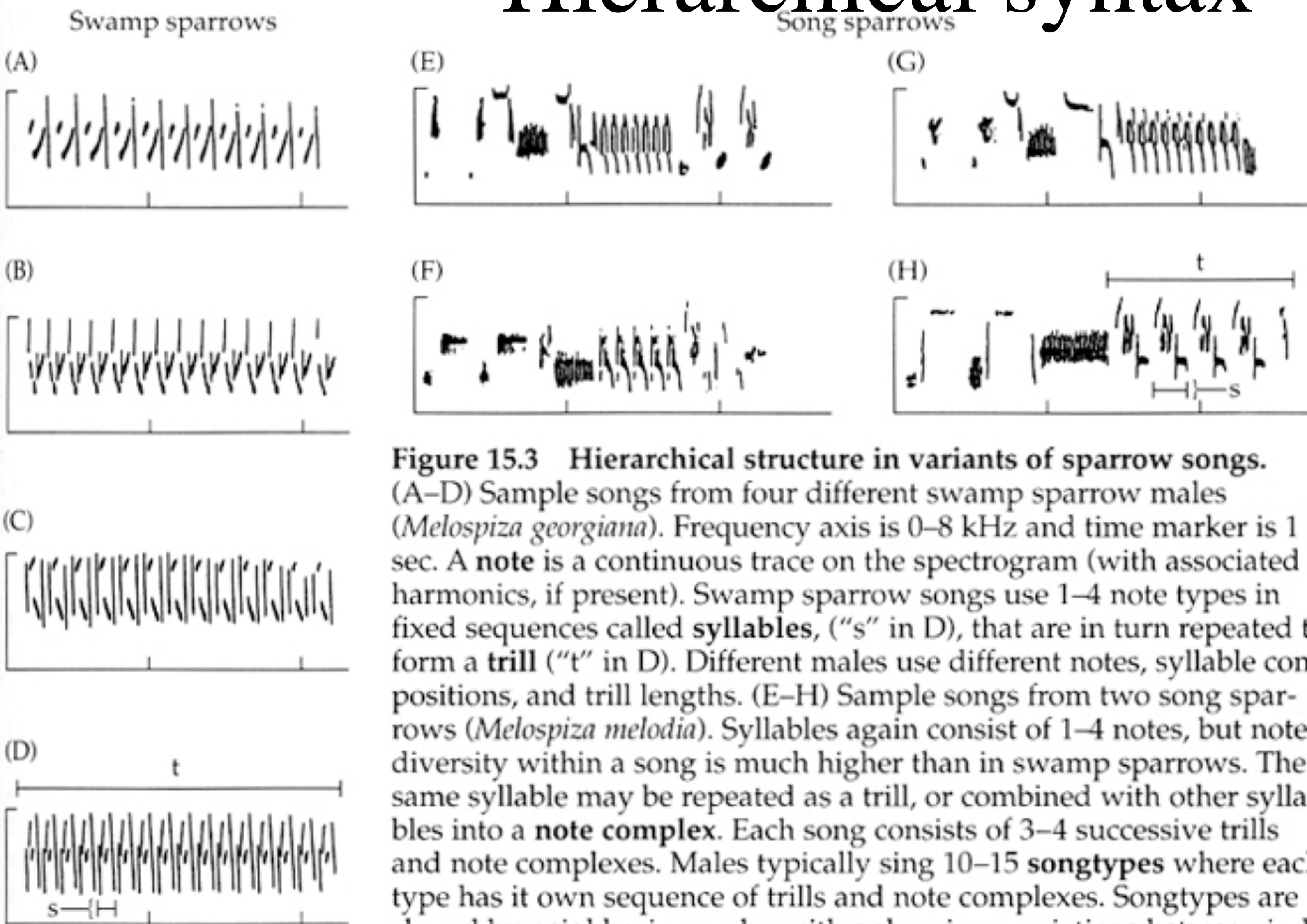
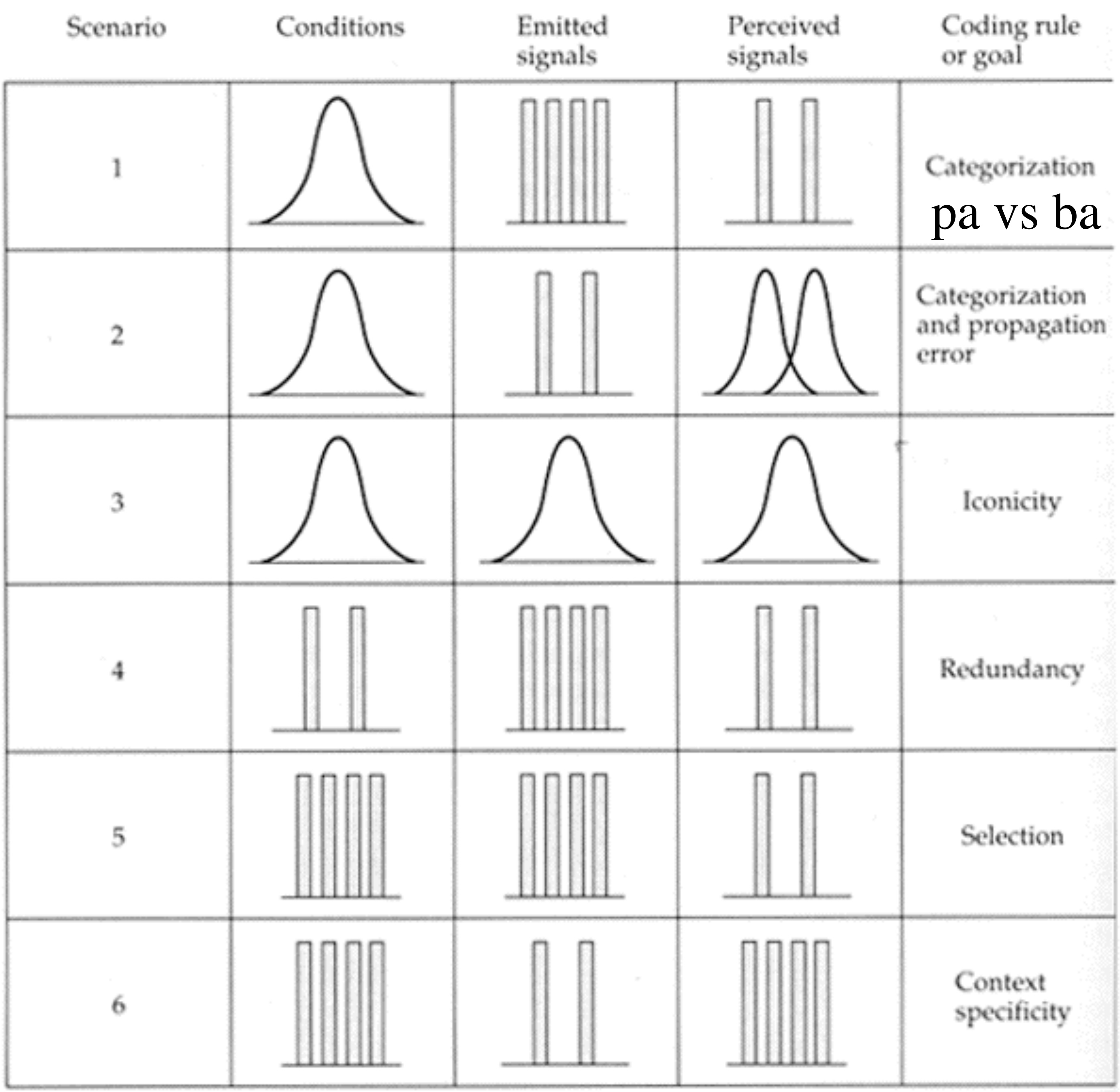


Figure 15.3 Hierarchical structure in variants of sparrow songs. (A–D) Sample songs from four different swamp sparrow males (*Melospiza georgiana*). Frequency axis is 0–8 kHz and time marker is 1 sec. A **note** is a continuous trace on the spectrogram (with associated harmonics, if present). Swamp sparrow songs use 1–4 note types in fixed sequences called **syllables**, ("s" in D), that are in turn repeated to form a **trill** ("t" in D). Different males use different notes, syllable compositions, and trill lengths. (E–H) Sample songs from two song sparrows (*Melospiza melodia*). Syllables again consist of 1–4 notes, but note diversity within a song is much higher than in swamp sparrows. The same syllable may be repeated as a trill, or combined with other syllables into a **note complex**. Each song consists of 3–4 successive trills and note complexes. Males typically sing 10–15 **songtypes** where each type has it own sequence of trills and note complexes. Songtypes are shared by neighboring males with only minor variations between individuals in note shape and number of notes per syllable. Songs E and F are different song types from one male, and G and H are the corresponding song types from a neighbor. (From Marler and Peters 1988.)

Coding schemes



Rule

Group recognition

Iconic aggressive signals

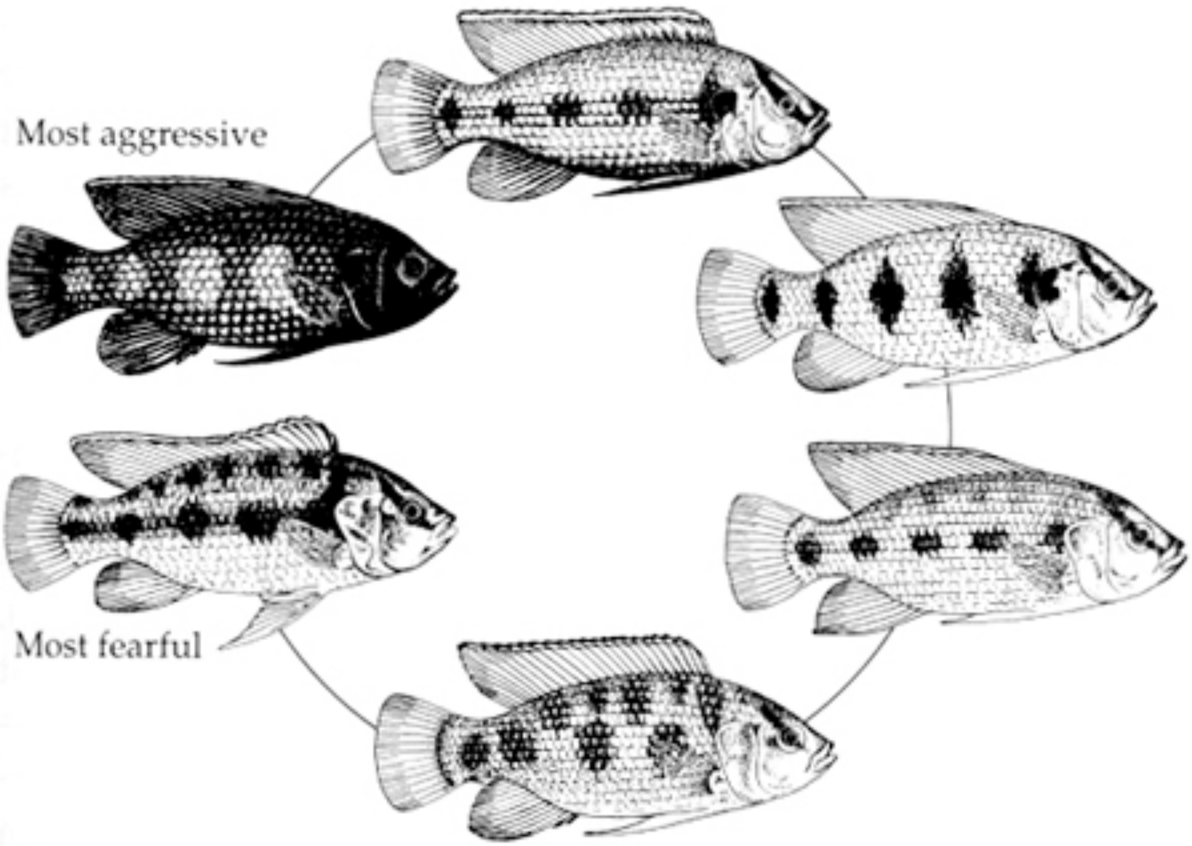


Figure 15.12 Iconic agonistic signals in cichlid fish. Examples from a continuous range of spotting patterns in the cichlid *Hemichromis fasciatus*. Fish regulate the pattern by moving pigment within melanophores in the skin. In this figure, a clockwise movement shows an increasing likelihood that the displaying fish will flee or hide; a counterclockwise movement shows an increasing likelihood that a fish will attack. (After Wickler 1964.)

Compound coding schemes

- Combination mapping
  - Assign different combinations of signal parameters to each alternative condition for each question
  - Inefficient if there are many conditions or questions
- Parameter mapping
  - Variants of signal parameter A to conditions for question A, variants of B to conditions B
  - e.g. body size covary with pitch, energy reserves covary with calling rate
- Hierarchical mapping
  - Individual differences denote individual and mean differences denote group or species

Tamarin group calls

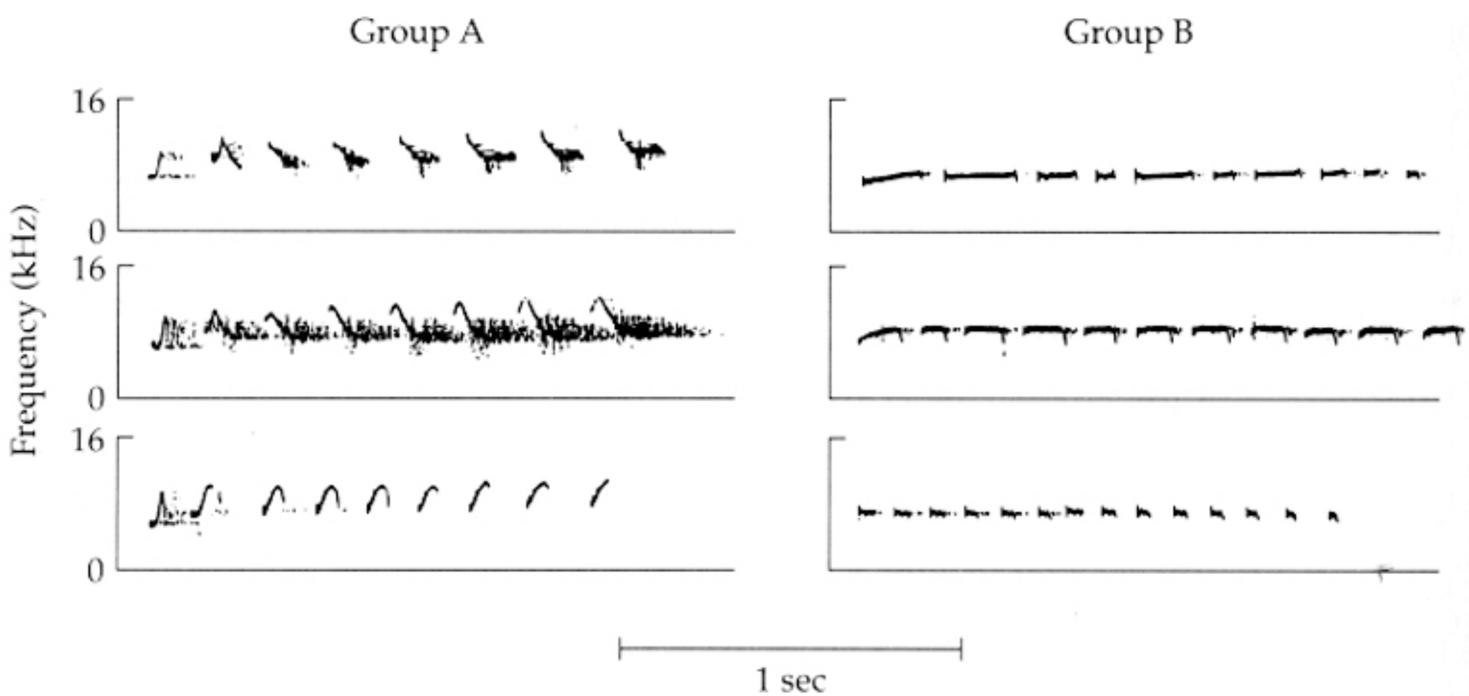


Figure 15.7 Group and individual signatures in calls of red-chested tamarins (*Saguinus labiatus*). Spectrograms of long calls of three individuals in Group A (left) and three individuals of Group B (right). Frequency axis indicates 0–8 kHz; the time marker represents 1 sec. Note similarities in the structure of long calls within each group and the slight variation around that group pattern, conferring individual signatures. Statistical analysis shows that different acoustic features are used to code for group versus individual identities. (From Maeda and Masataka 1987.)

Inferring sender coding schemes

- For discrete conditions and discrete signals, use contingency table analysis
- For discrete conditions and continuous signals, use discriminant function analysis
- For continuous signals and uncertain conditions, use clustering or principle component analysis

Inferring receiver coding schemes

- Determine how receiver categorizes the set of signal variants
  - Present alternatives in operant conditioning paradigm to determine which are perceived as same or different
  - Use habituation-dishabituation experiment
- Determine which condition is associated with each category by the receiver

Signal function and coding

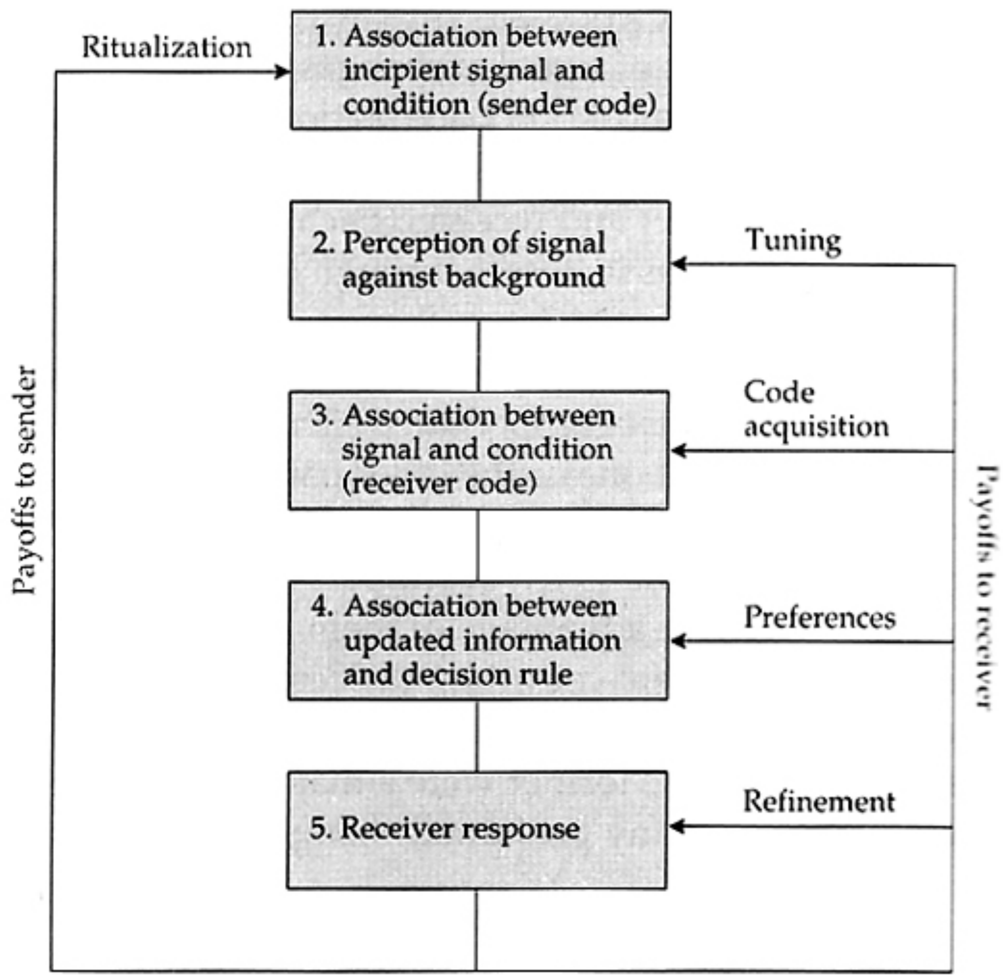
- Binary assignment
  - e.g. sex label, mated vs unmated
  - need only two signals
- Binary recognition
  - decide own vs other, e.g. offspring recognition
  - need many signals
  - Receiver needs template to match

Signal function and coding

- Binary comparison
  - opponent fighting ability, threshold mate choice, best-of-n mate choice
  - often use continuous signals with threshold
  - must compare two values and make judgment
- Manifold decisions (many possible answers)
  - iconic rules - Honeybee language
  - manifold recognition requires pairwise associations

Signal Evolution

Figure 16.1 A model of the process of signal evolution. Signal evolution begins with the association between an incipient signal (such as an unintentional sender cue) and a condition. Receivers must be able to perceive the cue, and recognize its association with the condition. Receivers then incorporate the information into a decision rule and a response. If receivers benefit from their response, they will fine-tune their sensitivity, recognition code, decision rule, and response. If senders benefit from the response, the cue will be modified via ritualization to maximize information transfer and transformed into a true signal.



Signal Ritualization

- Refinement of an inadvertent cue into a signal
- Requires fitness benefits to sender
- Involves
  - Simplification or reduction of number of components
  - Exaggeration of remaining components
  - Repetition of the display
  - Stereotypy during repeated renditions
- Leads to coevolution between receiver and sender
- May lead to emancipation of signal from condition that gave rise to original cue

Ritualized preening in duck courtship

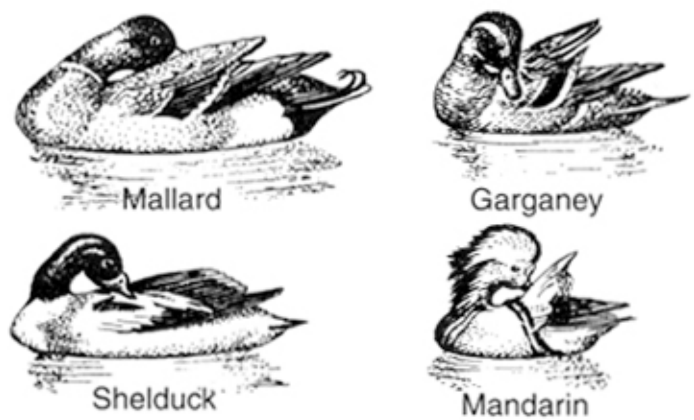


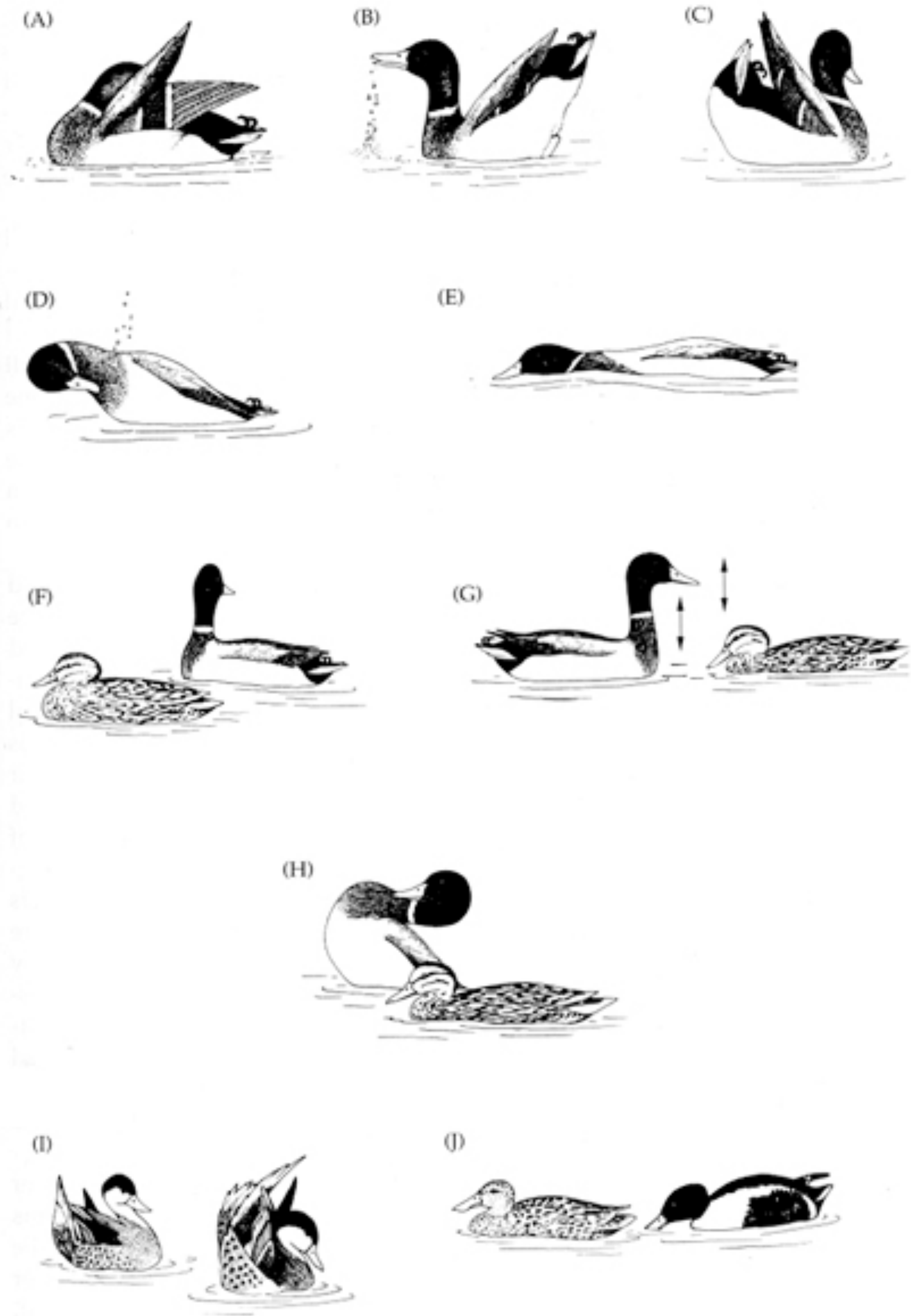
FIGURE 19.8 Mock preening by courting male ducks, a display thought to have evolved from displacement preening. The movements emphasize the bright markings on the wings. (Modified from N. Tinbergen 1951.)

Shelduck preens in conflict situations, mallard preening is partially ritualized during courtship, garganey and mandarin ducks simply point to colored wing patches

Ritualized courtship in ducks

Mallards use 8 displays

Bahama pintail and shoveler use 1 or 2 displays

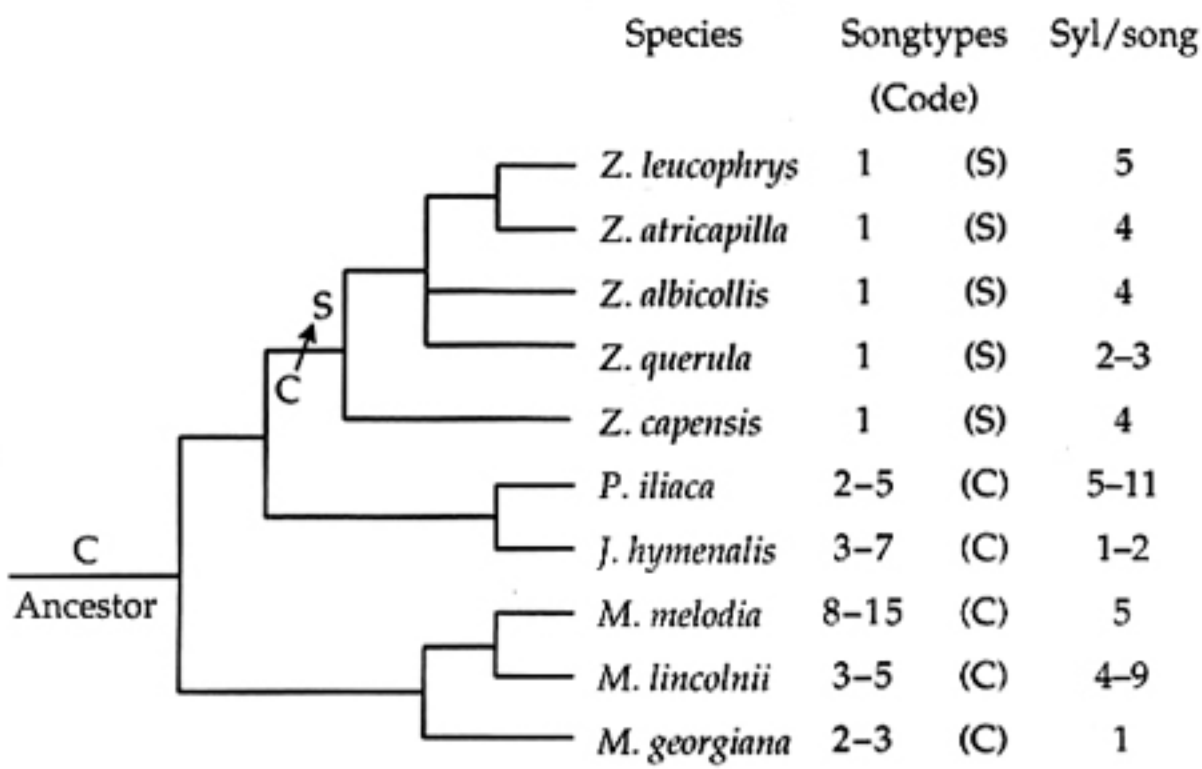


The comparative method

- Goal: infer trait evolution using behavior of extant species
- Derive phylogenetic tree from independent data
- Assign trait values to ancestral nodes by minimizing the number of possible changes, i.e. use parsimony
- Deduce where evolutionary change must have occurred

Repertoire evolution in sparrows

Figure B Phylogenetic tree of some Emberizine sparrow species based on allozyme data. Genera are *Zonotrichia*, *Passerella*, *Junco* and *Melospiza*. S = simple song repertoire; C = complex repertoire.



Song evolution in Oropendolas

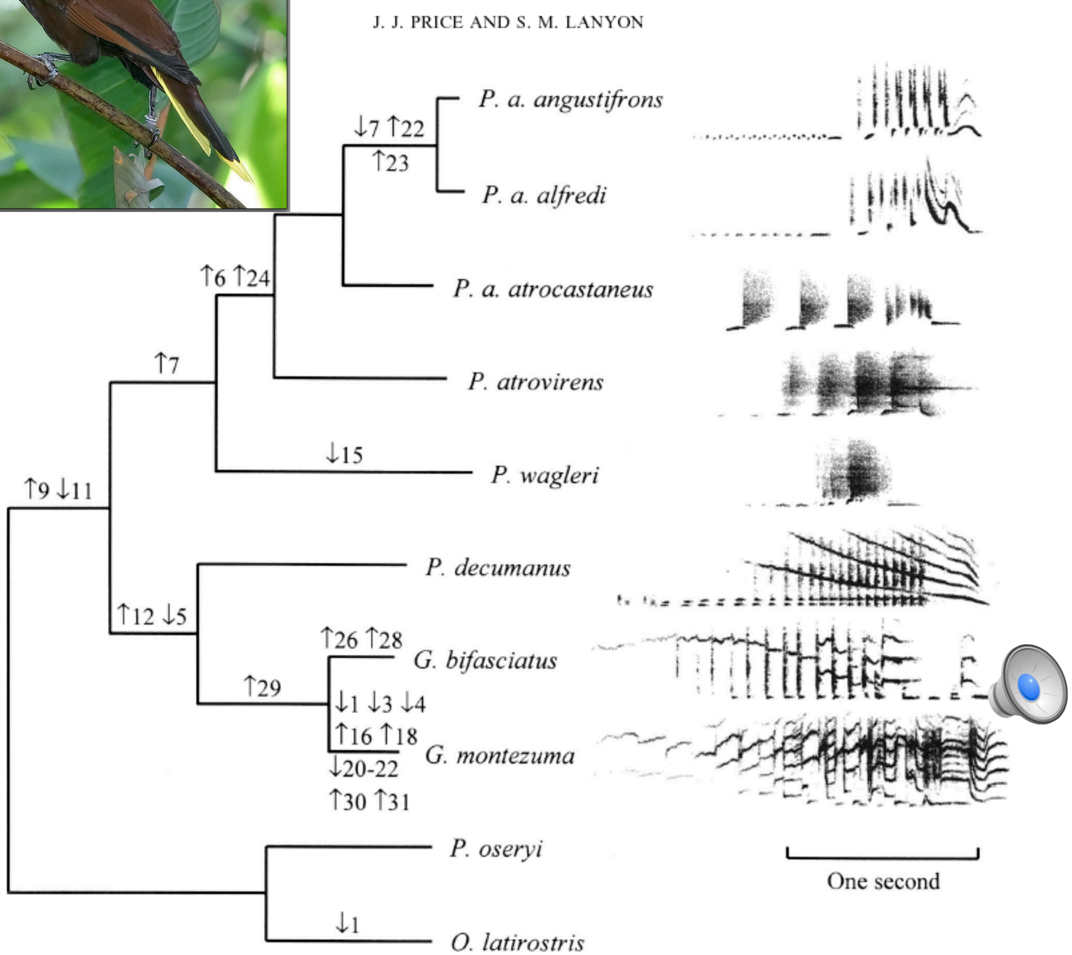
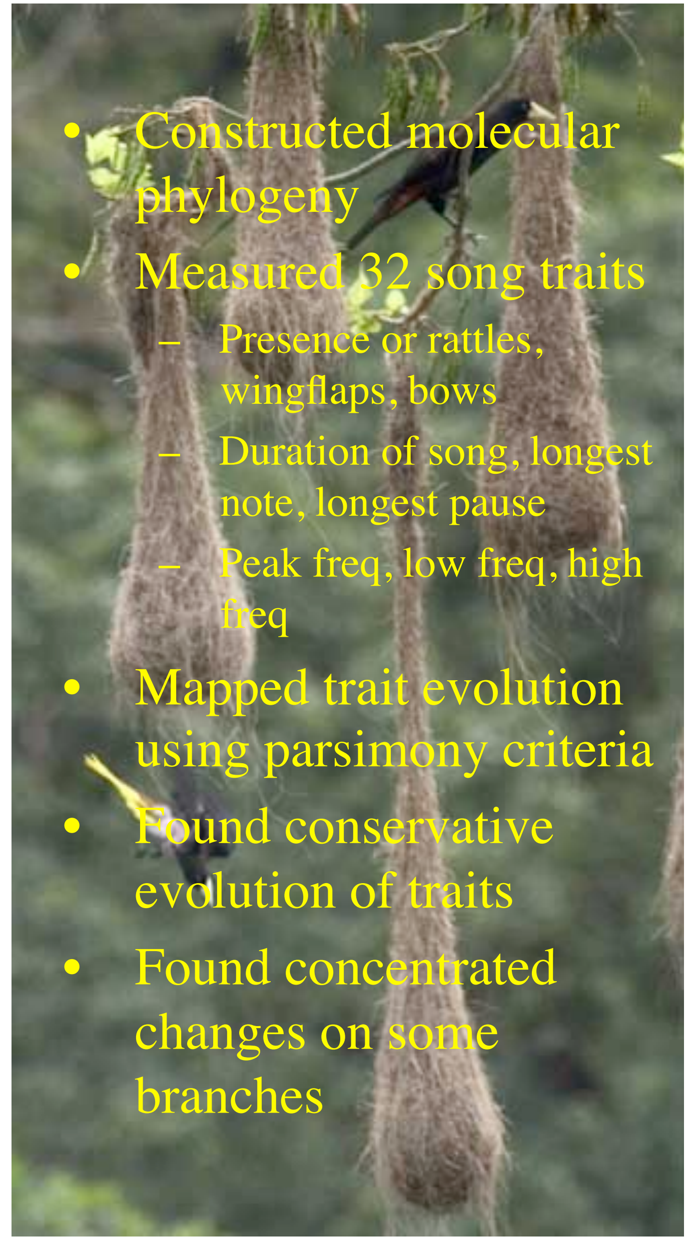


FIG. 2. Unambiguous evolutionary changes in oropendola songs reconstructed on the molecular tree. Arrows and character numbers on branches show the gain/increase (up arrows) or loss/decrease (down arrows) in particular song characters. Spectrograms show typical song patterns for taxa; those of *P. oseryi* and *O. latirostris* are not shown because these species have multiple species-typical songs. Subspecies of *P. decumanus* are collapsed into a single branch because their songs did not differ in any consistent way. Changes at the base of the *Psarocolius* group are supported by additional comparisons to cacique (*Cacicus*) taxa. Branch lengths on the tree reflect molecular changes.

Price and Lanyon. 2002. Evolution 56:1514-1529.

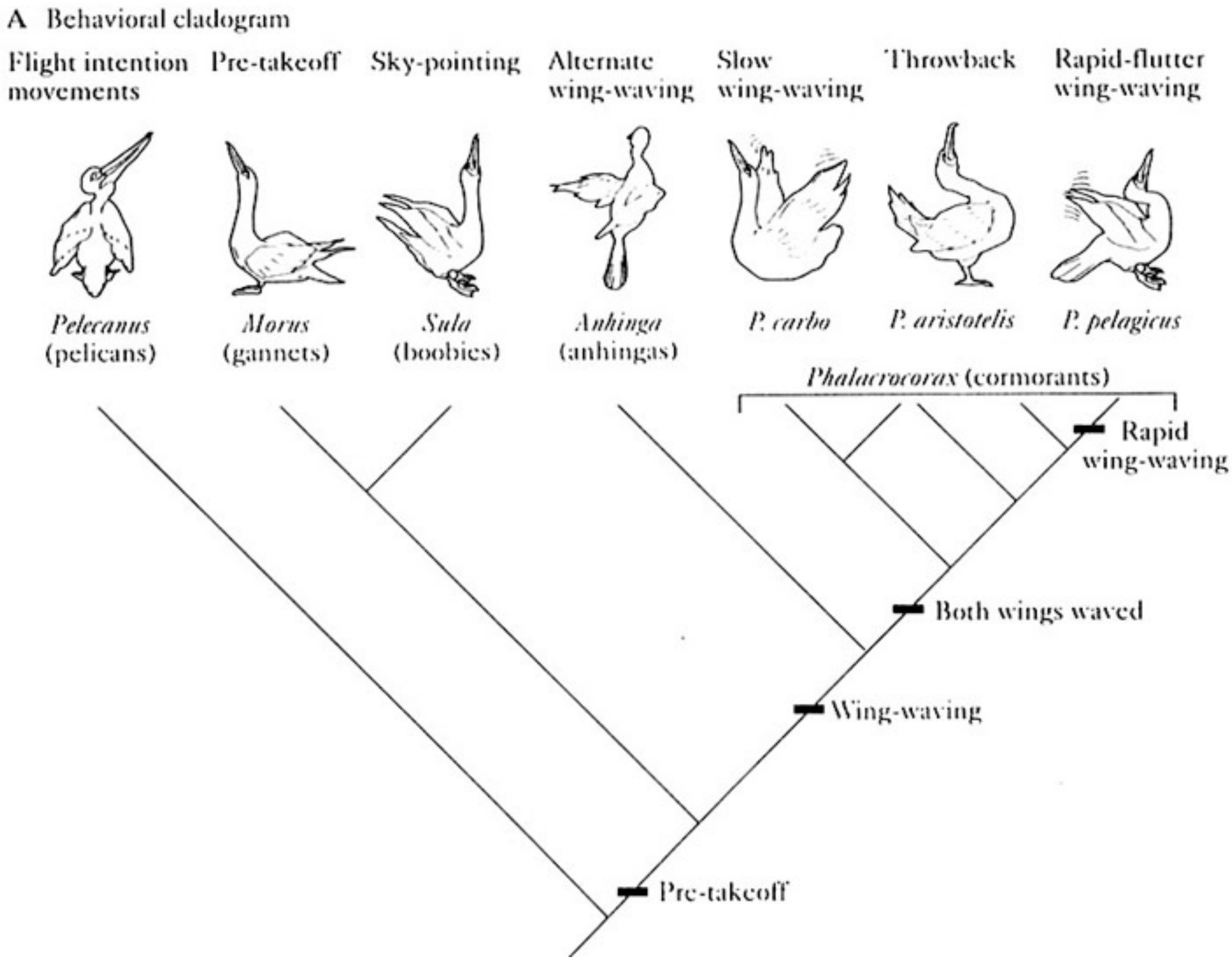


- Constructed molecular phylogeny
- Measured 32 song traits
  - Presence or rattles, wingflaps, bows
  - Duration of song, longest note, longest pause
  - Peak freq, low freq, high freq
- Mapped trait evolution using parsimony criteria
- Found conservative evolution of traits
- Found concentrated changes on some branches

Sender precursors of visual signals

- Intention (preparatory) movements
- Motivational conflict
- Autonomic processes with visual components
- Co-option from other displays

Flight intention and courtship in pelecaniforms



Food advertisement and pheasant courtship displays

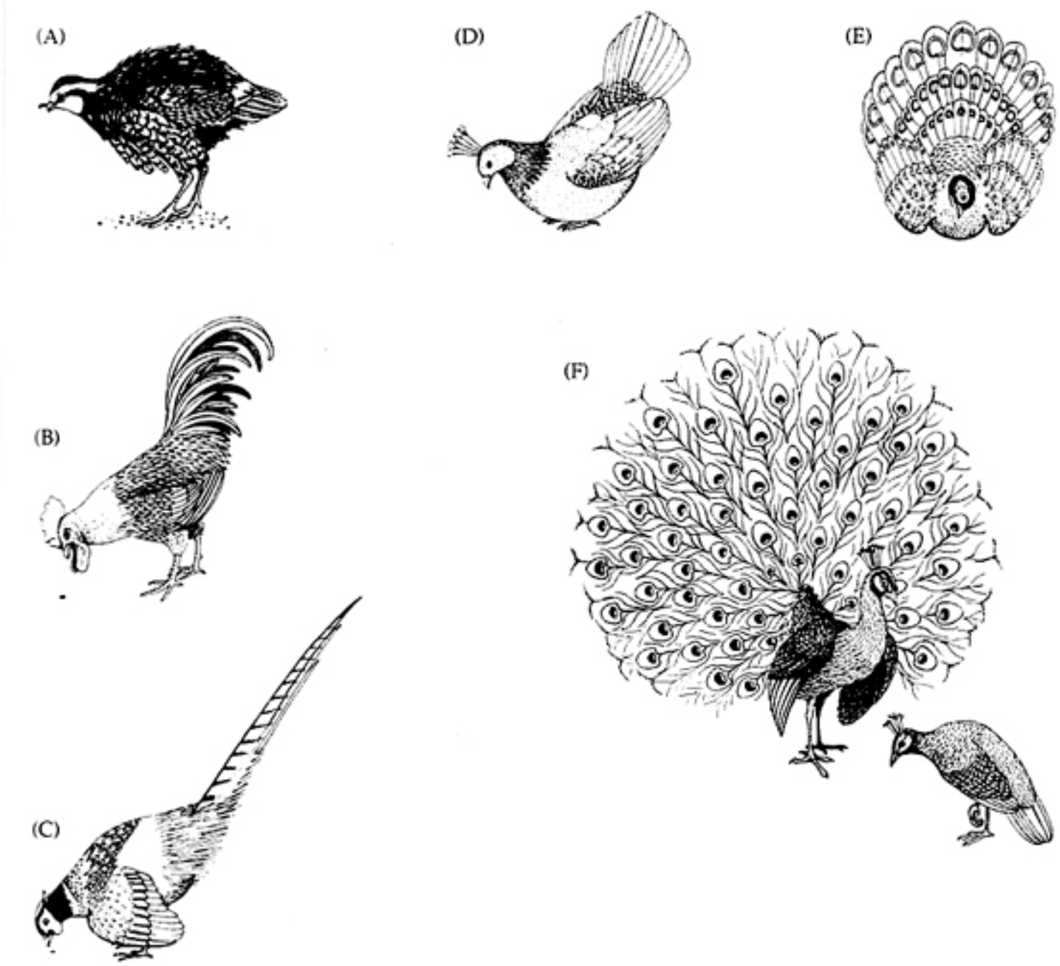
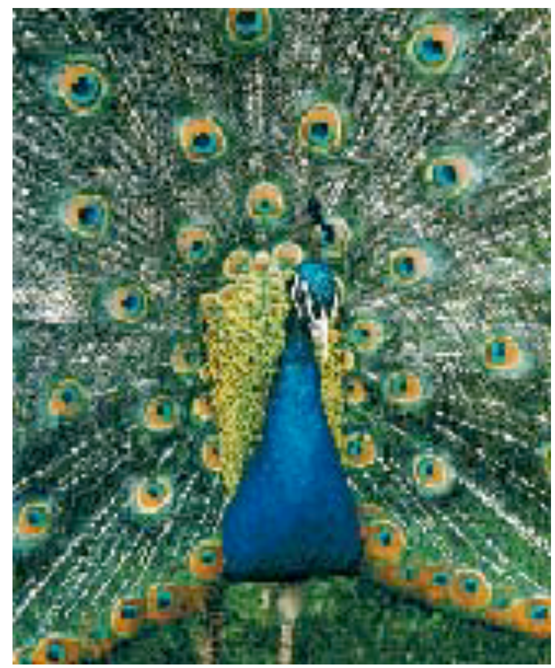
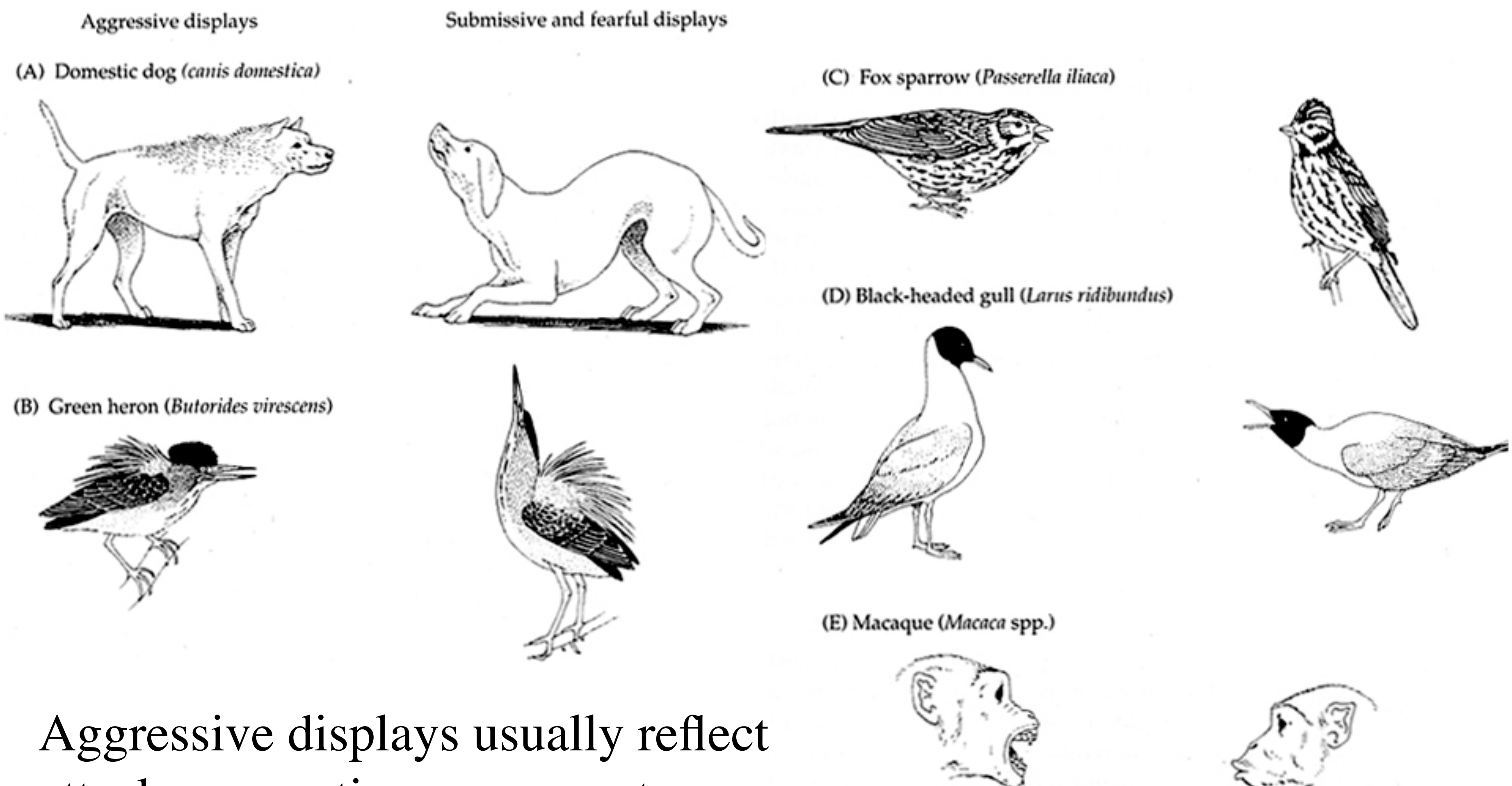


Figure A Degrees of ritualization in the courtship displays of pheasants (Phasianidae) from a food-advertising source. (After Brown 1975; Schenkel 1956.)

Males give food calls and feed mates in Bobwhite quail

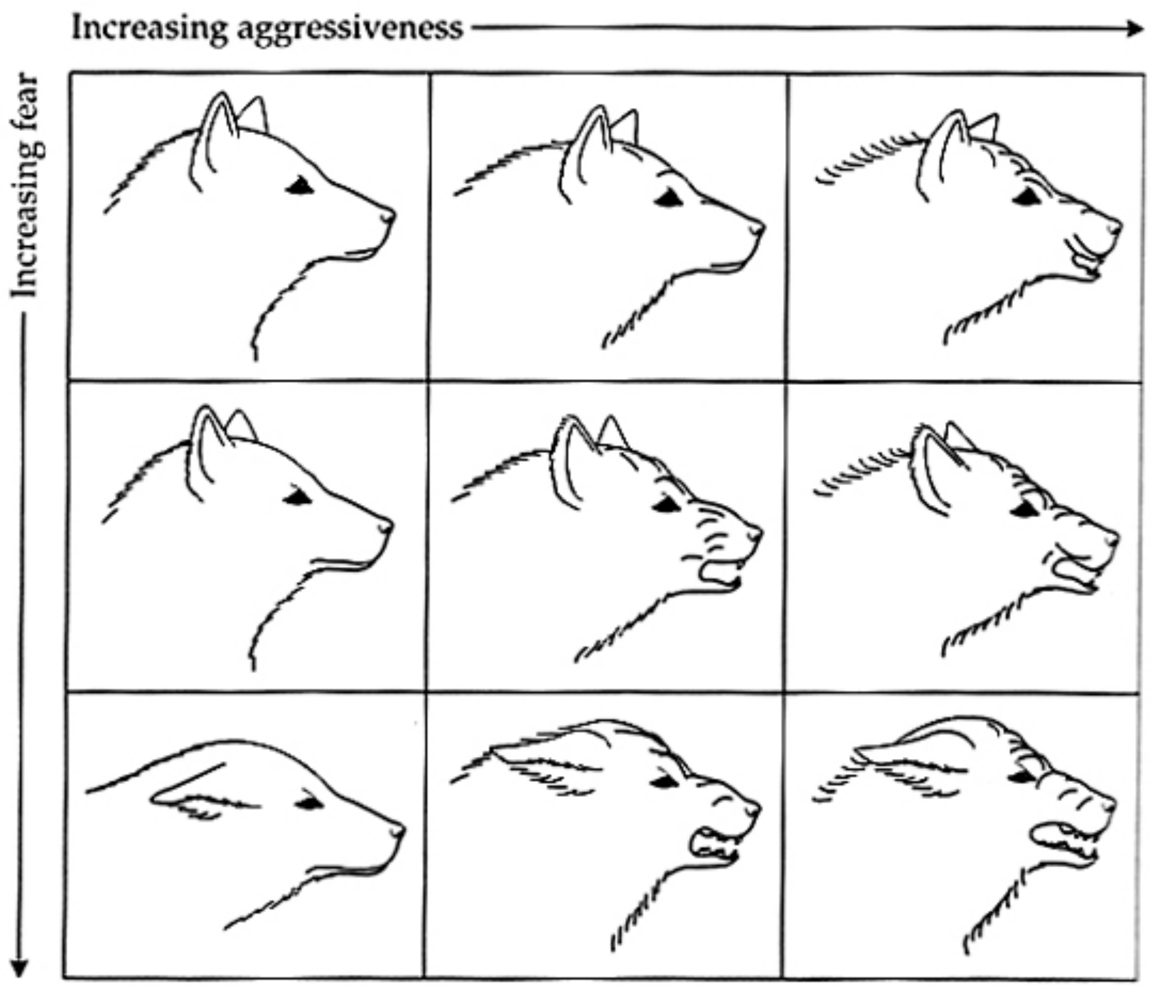


Intention movements and antithetical displays

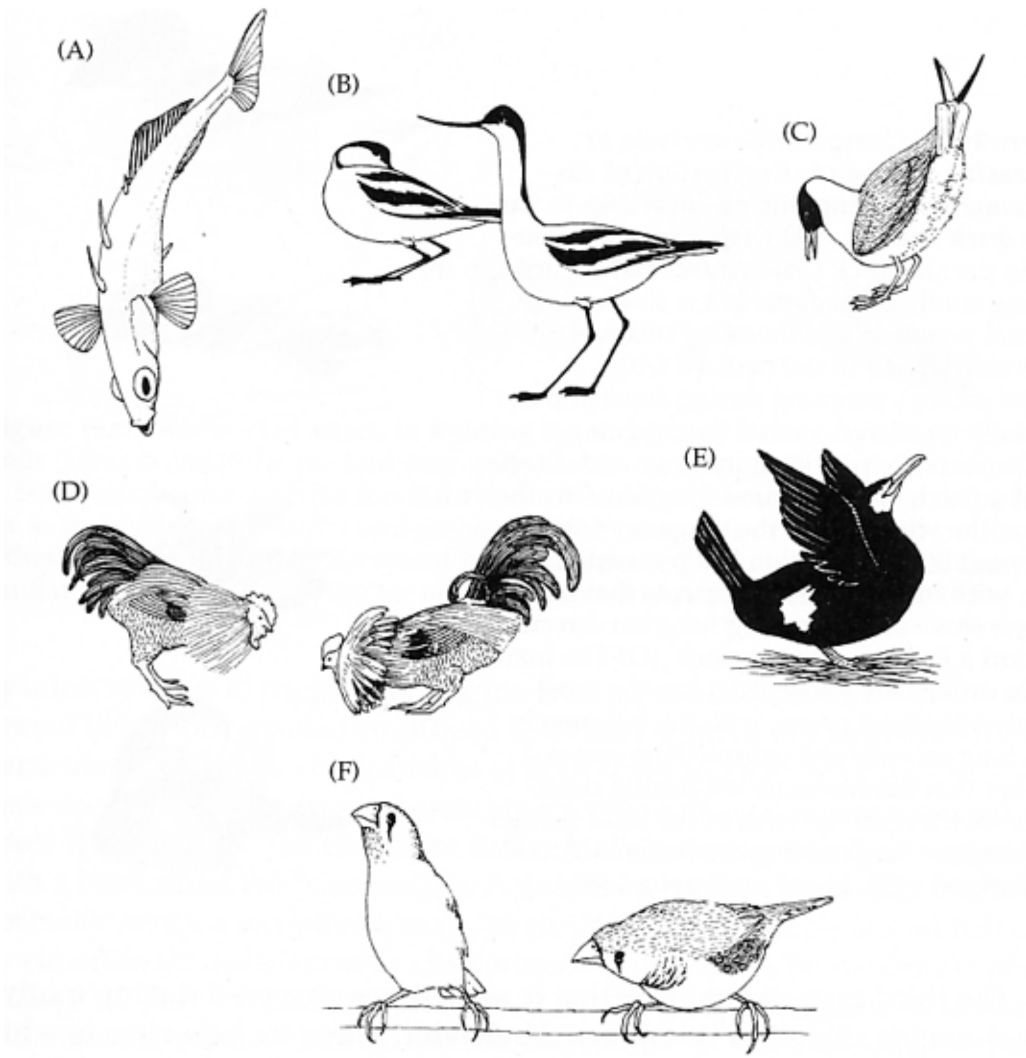


Aggressive displays usually reflect attack preparation movements

Motivational conflict in wolves



Displacement Acts



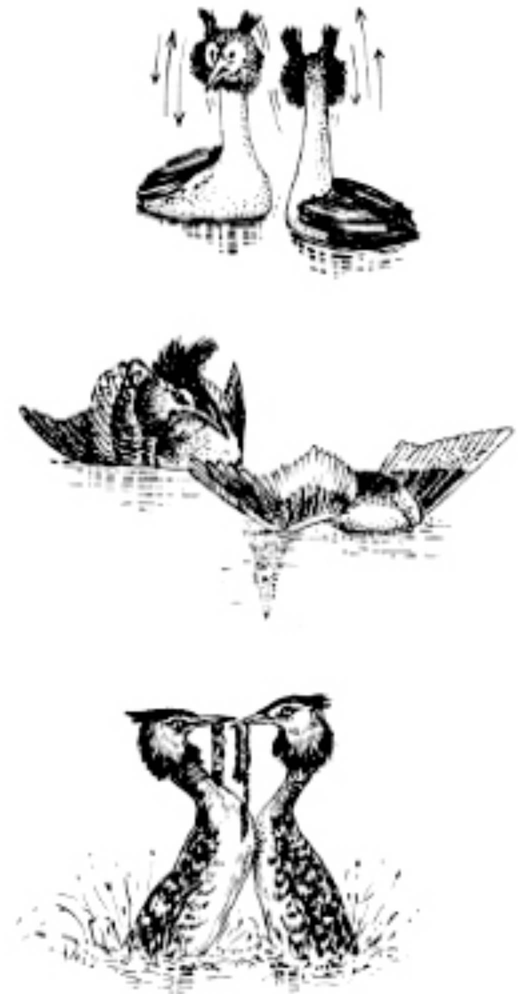
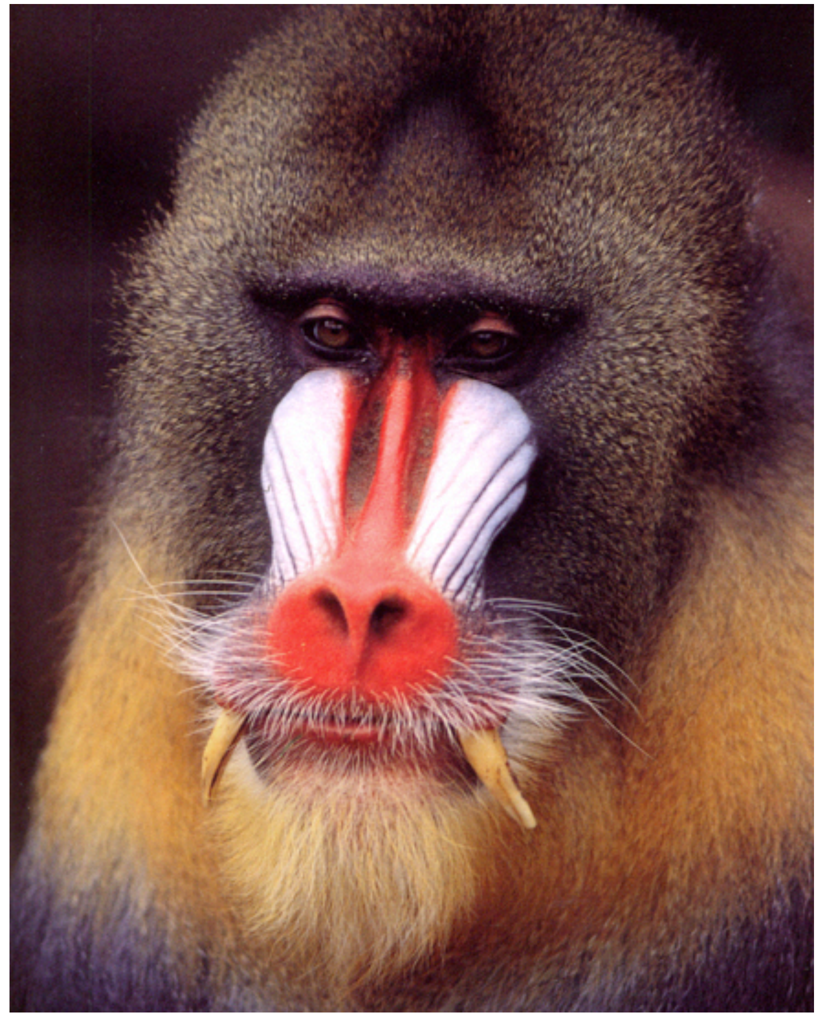


FIGURE 19.9 Courtship in the great crested grebe. This part of the courtship ceremony, the penguin dance, evolved from displacement nest building. The mates dive for weeds to present to one another.

Autonomic responses can be coopted as displays

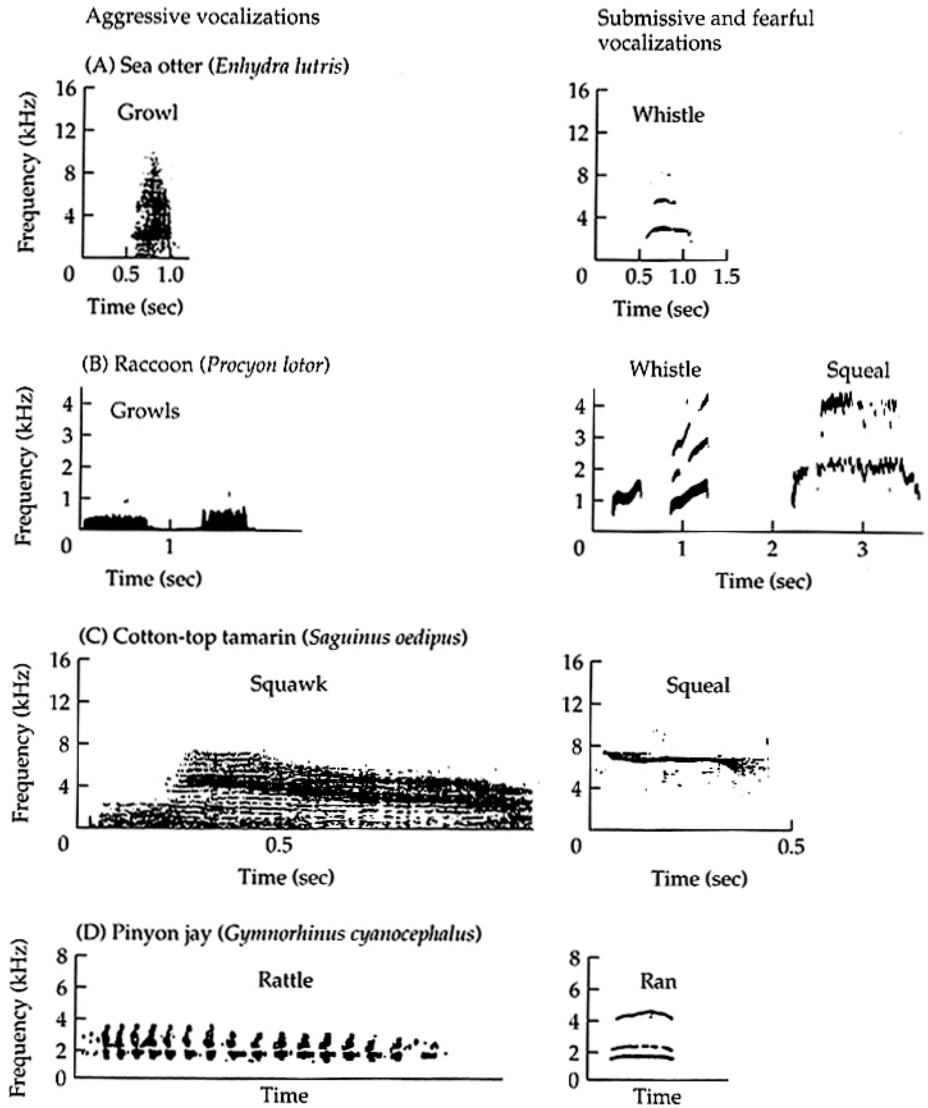


Sender precursors of auditory signals

- Respiration
  - High tension vocal chords = whistle
  - Low tension = harmonic series
- Locomotory and foraging movements
  - Mosquito mate detection
  - Percussion in beaver, kangaroo rats, woodpeckers
- Visual or tactile courtship displays
  - Aerial dives in woodcock, hummingbirds, manakins
  - Stridulation in orthopterans
- Defensive antipredator acts
  - rattlesnake, click beetle, lizard and salamander hisses

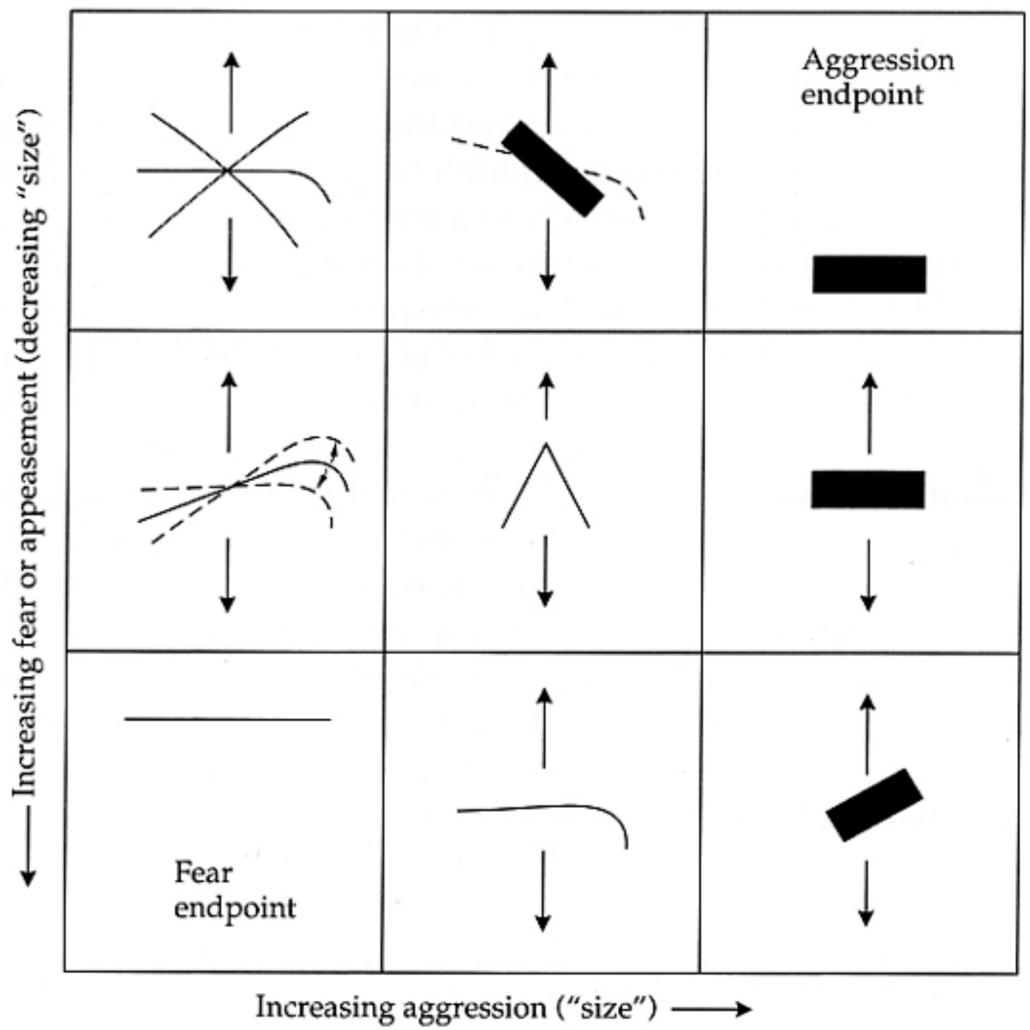
Antithetical vocalizations

Aggressive:
Broad band,
Low frequency



Submissive:
Tonal, high
frequency

Morton’s motivation-structure “rules”



Sender precursors of olfactory signals

- Dietary signals
  - Secondary plant defense compounds
- Reproductive precursors and products
  - Androgens in urine, saliva, sweat (boars)
  - Estrogen and metabolites in female urogenital secretions
- Defensive chemicals
  - Alarm substances (fish, ants, bees and wasps)
- Novel mate attraction pheromones

Bark beetle mating pheromones

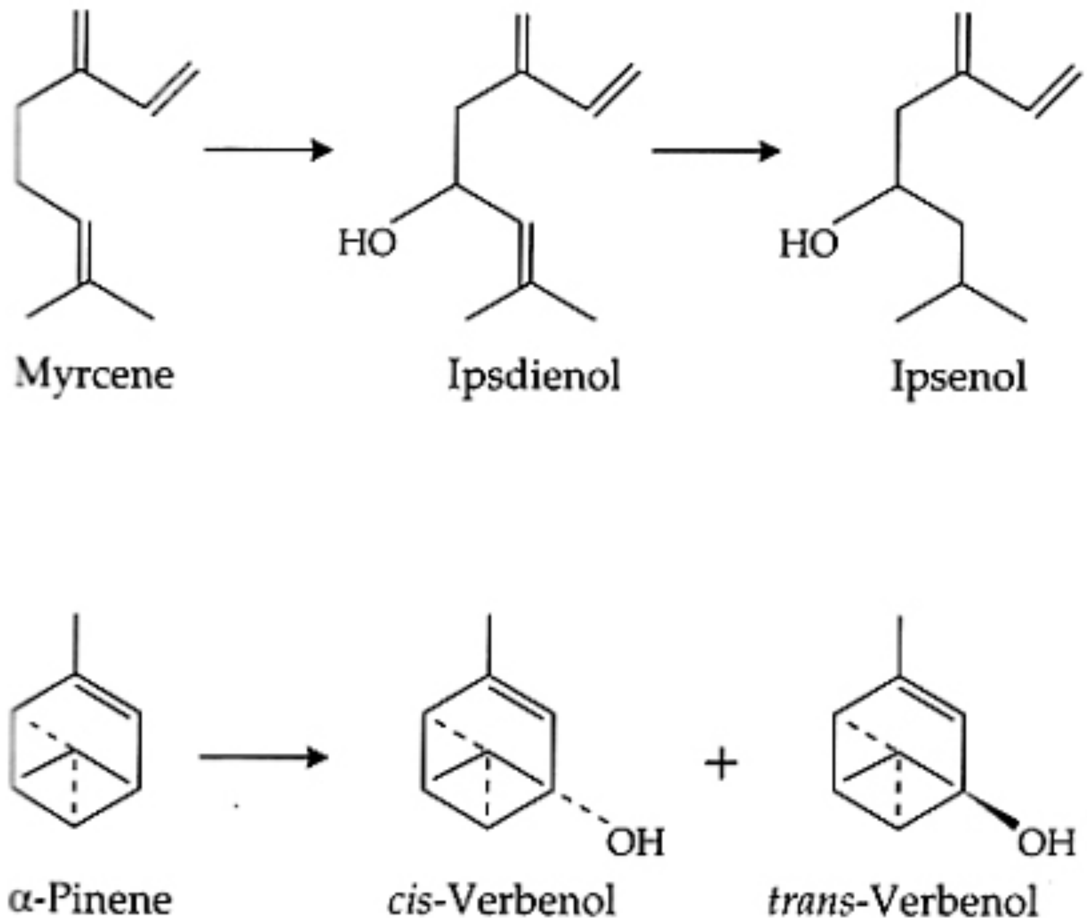
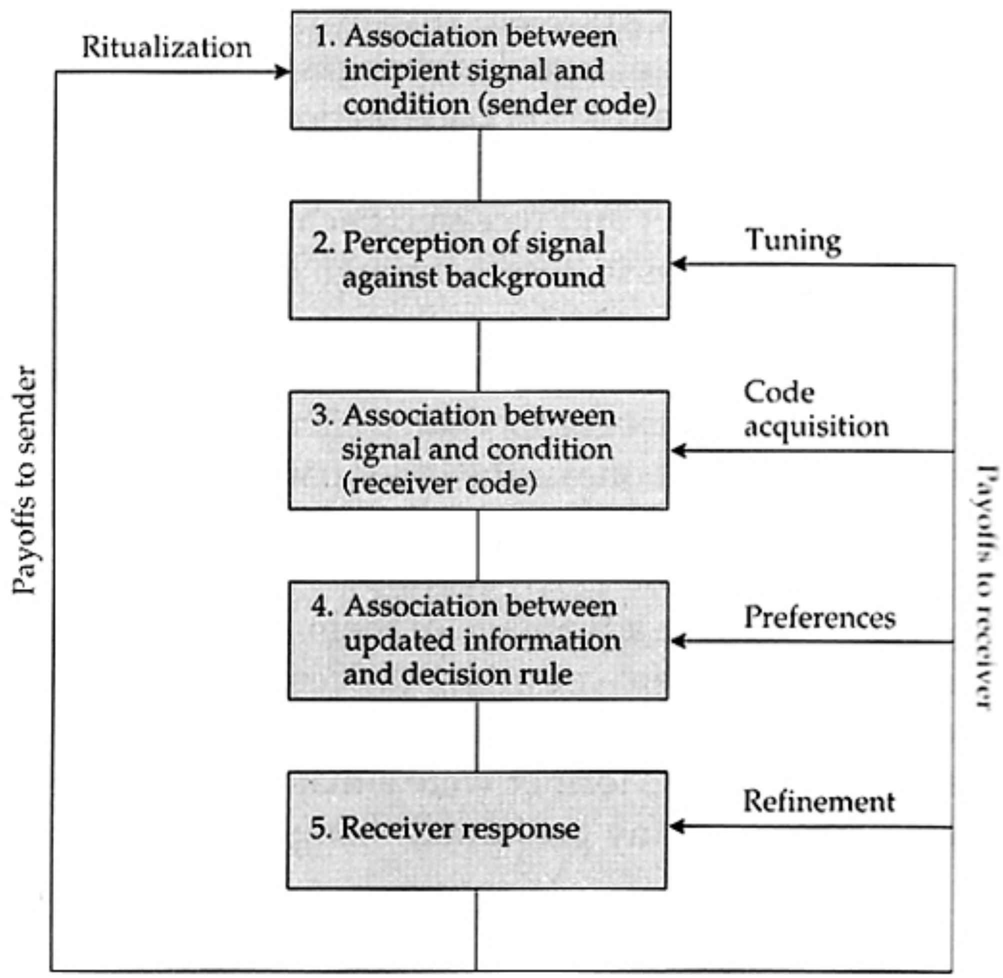


Figure 16.13 Pheromones derived from plant compounds. Proposed pathways for the conversion of plant monoterpenes to the aggregating pheromones of *Ips* bark beetles. Only the male produces ipsdienol and ipsenol. Once he has attracted and mated with a female, both produce verbenol, which deters further arrivals. (After Blomquist and Dillwith 1983.)

Which came first, signal or perception?

Figure 16.1 A model of the process of signal evolution. Signal evolution begins with the association between an incipient signal (such as an unintentional sender cue) and a condition. Receivers must be able to perceive the cue, and recognize its association with the condition. Receivers then incorporate the information into a decision rule and a response. If receivers benefit from their response, they will fine-tune their sensitivity, recognition code, decision rule, and response. If senders benefit from the response, the cue will be modified via ritualization to maximize information transfer and transformed into a true signal.



Receiver bias and feature detectors

- Feature detectors are receiver refinements that improve signal detection in noise
  - e.g. color preferences
  - movement detection
- Feature detectors allow for invariant responses and require no learning
- Provide explanation for sign stimuli and supernormal stimuli

Feature detectors

Spot Slanted line Motion

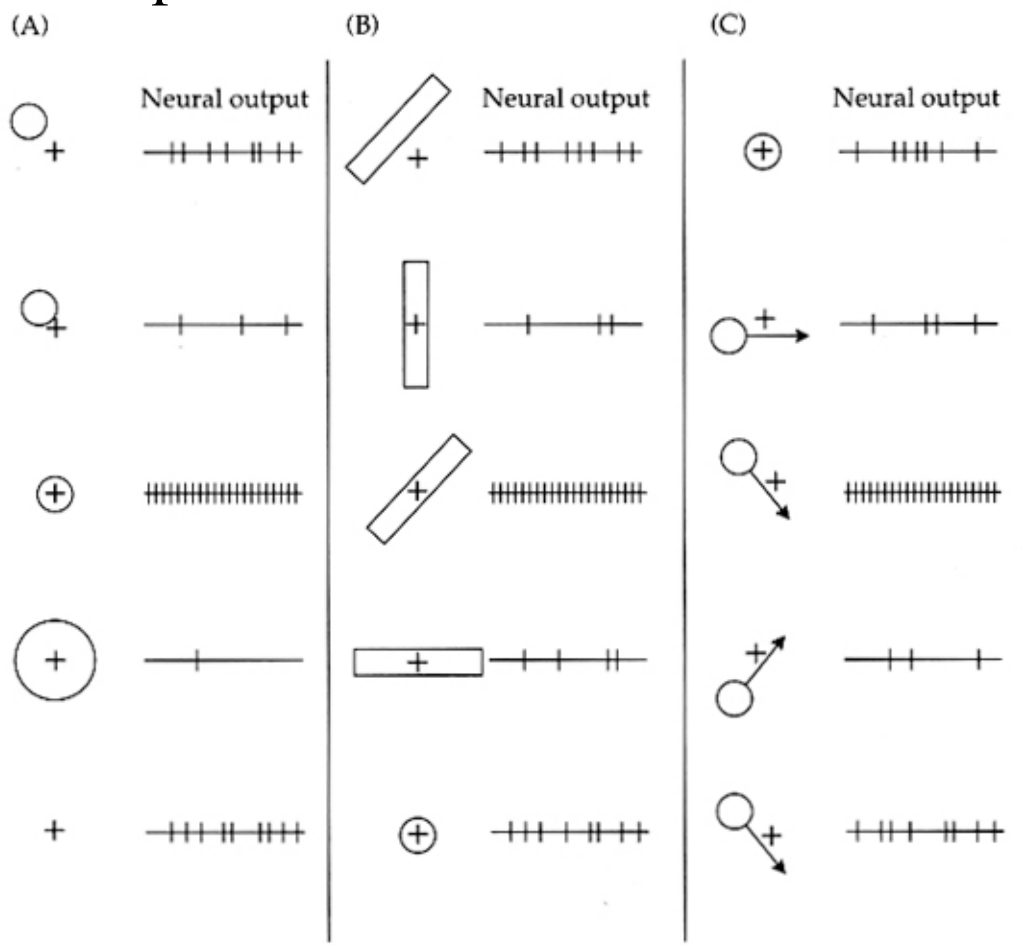
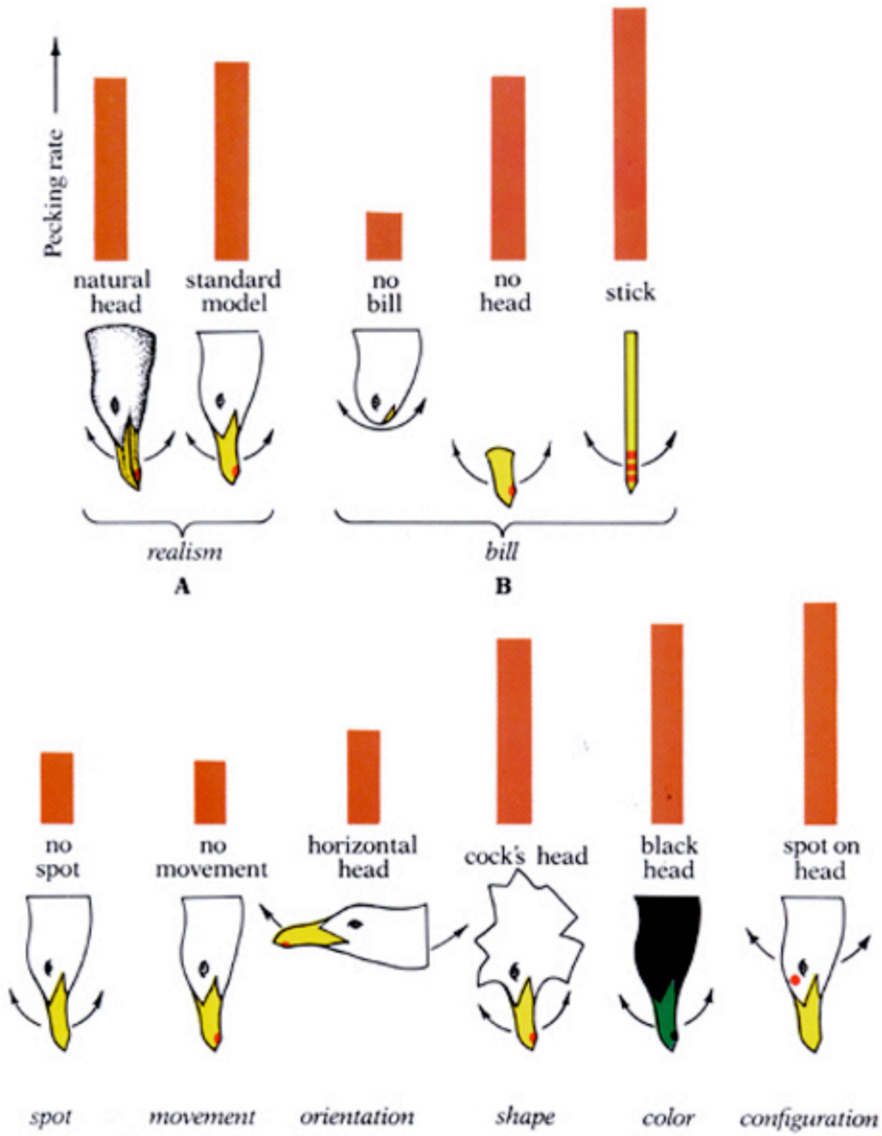


Figure 16.15 Three simple visual feature detectors. A spot detector (A), slanted line detector (B), and motion detector (C) identified in vertebrate eyes by shining light on the retina and recording from nerves associated with single photoreceptors

Innate releasing mechanisms



Herring gull chicks use a moving red spot on bill as a **sign stimulus** to recognize their mother.

A yellow stick with red spots acts as a **super normal stimulus**.

Receiver precursors to signal evolution

- Sensory drive (Endler)
  - Environment influences signal form and receiver design
  - Favors senders giving conspicuous signals
- Sensory bias or exploitation (Burley, Ryan)
  - Receivers have latent preferences, e.g. females like to eat red berries and prefer red-legged males
  - Senders produce signals to exploit this preference

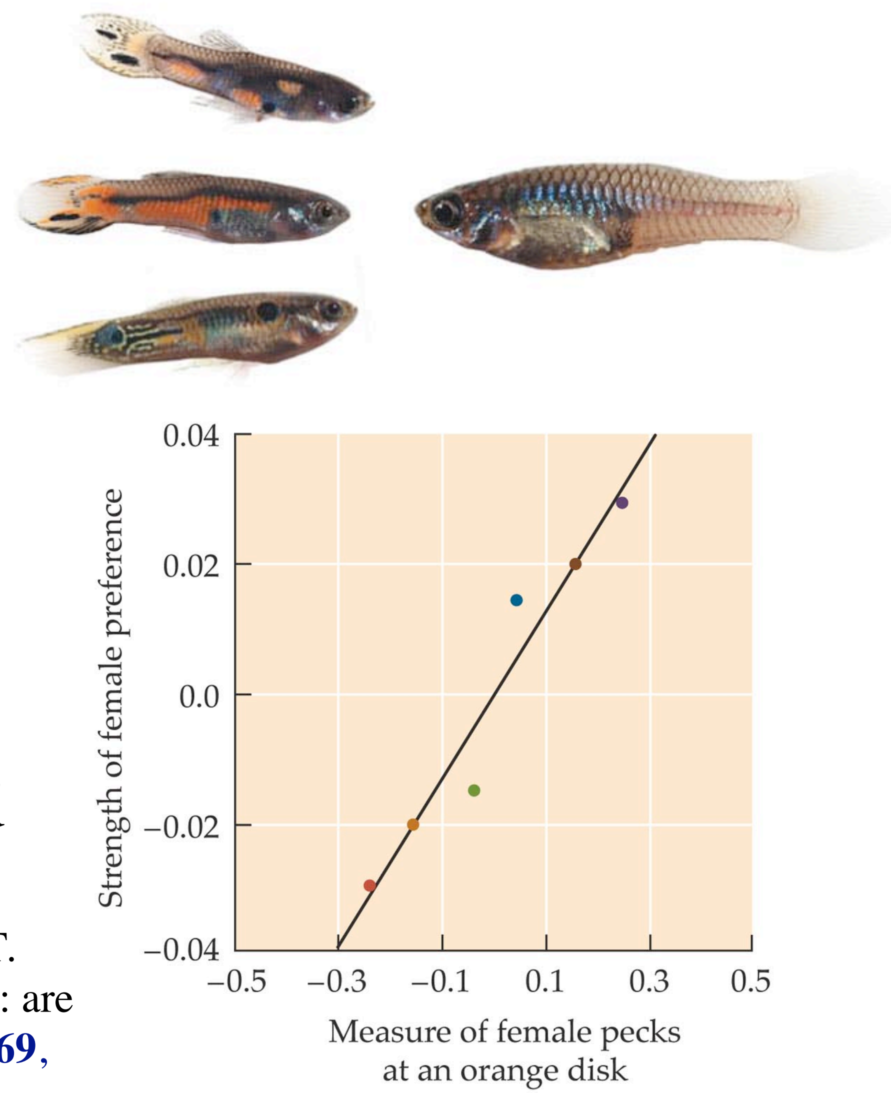
Sensory bias in guppies

(A)

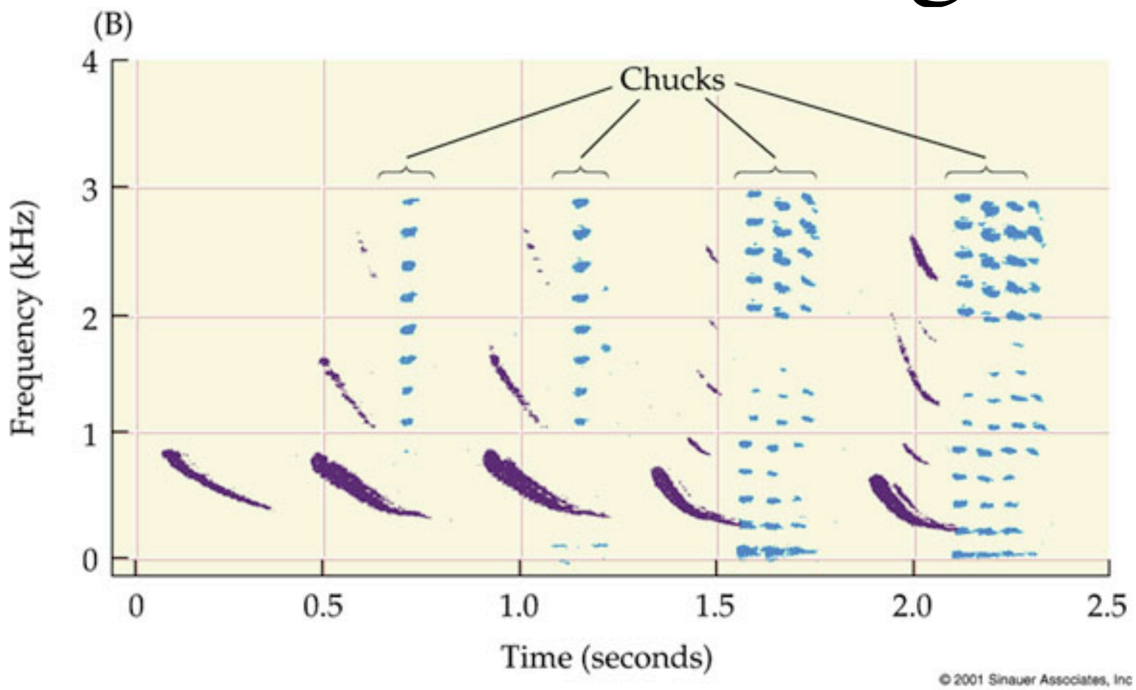
Female guppies prefer orange food items

Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. 2002 A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond.* B **269**, 475–481

(B)



Female choice in Túngara frogs



- Calls consist of ‘whines’ and ‘chucks’
- Females prefer males with deeper chucks
- Chuck frequency constrained by male body size

Sensory exploitation in tungara frogs

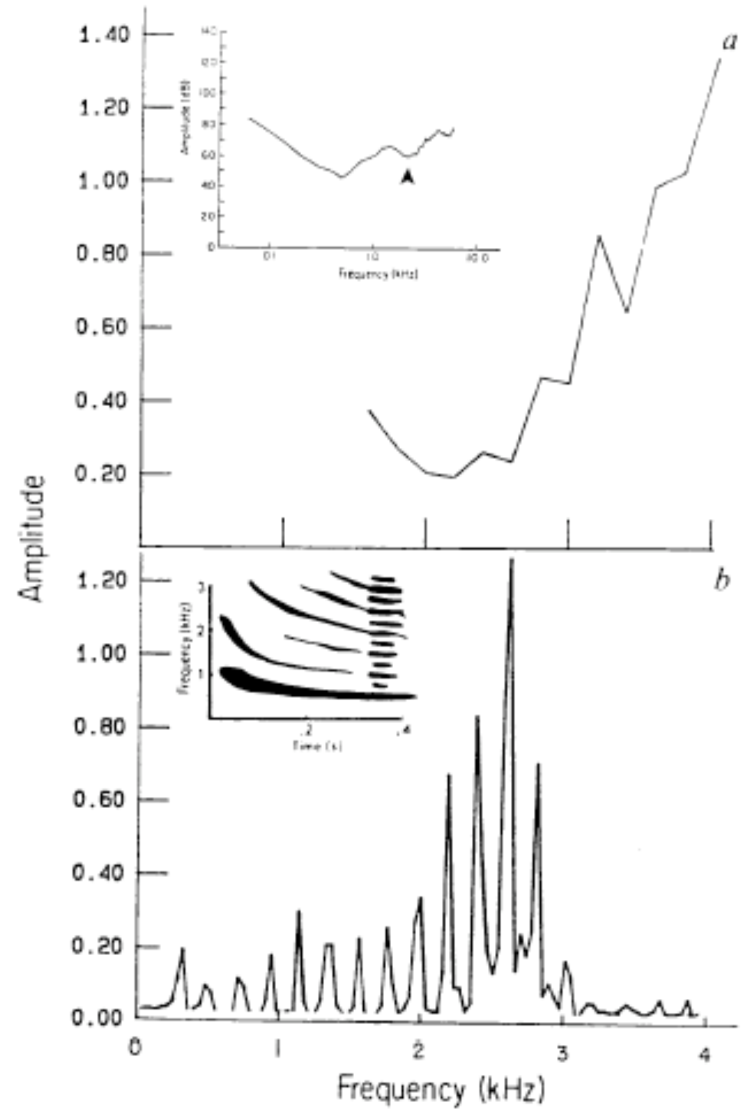


FIG. 1 *a*, The mean audiogram of the basilar papilla of *P. pustulosus* derived from five individuals. Audiograms represent thresholds as a function of frequency, determined for sinusoidal, closed-field stimuli using 1–2 MΩ glass electrodes. The truncation of the audiogram below 1.5 kHz to eliminate influences of amphibian papilla neurons and the slight broadening of the tuning curve resulting from averaging biases the results toward the null hypothesis. Insert, audiogram from a single frog; basilar papilla best frequency is marked by arrow. Male and female audiograms did not differ. *b*, Representative Fourier spectrum of a chuck. Insert, sonogram of a whine plus a chuck.

Sensory bias predicts preference precedes trait evolution