Communication and Vocal Learning

- What is communication?
- Why communicate?
  - Behavioral ecology vs evolutionary biology
  - What information is conveyed?
- When does vocal learning occur?
- Is vocal learning a single trait?

How would you define animal communication?

i.e., what is necessary for animal communication to occur?

Definitions of communication

- Wilson (1975) {sociobiology}
  "..communication occurs when the action of or cue given by one organism is perceived by and thus alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants."

Definitions of communication

- Hailman (1977) {ethology}

  "Communication is the transfer of information via signals sent in a channel between sender and a receiver. The occurrence of communication is recognized by a difference in the behavior of the reputed receiver in two situations that differ only in the presence or absence of the reputed signal… the effect of a signal may be to prevent a change in the receiver's output, or to maintain a specific internal behavioral state of readiness."

Definitions of communication

- Dusenbery (1992) {sensory ecology}
  “The term ‘true communication’ is restricted to cases in which the transmitting organism engages in behavior that is adaptive principally because it generates a signal and the interaction mediated by the signal is adaptive to the receiving organism as well.”

Definitions of communication

- Krebs and Davies (1993) {behavioral ecology}

  "..the process in which actors use specially designed signals or displays to modify the behavior of reactors."

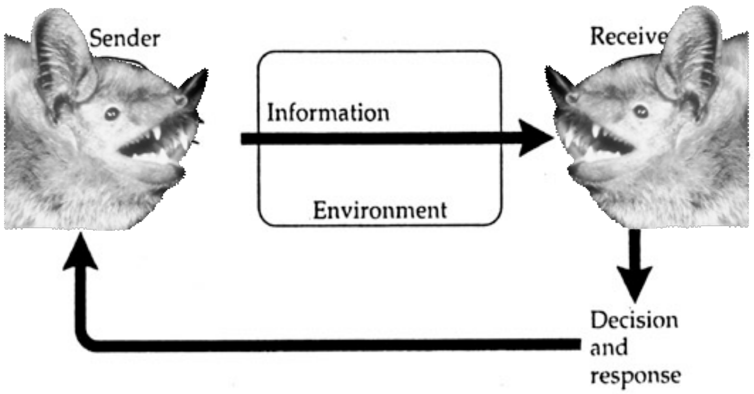
- Kimura (1993) {neuropsychology}

  "The term is used here in a narrower sense, to refer to behaviors by which one member of a species conveys information to another member of the species."

Definitions of communication

- Johnson-Laird (1990) {cognitive psychology}
  “Communication is a matter of causal influence…the communicator (must) construct an internal representation of the external world, and then..carry out some symbolic behavior that conveys the content of that representation. The recipient must first perceive the symbolic behavior, i.e. construct its internal representation, and then from it recover a further internal representation of the state that it signifies. This final step depends on access to the arbitrary conventions governing the interpretation of the symbolic behavior.”

What is communication?



Sender intentionally produces a signal to convey information to a receiver

- Signal must be perceived by a receiver despite attenuation or degradation caused by transmission through the environment
- Signal transmission depends on the sensory modality used (e.g. hearing, vision, smell)
- Receiver must discriminate among signal variants and infer meaning as appropriate

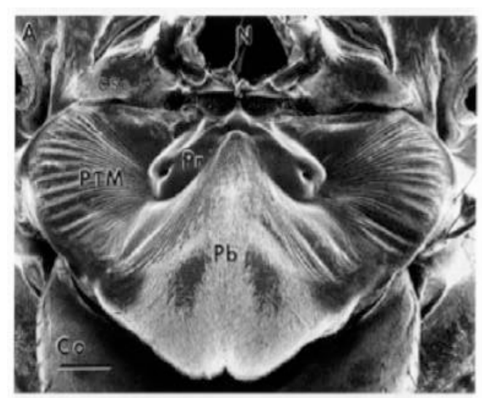
Implications

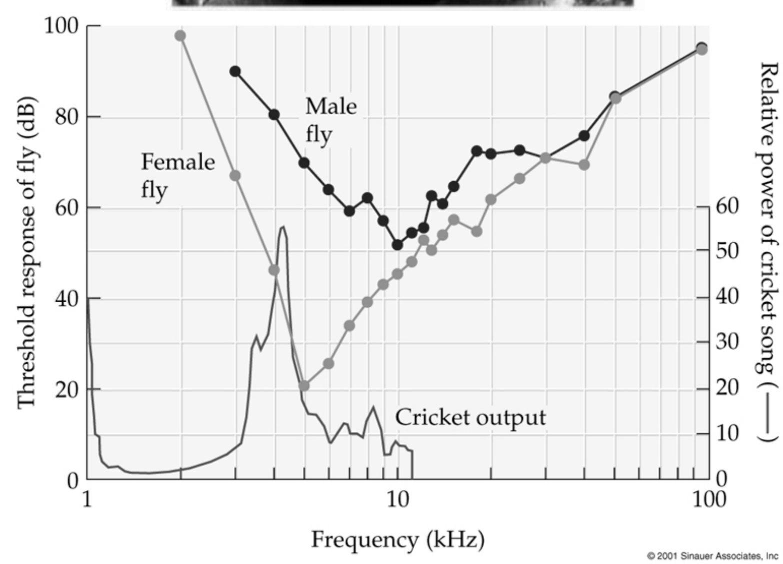
- Communication is never perfect
- Communication evolves when
  - senders create more distinctive signals
  - receivers acquire greater discrimination ability
  - (note that behavioral ecologists rarely think about signal semantics because it is difficult to study what an animal is thinking)
- Which of these will happen depends on the relative costs to sender and receiver as well as constraints on signal production or reception

Sender Costs

- Conspicuousness to predators and parasites
- Energetic costs of signaling
  - High for auditory displays with high duty cycle
- Time lost in display
- Conflict with original function

Exploitation:
Ormia flies parasitize male crickets

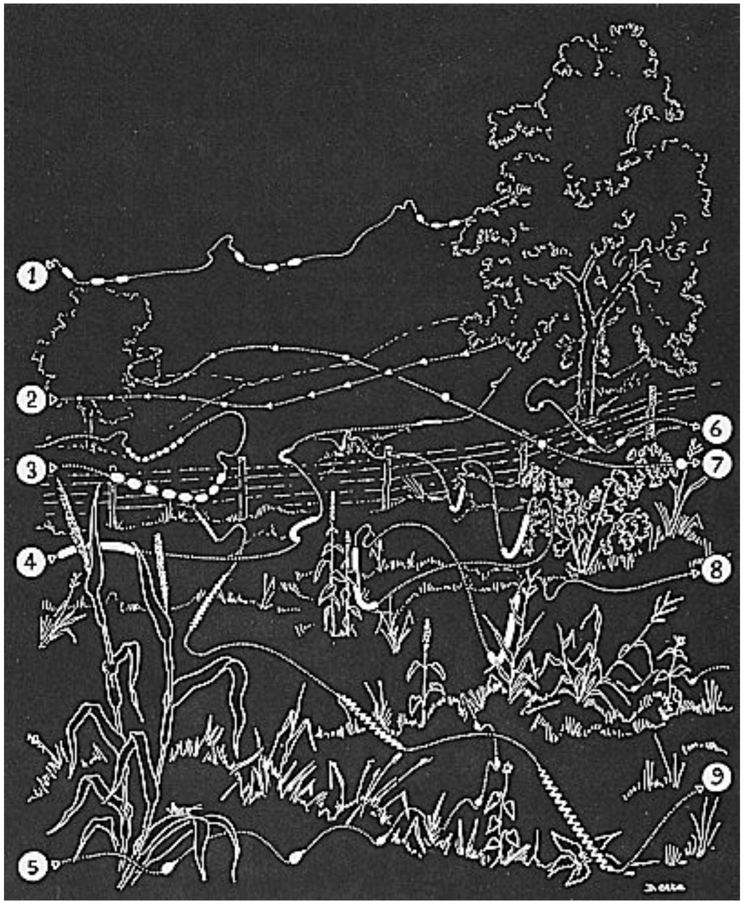




Receiver costs

- Vulnerable to predation while inspecting or comparing signals
  – Choosiness may decline in presence of predators
- Time lost in assessment
- Susceptible to manipulation

Manipulation: Female *Photuris* fireflies mimic *Photinus* males



Above are shown the flashes and flight paths of different species as they would appear in a time-lapse photograph (From: Lloyd, J. E. (1966). Univ. of Michigan Museum of Zoology, Misc. Pub. 130, 1-93)

Female *Photuris* firefly devours a male *Photinus* to obtain defensive compounds called lucibufagins.
Copyright © 1997 by Thomas Eisner

Constraints

- Phylogenetic
  - Implies insufficient time or genetic variation for evolution to modify trait
- Physical
  - Production of signal is impossible given the organism's morphology and physiology

Is learning a cost or constraint?

- Learning is often time-consuming and mistake-prone
  - restriction to critical period may minimize error
- Neural tissue required for learning and memory is often energetically costly to maintain
- Trade-offs in relative size of brain regions devoted to specific processing or memory tasks has been used to infer constraint

Constraints on sender learning: HVC and repertoire size

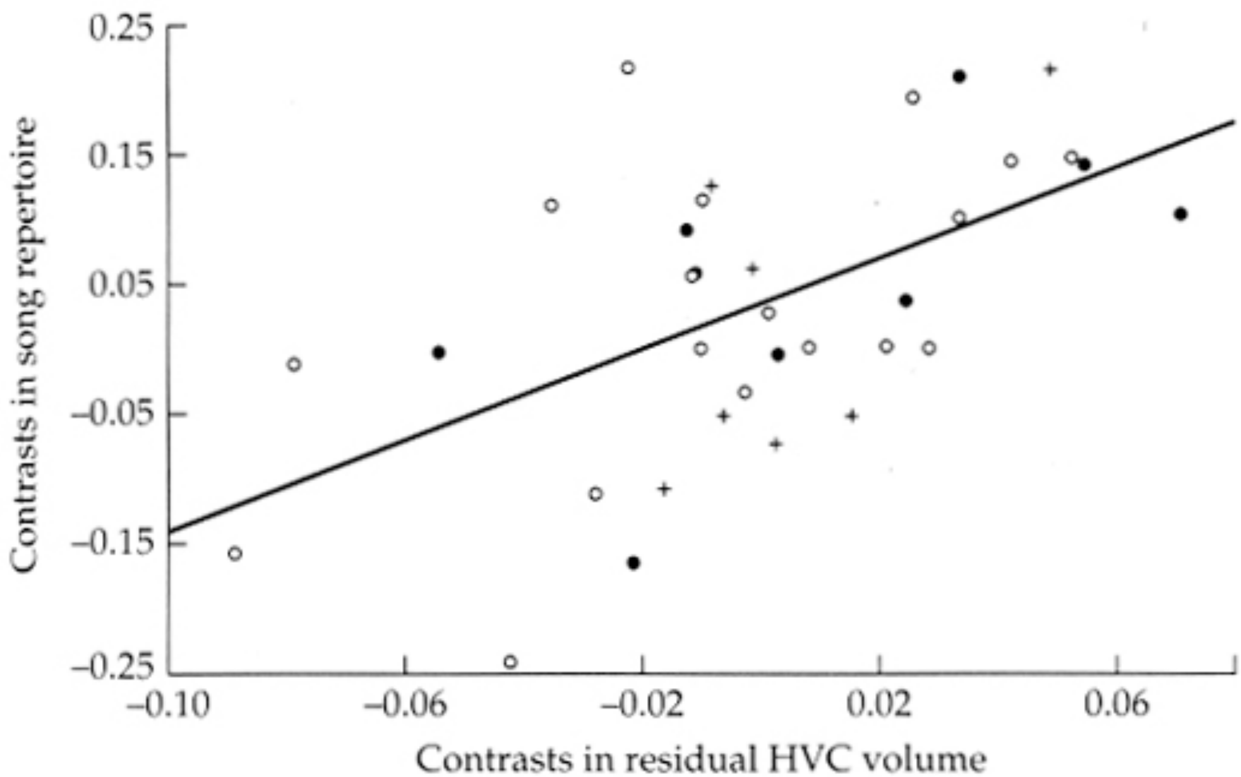
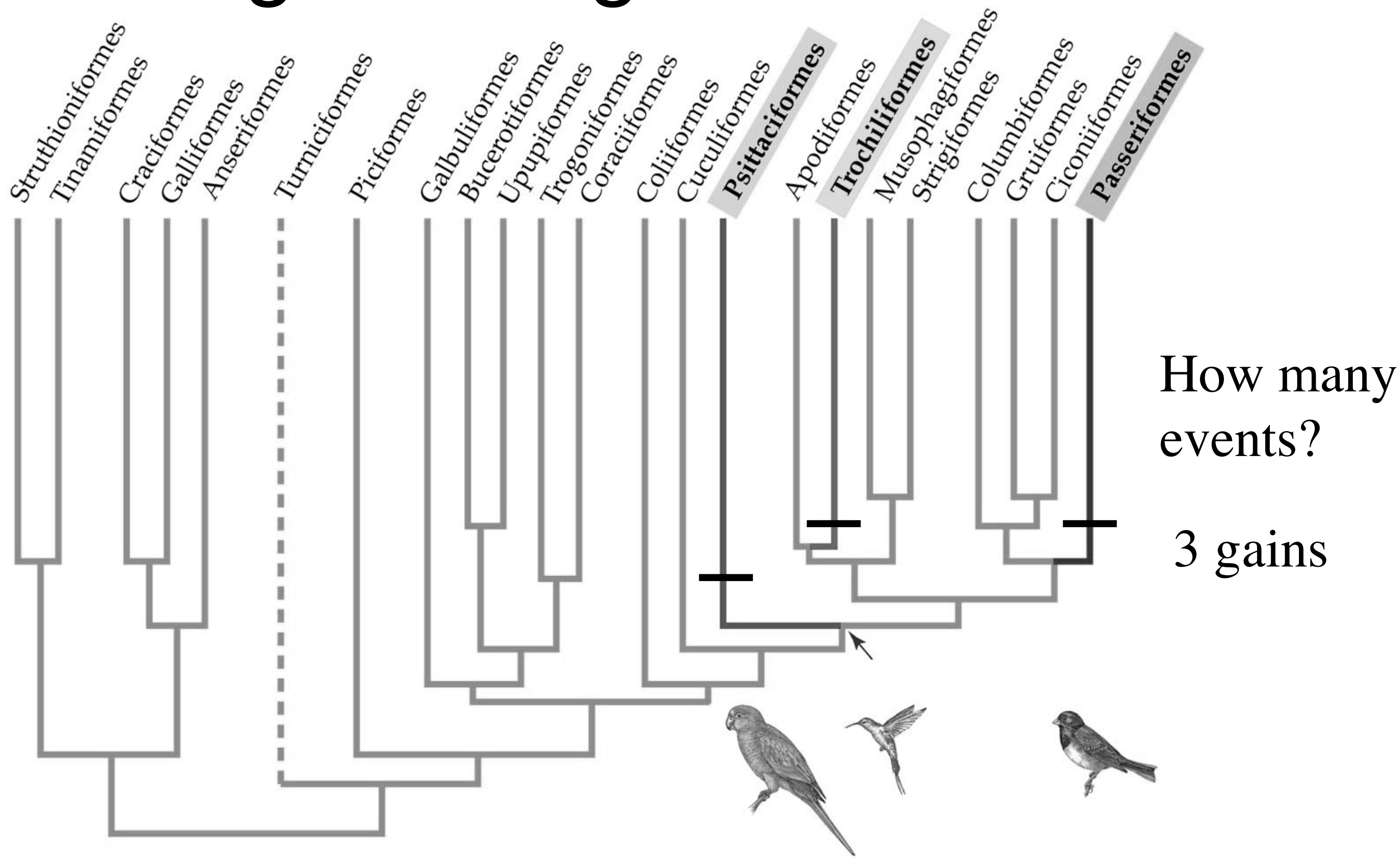


Figure 17.7 Relationship between HVC (higher vocal center) nucleus size and repertoire size in passerine birds. A larger repertoire size is associated with a larger brain area for vocal learning. Each point represents an independent contrast between two related species (●), genera (○) or families (+) with different repertoire sizes. The effect of overall brain size (telencephalon) on HVC volume has been statistically removed. (From DeVoogd et al. 1993.)

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
- Use trait value at next lower node to decide ambiguous nodes (if trait is discrete, otherwise use independent contrasts)

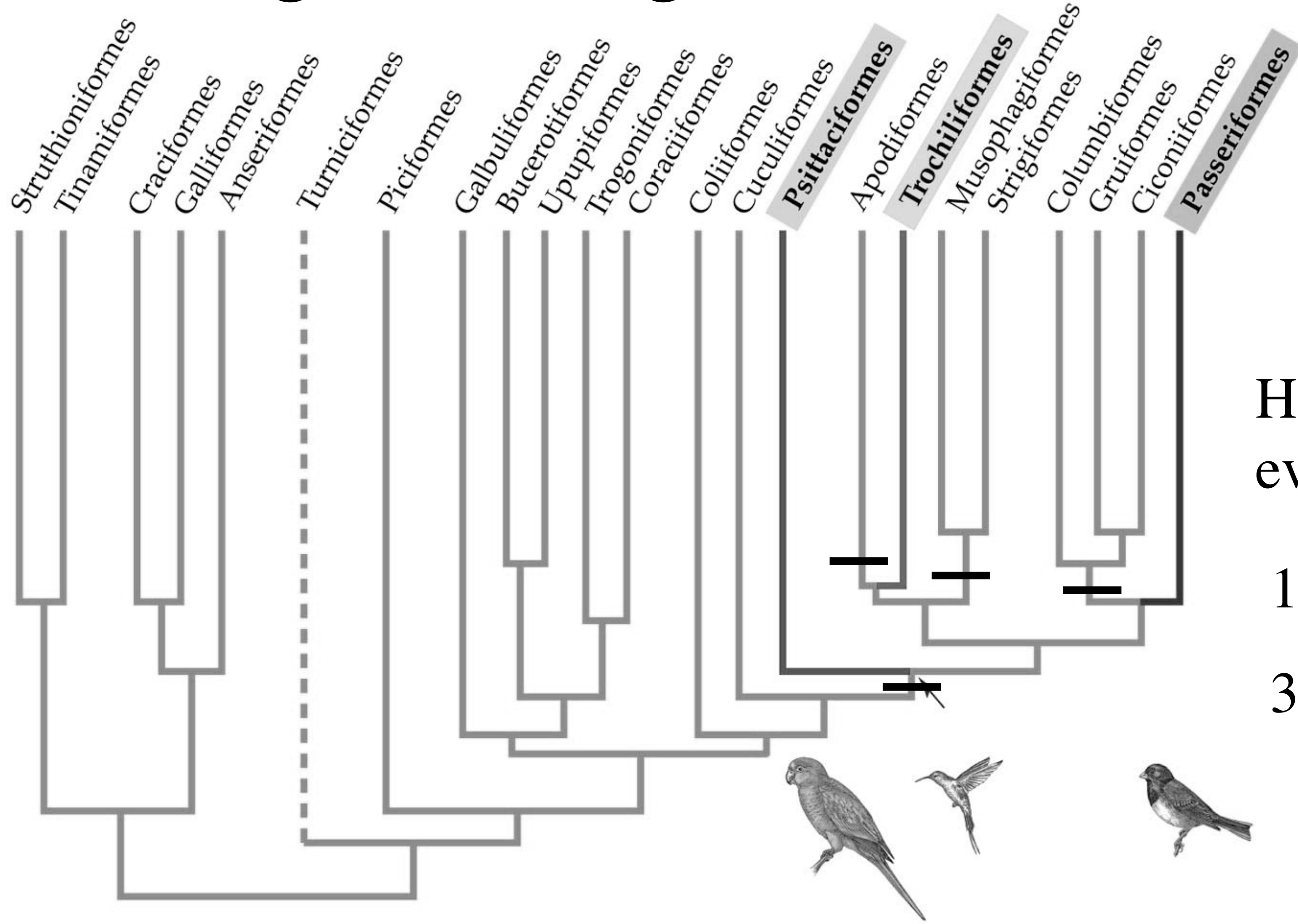
Song learning evolution in birds



ANIMAL BEHAVIOR, Eighth Edition, Figure 2.14 © 2005 Sinauer Associates, Inc.

- Note 1: need to consider outgroup to infer ancestral trait value
- Note 2: assume losses are equally likely as gains

Song learning evolution in birds



How many events?

1 gain,

3 losses

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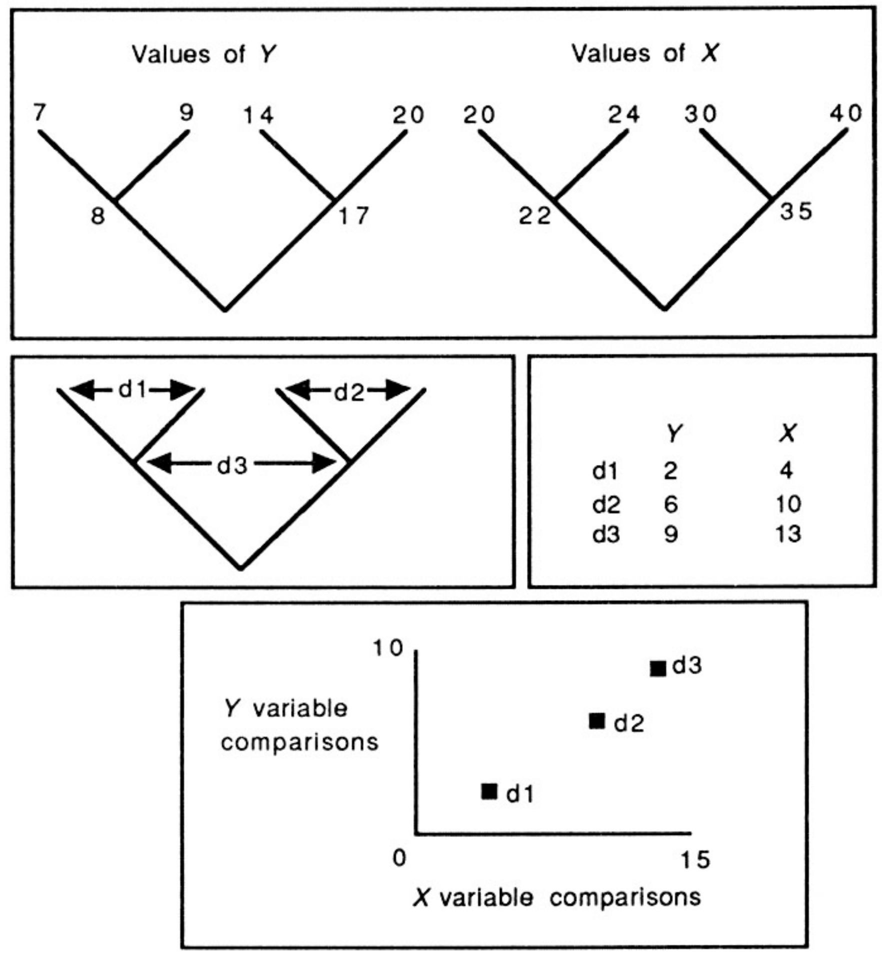
4 > 3, so this is less parsimonious

Measure trait evolution by independent contrasts

- Derive phylogenetic tree from independent data
- Estimate independent contrasts (d) for each trait
  - Assigning average trait values to ancestral nodes
  - Using the difference in trait values between derived taxa
  - Weight change by branch length (proportional to time)
- Regress contrasts through the origin

Under a Brownian motion model of evolution, d1, d2, and d3 provide independent comparisons. Path length differences are ignored in this illustration.



Primate repertoire size and sociality

- Scored repertoire size in adults only
- Repertoire size predicts grooming better than group size

McComb, K. and Semple, S. 2005 Coevolution of vocal communication and sociality in primates. Biology Letters 1:381-385.

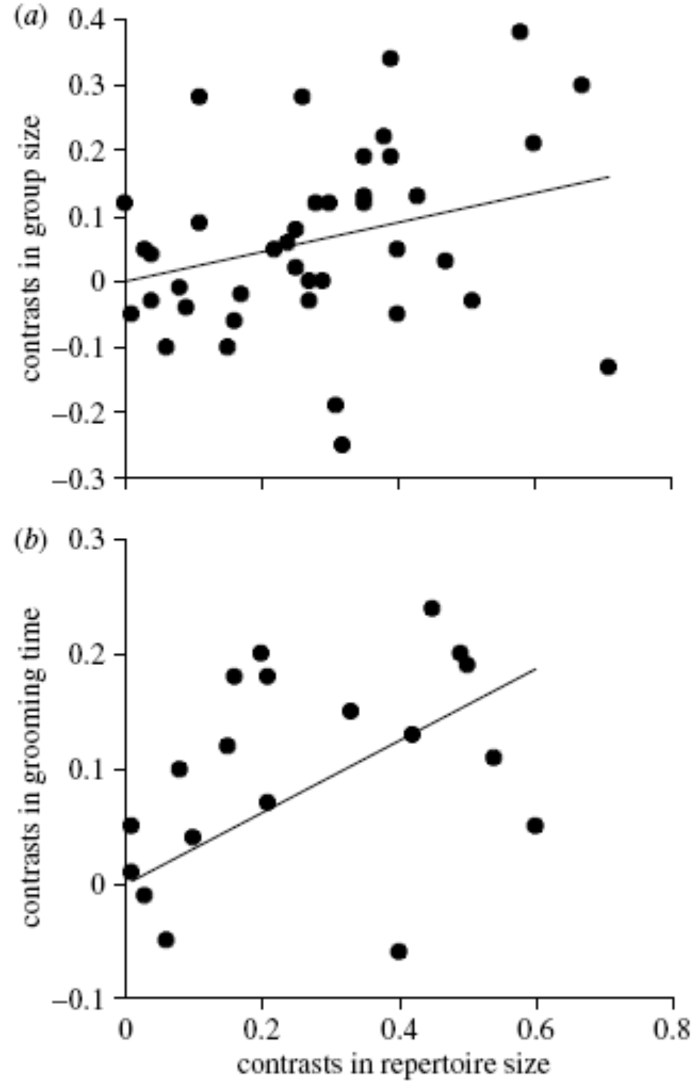


Figure 1. Relationships between (*a*) contrasts in repertoire size and contrasts in group size and (*b*) contrasts in repertoire size and contrasts in grooming time. Repertoire size was square root transformed, group size was log transformed and percentage grooming time was log+1 transformed.

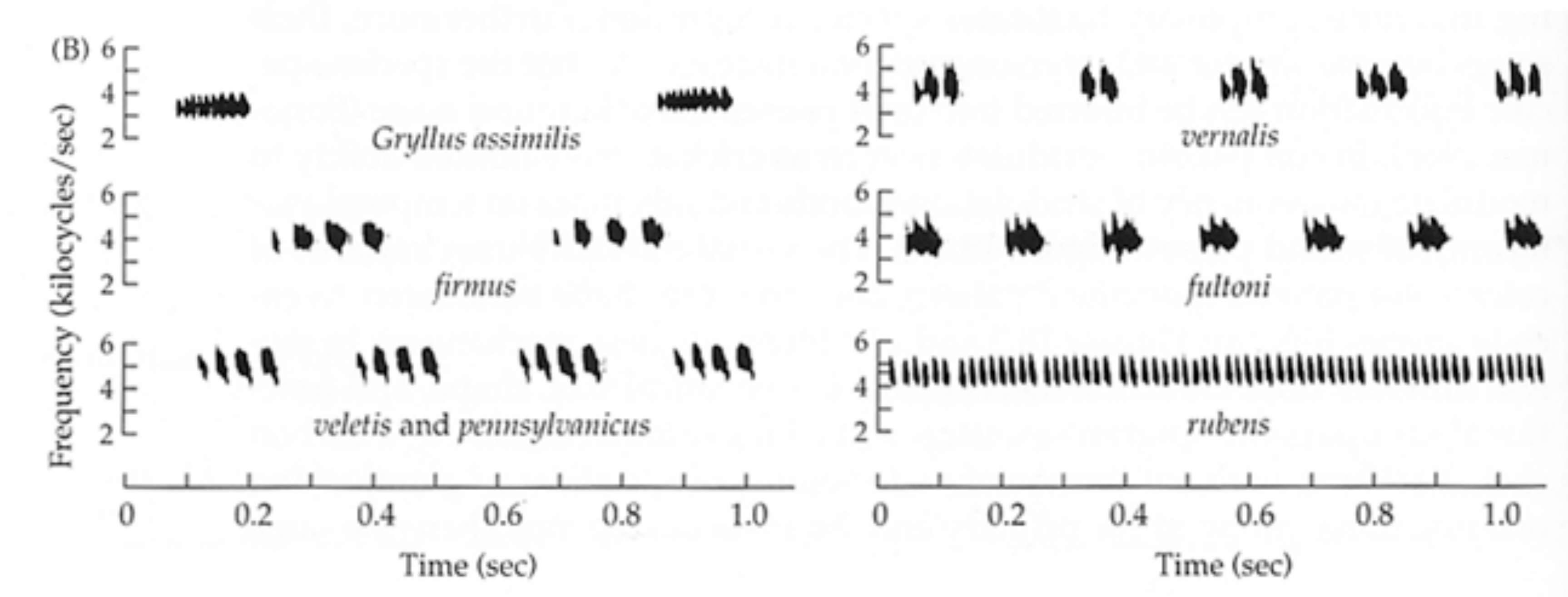
Why do animals communicate?

- Sexual advertisement
- Territory defense and conflict resolution
- Social integration
- Parental care
  - Recognition
  - Begging
- Transfer environmental information
  - Predator alarm
  - Food location

Sexual advertisement

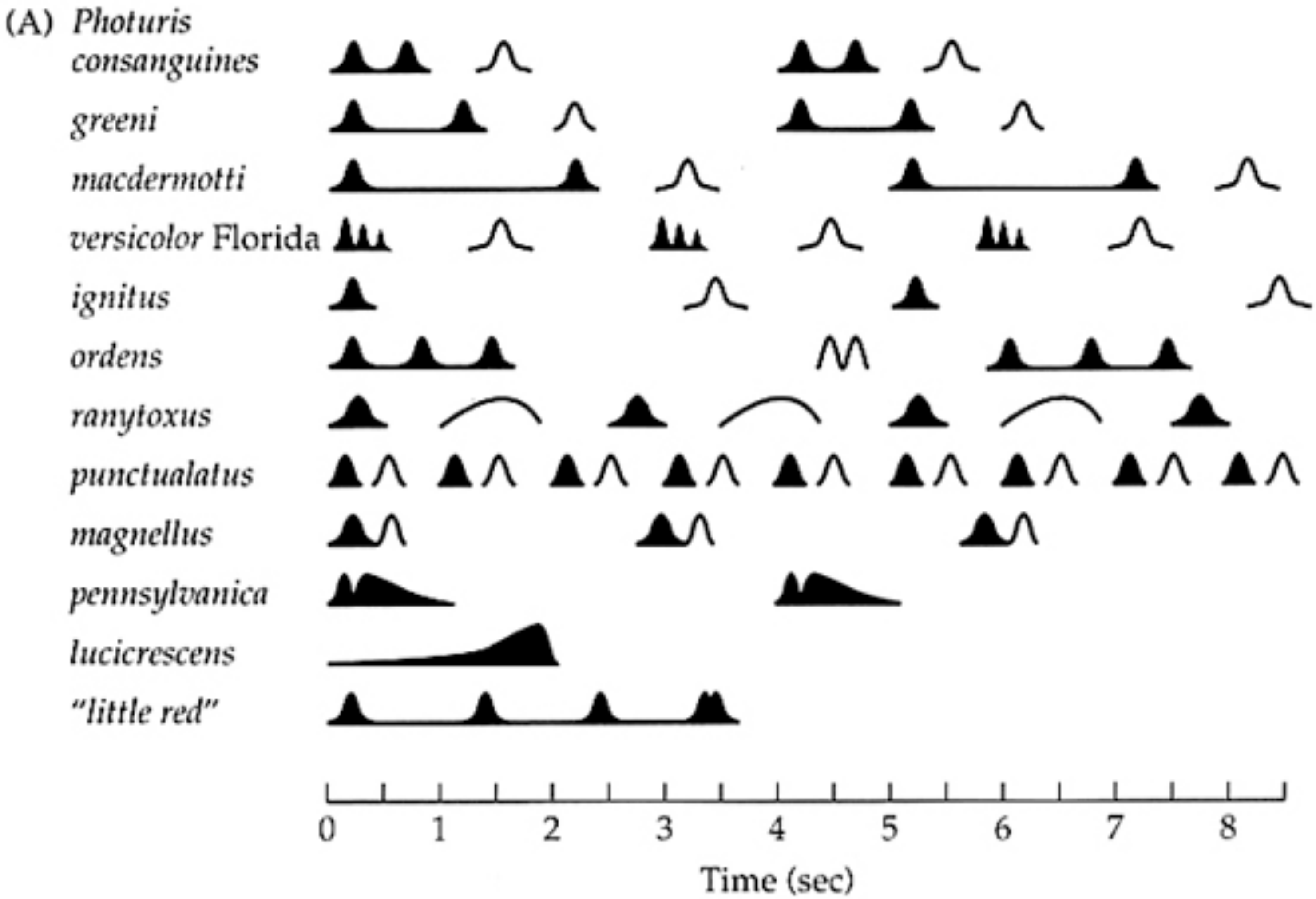
- Mate attraction
  - signals designed to attract potential mates from a distance
  - species specific and stereotyped
  - localizable: loud, high duty cycle
- Courtship
  - signals may be arbitrary and exaggerated
  - signals may depend on male condition and indicate male quality

Species differences in cricket calls

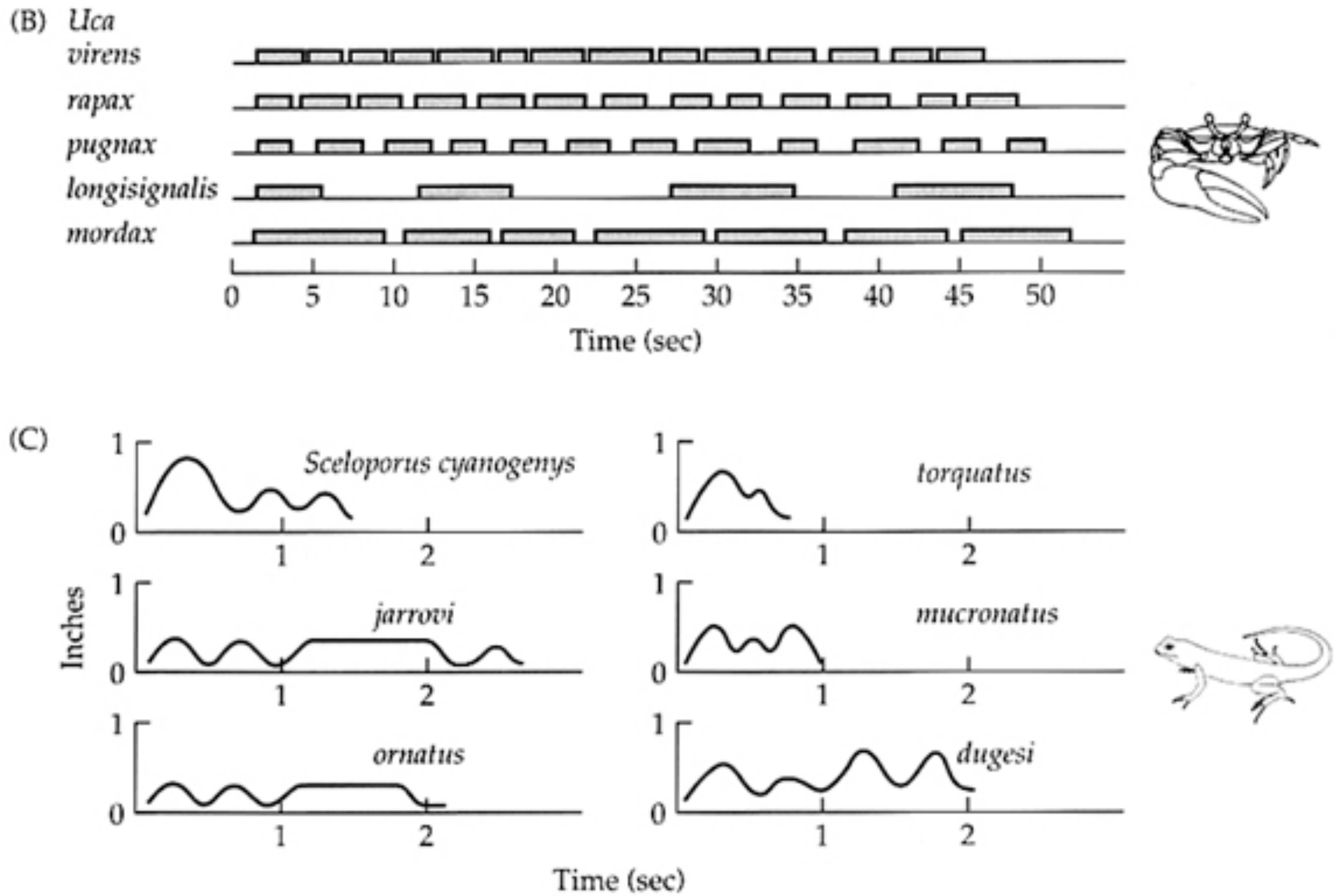


Species differences are encoded in temporal patterns

Species differences in firefly flashing signals

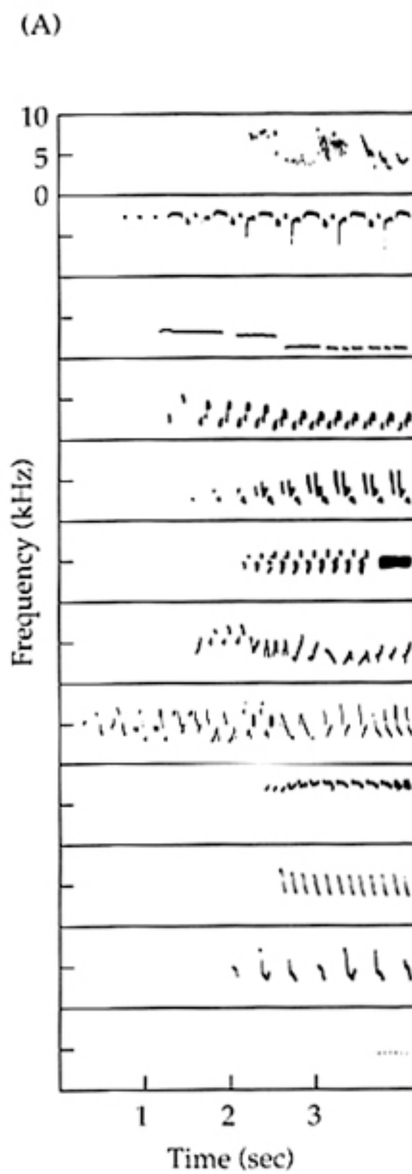


Species differences in fiddler crab and fence lizard displays



Species differences in bird song

Species differences are encoded in frequency range, INI, note structure



Species	Frequency range	Internote interval	Syntax	Frequency changes	Note structure
Erithacus rubecula	+	−	+	+	−
Regulus regulus	+	−	+	+	−
Zonotrichia albicollis	+	+	?	+	+
Lullula arborea	+	+	+	?	+
Seiurus aurocapillus	+	+	+	?	+
Emberiza citrinella	+	+	?	?	+
Phylloscopus trochilus	+	+	+	?	+
Passerina cyanea	?	+	−	?	−
Regulus ignicapillus	+	+	−	−	+
Parus palustris		+	−	−	+
Phylloscopus collybita	+	−	−	−	+
Phylloscopus bonelli	+	−	−	−	+

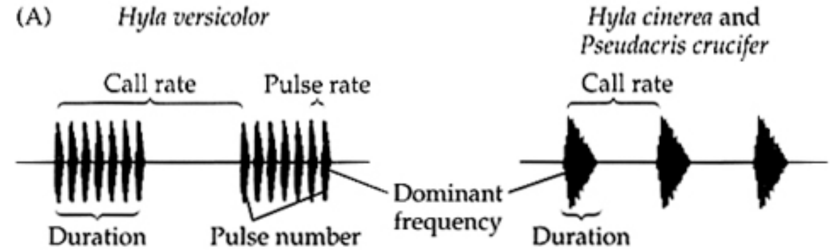
Static vs dynamic calling displays

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

Dynamic components:
Convey information about individual differences.
Females typically prefer extremes and may be used in male-male interactions.

Tree frog example

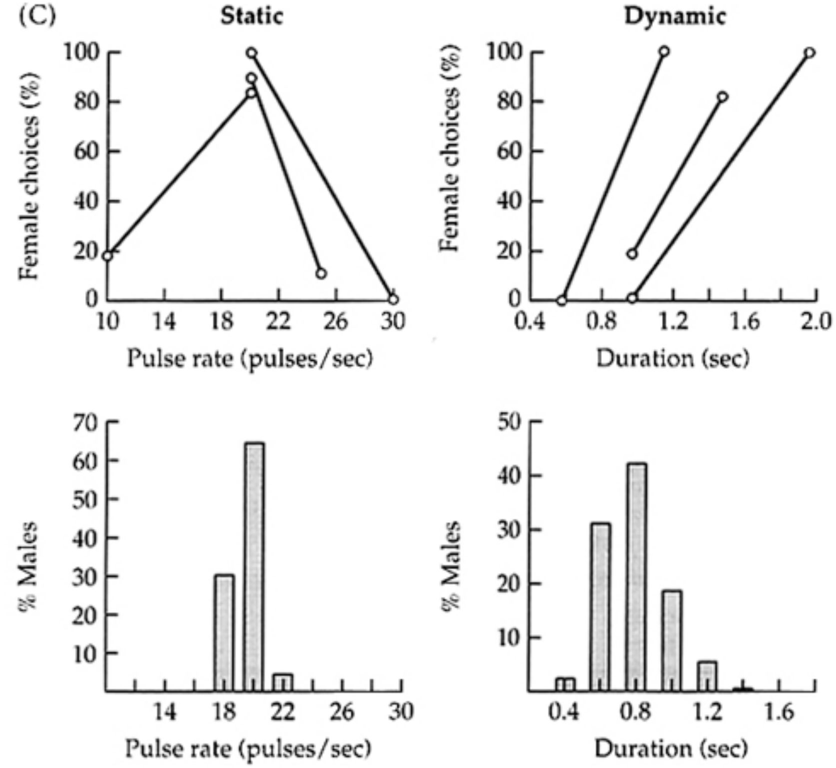
(A)



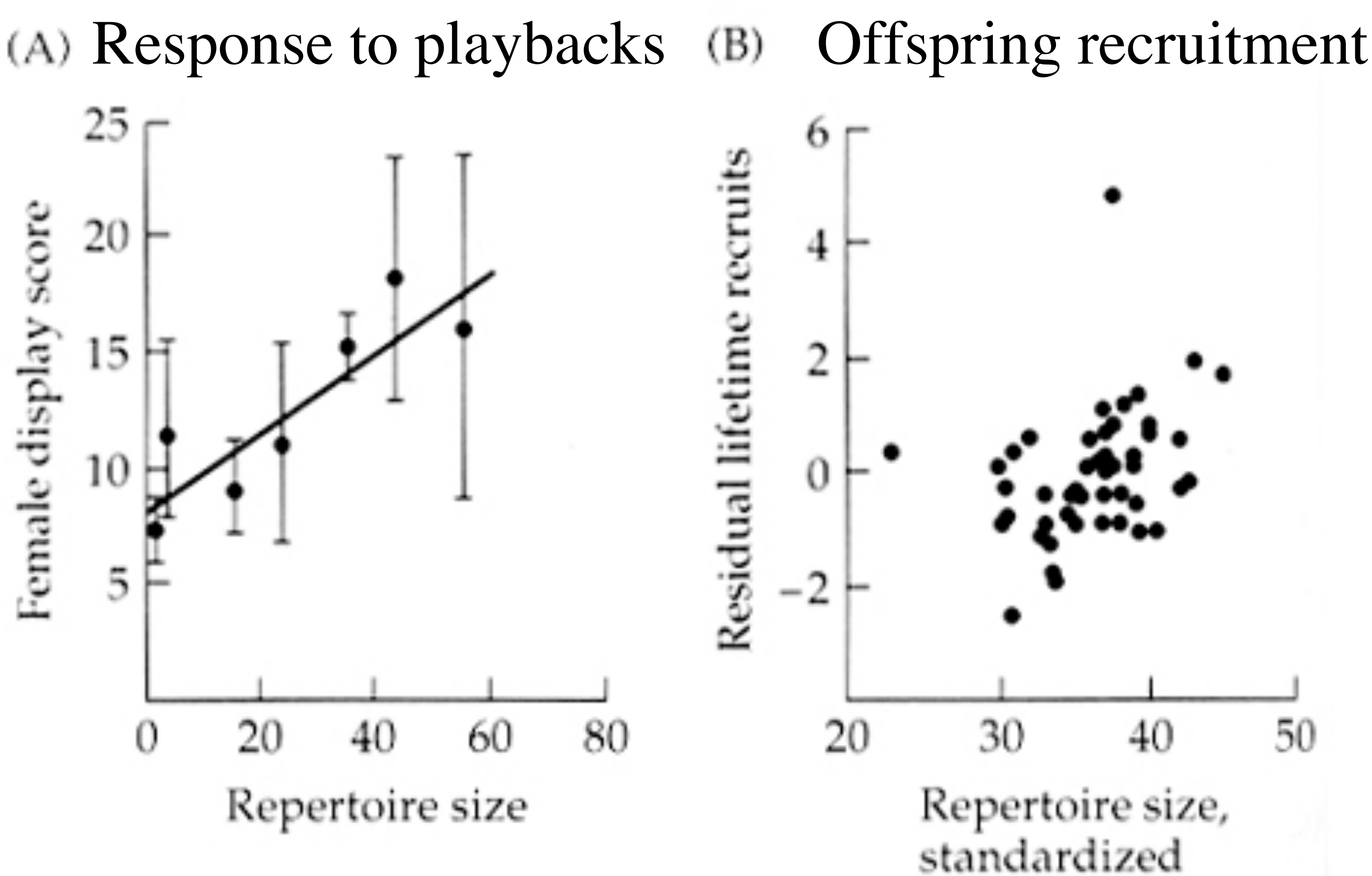
(B)

	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

(C)

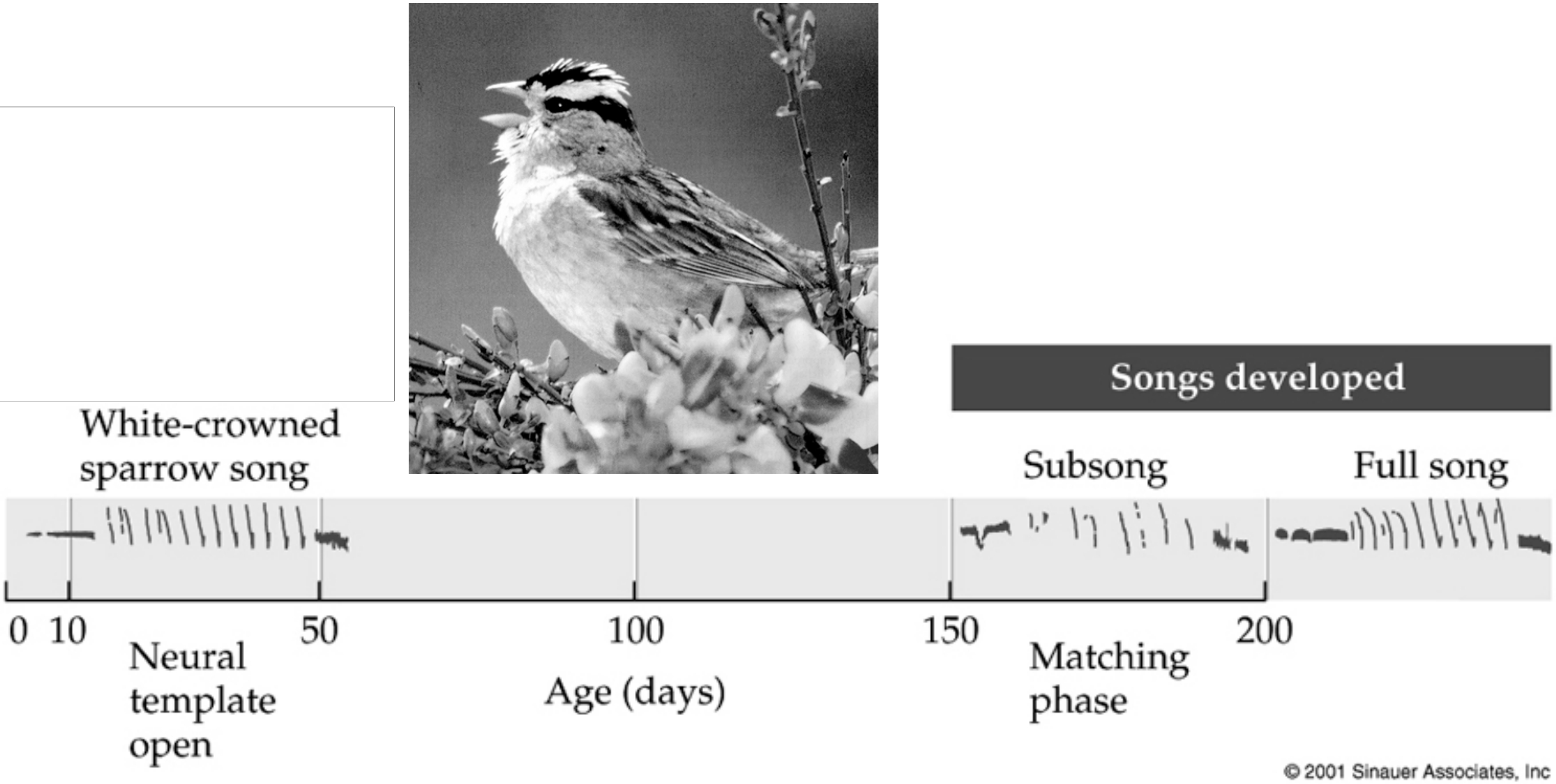


Female preference for repertoire size in *Acrocephalus* warblers



Repertoire size may reveal condition during early development when males learn songs

Critical period learning:
white-crowned sparrows (and other oscines)



Females typically prefer the song that they heard when they were young. Young males learn their song between 10-50 days of age (critical period) based on tutoring experiments with taped songs.

Song dialects

Song dialects in white-crowned sparrows

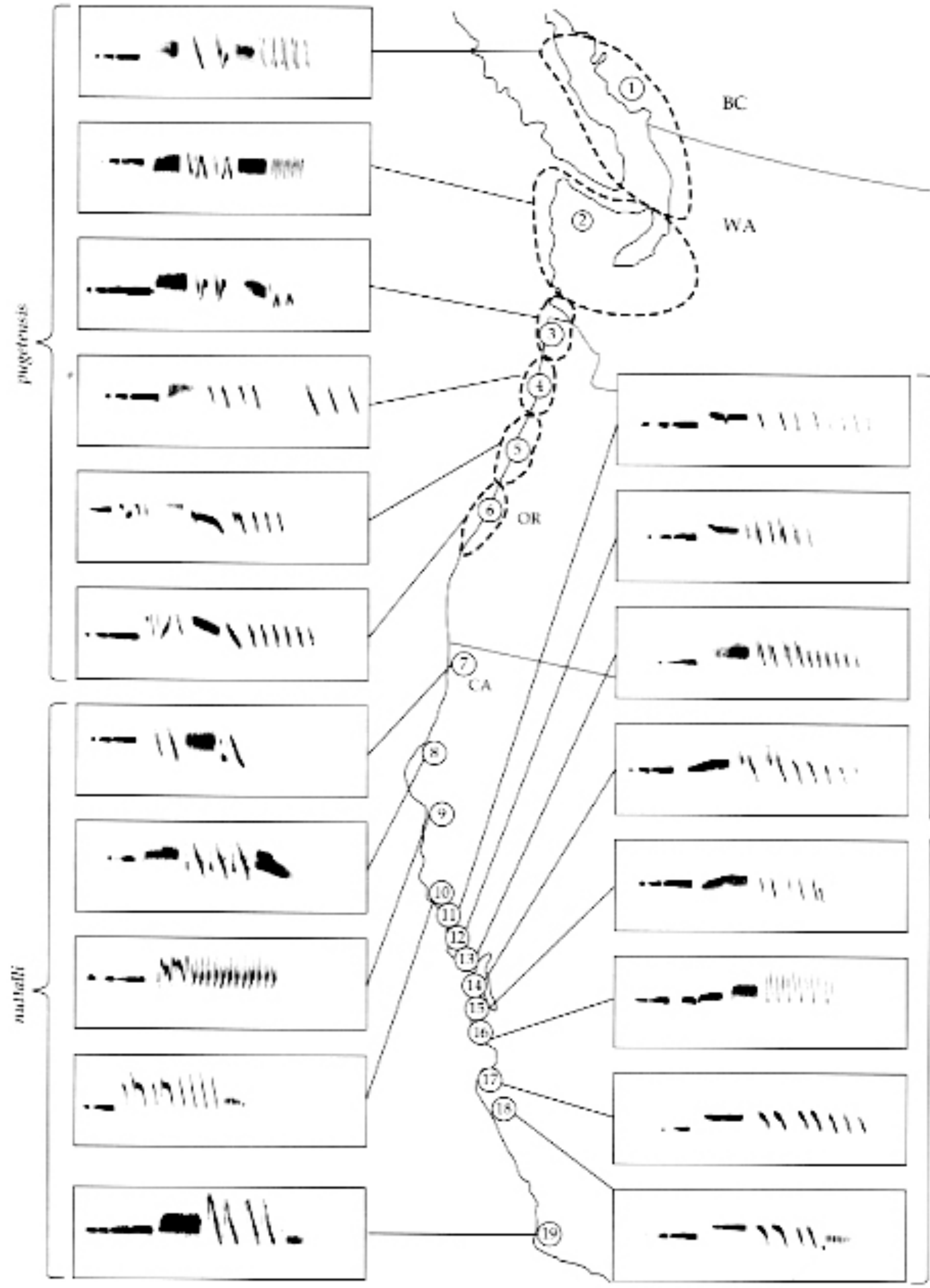
•Song learning used to match neighbor's song after juvenile settlement

•Result in song 'dialects'-patchwork variation

• Matching neighbors song appears to be important for obtaining territories and mates

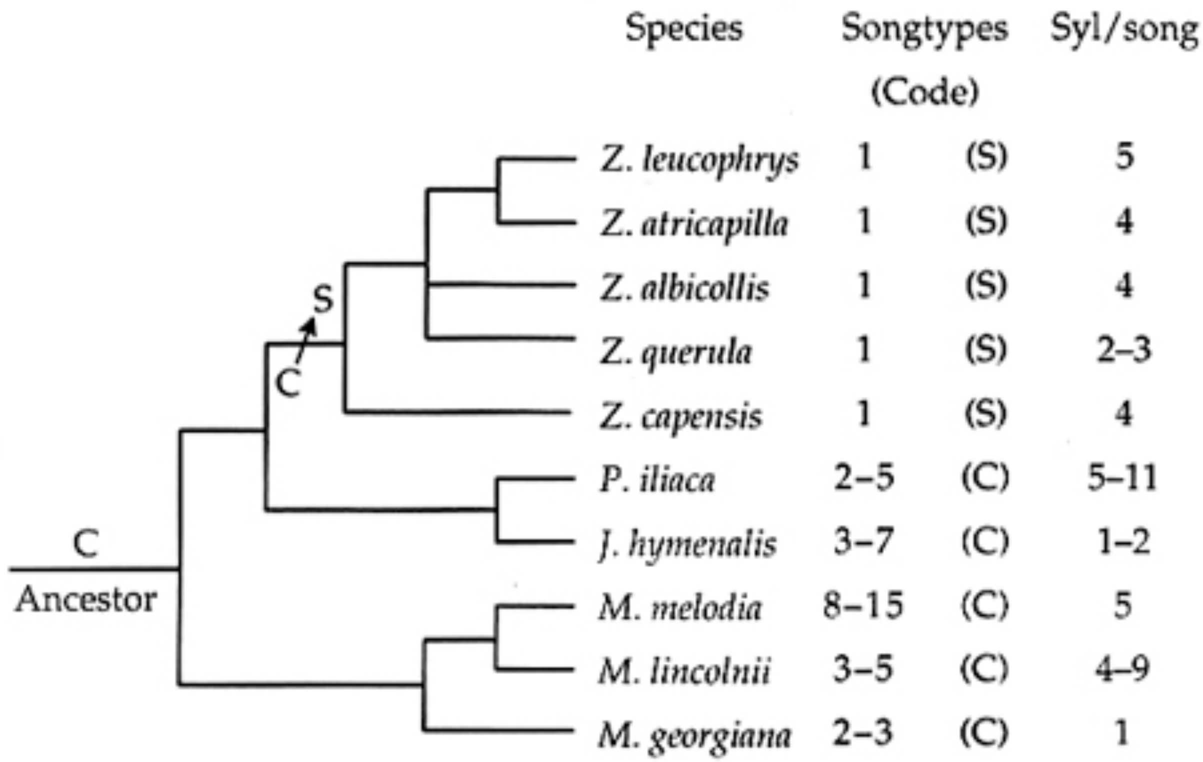
•Dialects more common in stable environments like the tropics

- •Smaller dialects in sedentary populations of WCS
- •Larger, looser dialects in migratory populations



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.



Simple repertoire of white-crowned sparrow is derived

Singing strategies in territorial songbirds

Table 22.1 A summary of the mean values of song variables for songbird species employing different types of singing strategies

Song variable	Singing Strategies			
	One songtype	Bout	Mixed	Infinite[a]
Size of songtype repertoire	1.0	8.1	20.2	∞
No. of syllable types per song	3.8	4.6	7.0	3–∞
Song duration (sec)	6.1	1.8	2.0	0.3–∞
Intersong interval (sec)	6.6	5.7	5.2	0–10.5
Duty cycle (%)	31	27	24	22–100
Song delivery rate (per min)	7.2	12.3	12.4	–∞–130.4
No. of species	24	34	28	15

Source: Based on data from Read and Weary 1992.

[a]Minimum and maximum values are given for infinite repertoire species. e.g. mockingbird, thrasher

Some singers have multiple song types in repertoires

- -Mixed-mode singing = ABCDABCDABCD
- -Bout signing = AAAABBBBCCCCCCDDDD
- -Infinite = really big number of songtypes

Song matching reveals motivation

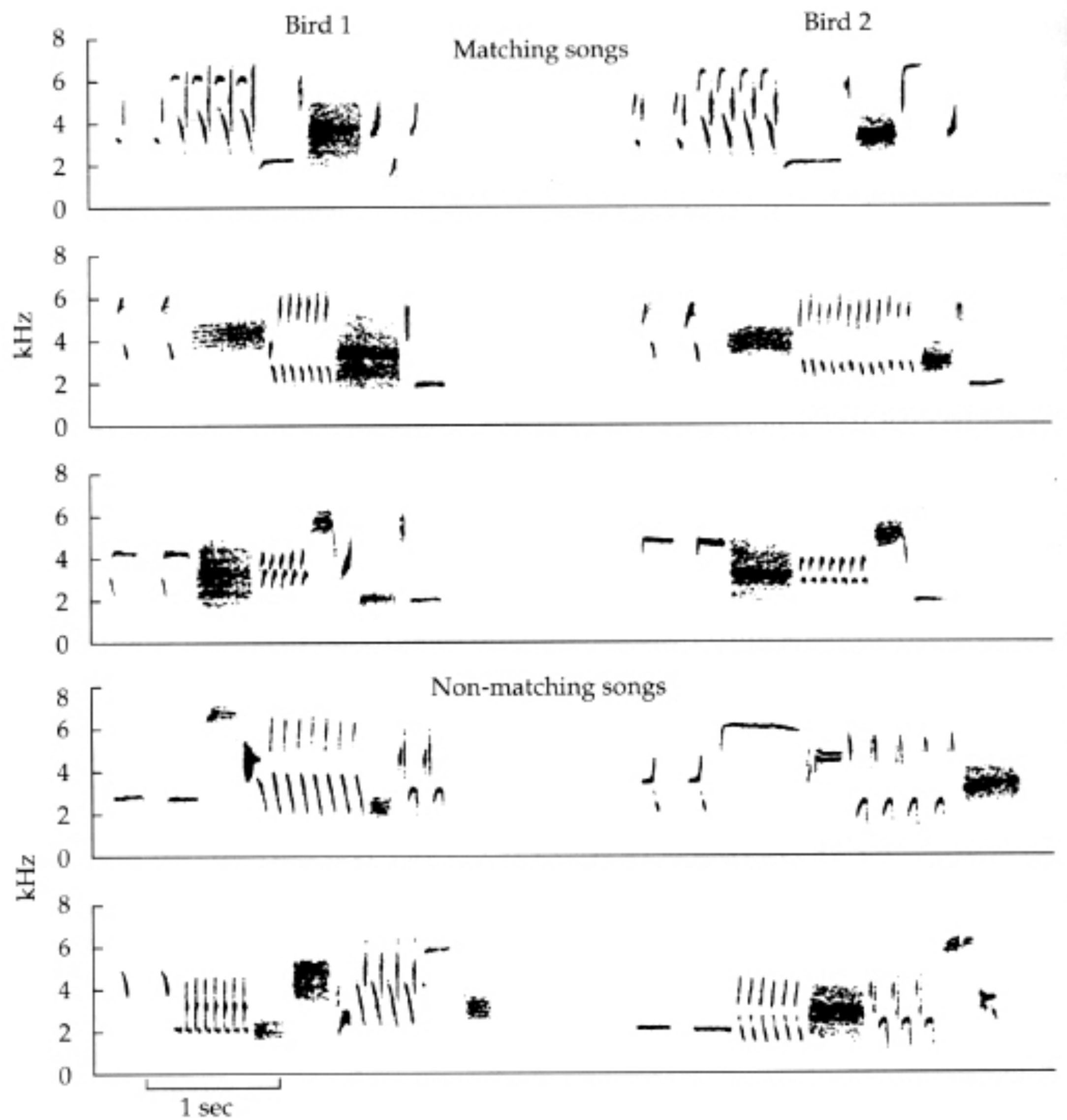
<u>Song matching in song sparrows</u>

Neighbors share some, but not all, songs in their repertoire

In contests, individuals can
-songtype match,
-repertoire match, or
- fail to match

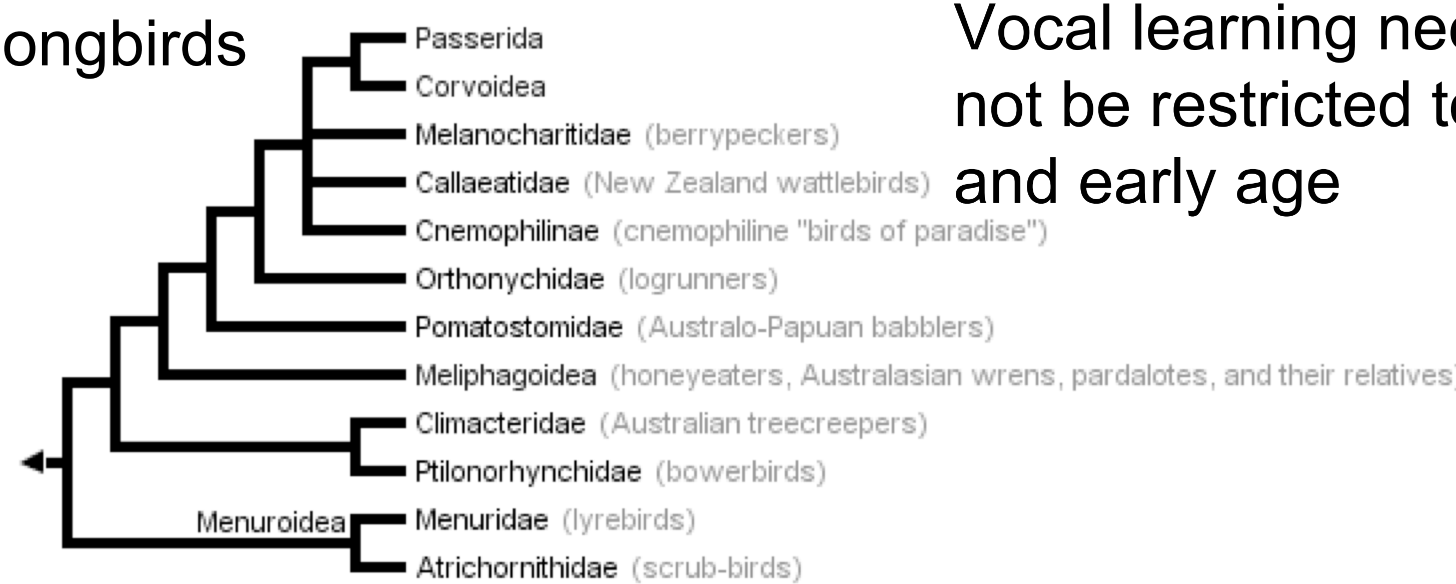
Interactive playbacks show rate of singing, rate of songtype switching, and type of matching all indicate aggressive motivation

Intruders with larger repertoires who can match songtypes are more successful at gaining territories



Lyrebird: mimicry in a basal oscine

Oscine songbirds

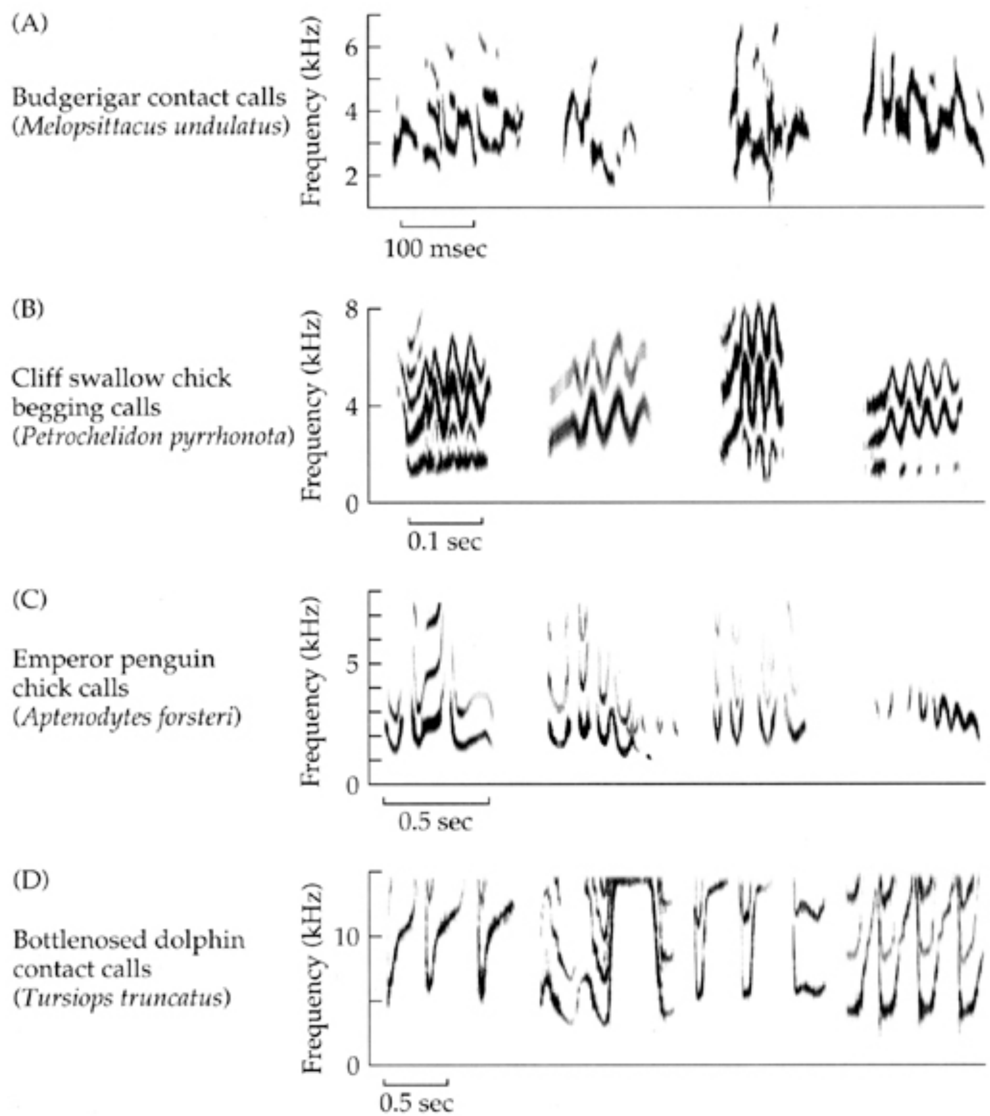


Vocal learning need not be restricted to and early age

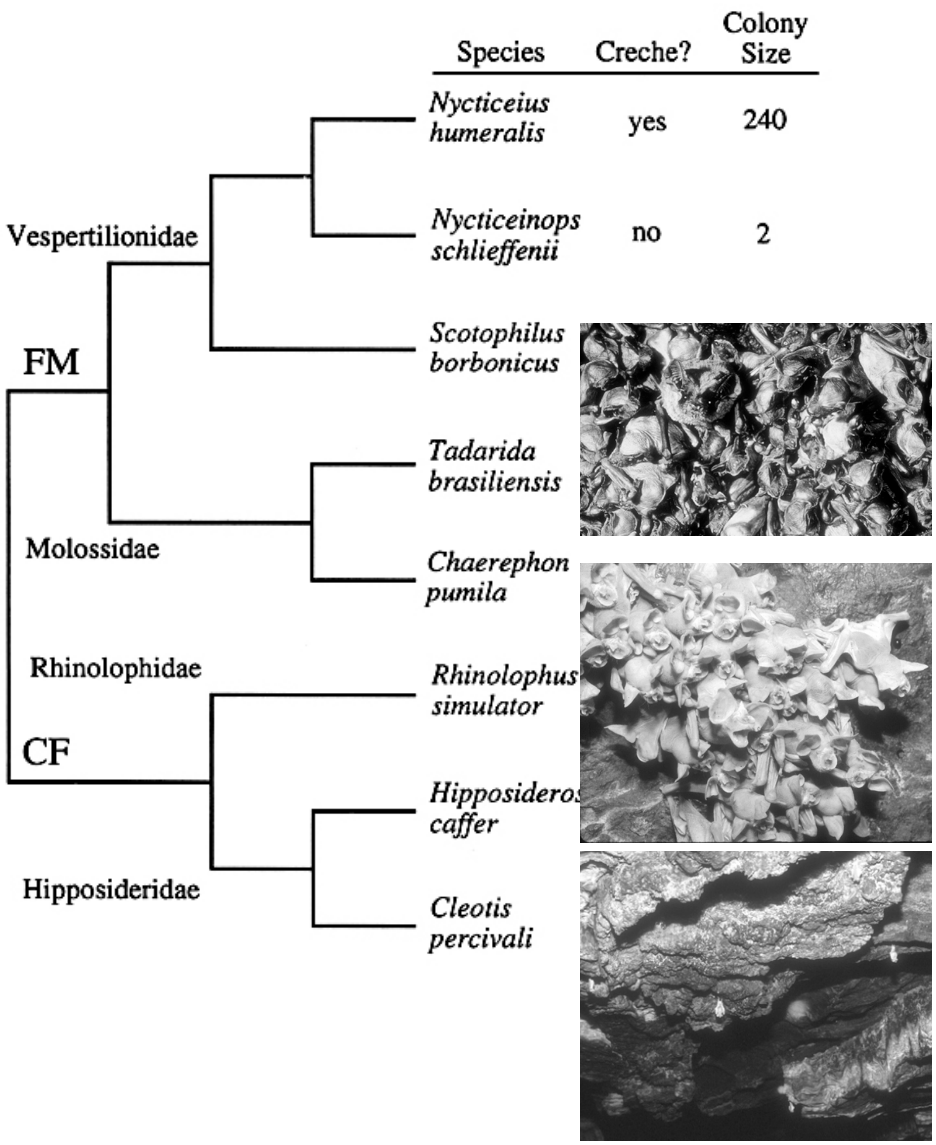
Social Integration

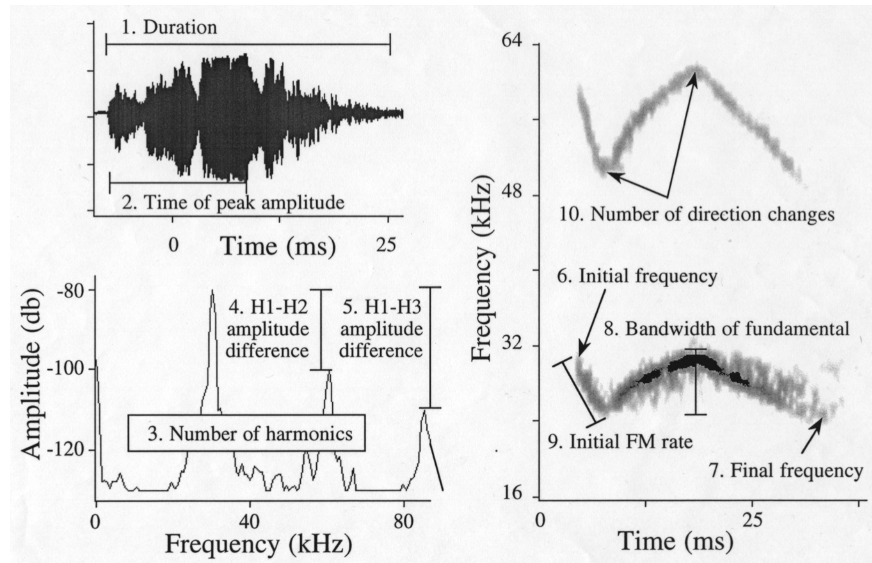
- Parent-offspring integration
- Group integration
- Male-female integration

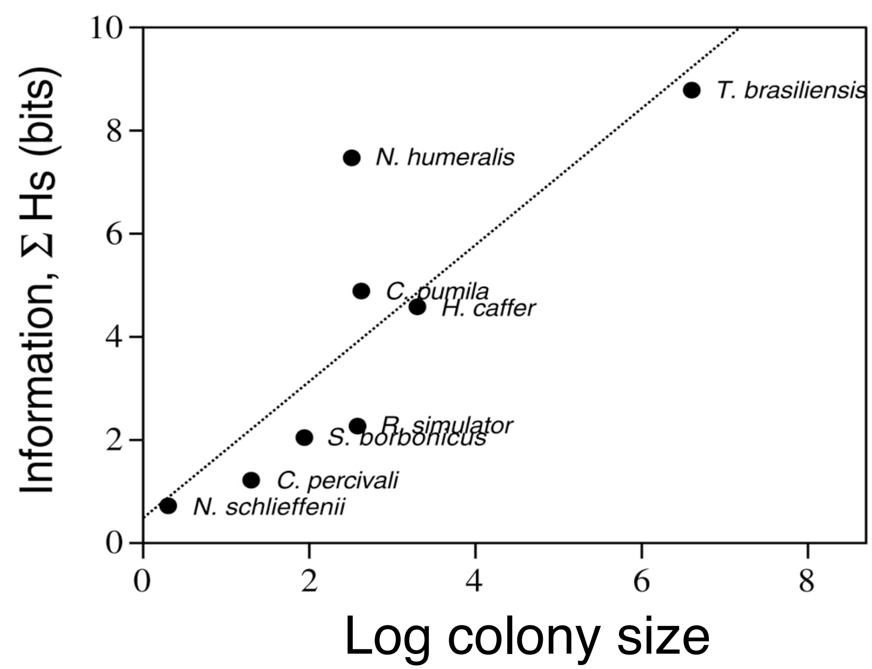
Vocal signatures



Call complexity increases with colony size





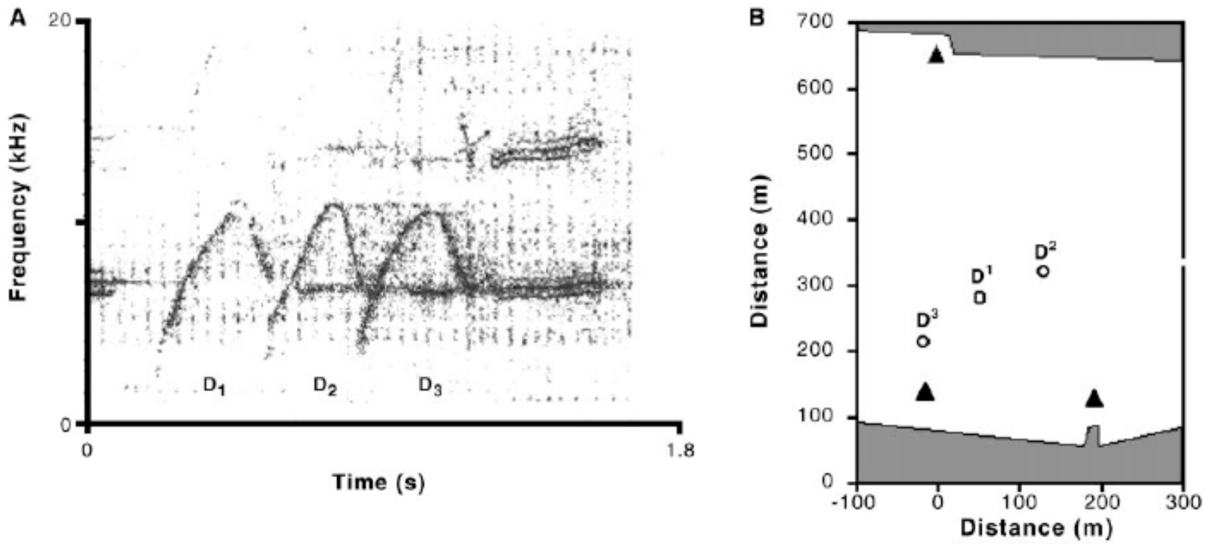


Group recognition vocalizations

- Social group cooperation requires a recognition mechanism to exclude cheaters
- Coordinates group movement in terrestrial vertebrates
  - Often involves call convergence, presumably by vocal learning
- Examples
  - Bottlenose dolphins
  - Killer whales
  - Spear-nosed bats
  - Parrots
  - Vervet monkeys
  - Chimps

Whistle matching in dolphins

Fig. 3. A matching whistle interaction that involved three individuals. (A) Spectrogram of the produced whistles. (B) Plot of the array geometry with the locations of each of the dolphins that produced whistles D_1, D_2, and D_3 in (A). Gray areas at the top and the bottom of the plot represent the shoreline. Circles, animals; triangles, hydrophones (25).



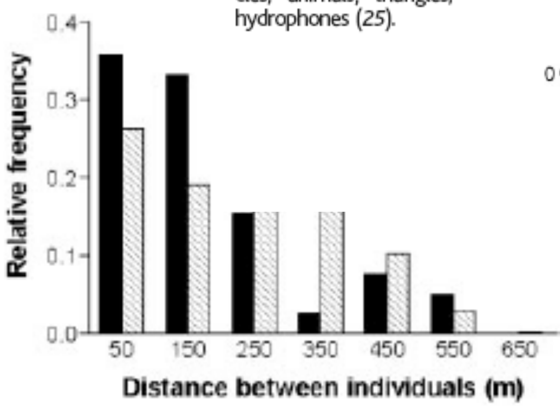
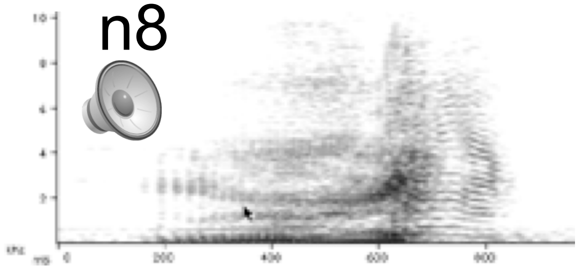


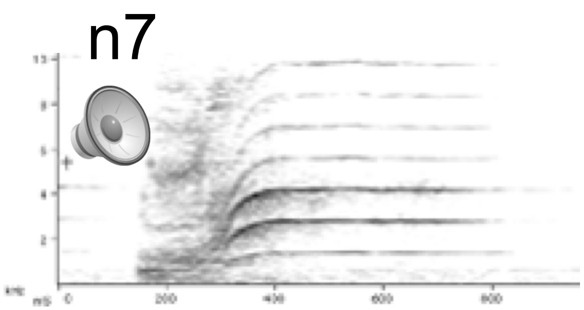
Fig. 2. Distributions of the distances between dolphins in matching (solid bars) and non-matching (hatched bars) whistle interactions.

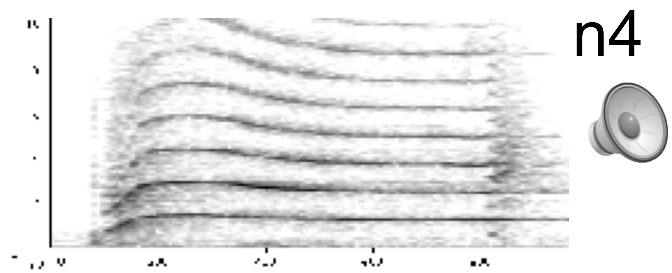
- Free-ranging animals produce matching whistles in response to nearby calls
- Propose that individuals are signaling to known individuals

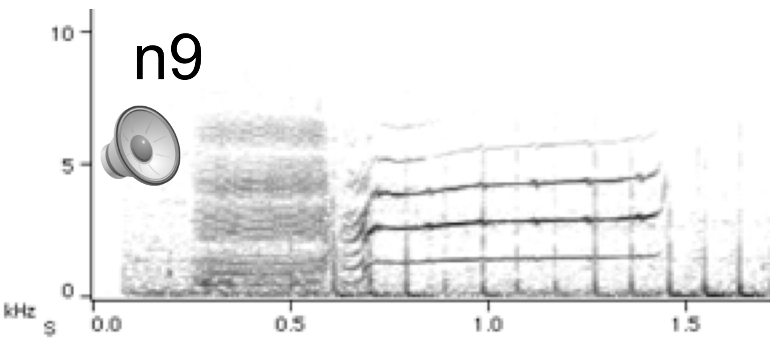
Janik VM 2000 Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289: 1355-1357.

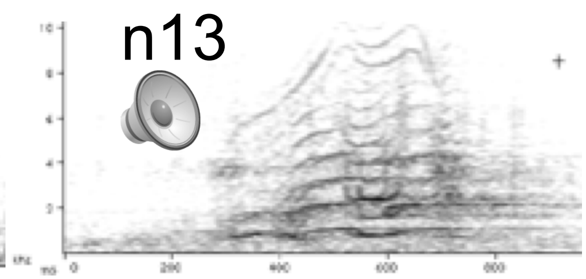
Killer whale dialects

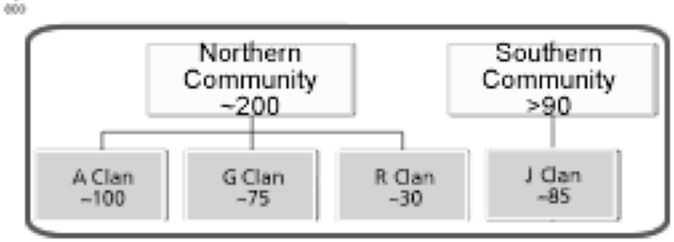










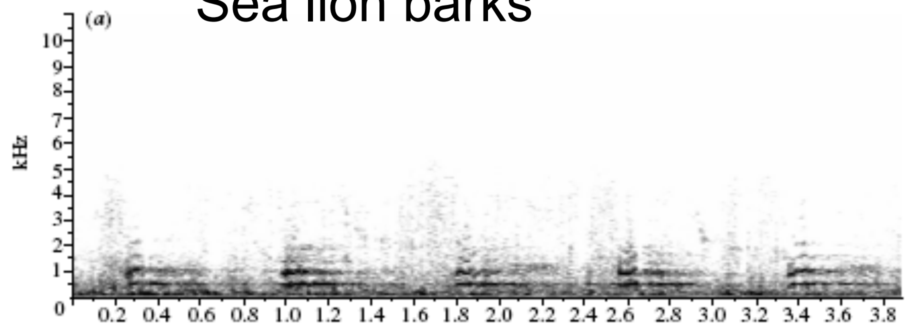


http://www.killerwhale.org/fieldnotes/chat.html

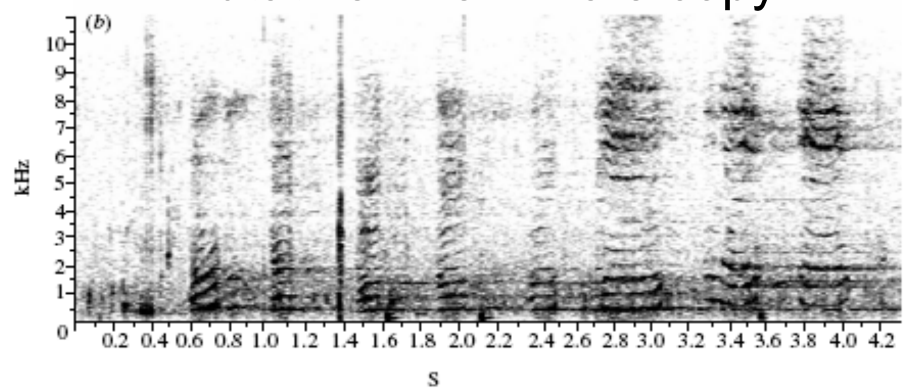
Vocal mimicry by a killer whale?

Canada's lonely killer whale dies
Saturday, 11 March 2006

Sea lion barks

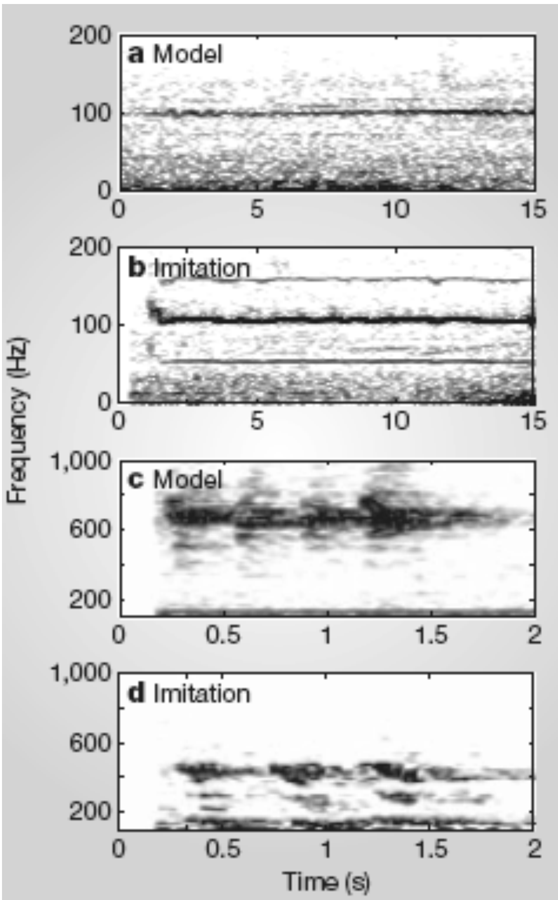


Putative killer whale copy



Foote AD, Griffin RM, Howitt D, Larsson L, Miller PJO, et al. 2006 Killer whales are capable of vocal learning. Biology Letters 2: 509-512.

Vocal mimicry in African elephants?



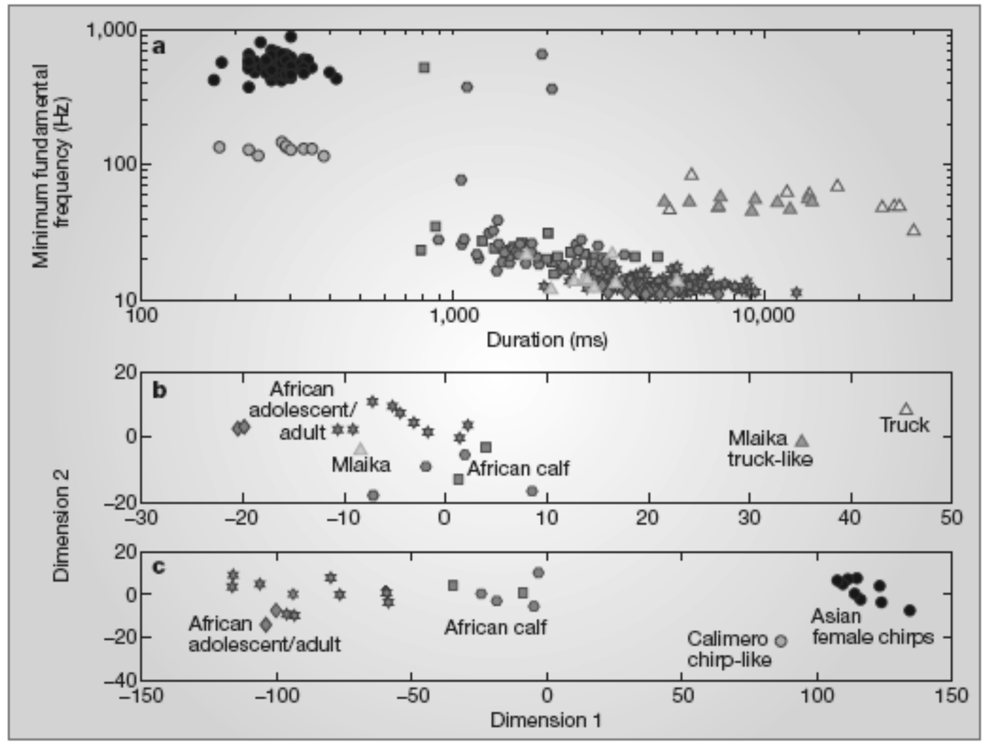
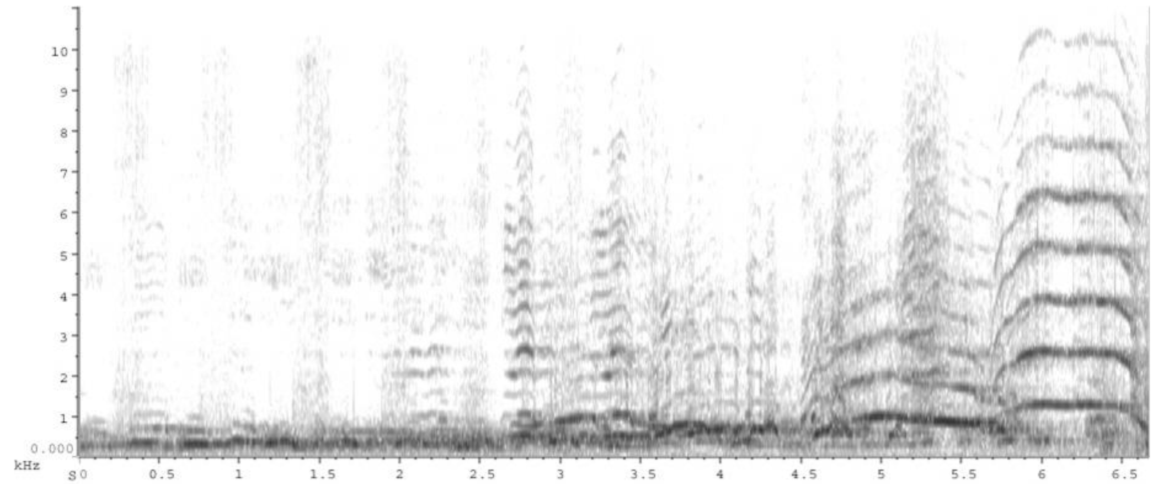


Figure 2 Imitation of sounds by the African elephants Mlaika and Calimero. Mlaika's imitations (green triangles) are similar to truck sounds (light-blue triangles) and differ from her normal calls (yellow triangles), which are similar to the sounds made by other African elephants (dark blue symbols: stars, adult female; diamonds, adult male; squares, female calf; hexagons, male calf). Calimero makes chirp-like sounds (pink circles) similar to the chirps of the Asian elephants (red circles) who lived with him. **a**, Scatterplot of frequency versus duration for ten calls from each source. **b**, Multidimensional scaling plot of means for each source in **a**, apart from the chirp sounds. **c**, Multidimensional scaling plot of individual means from chirps of nine female Asian elephants and Calimero's chirp-like calls. Dimension numbering represents different combinations of acoustic features; for methods and further details, see supplementary information.

Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S 2005 Elephants are capable of vocal learning. Nature 434: 455-456

Chimpanzee pant hoots



Crockford C, Herbinger I, Vigilant L, et al. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? Ethology 110: 221-243

- Found acoustic differences among individuals and among three contiguous groups in Tai Forest, Ivory Coast. A fourth group 70 km away was less distinct.
- Pairwise comparisons did not correlate with relatedness.
- Propose that calls converge to maximize differences among contiguous groups

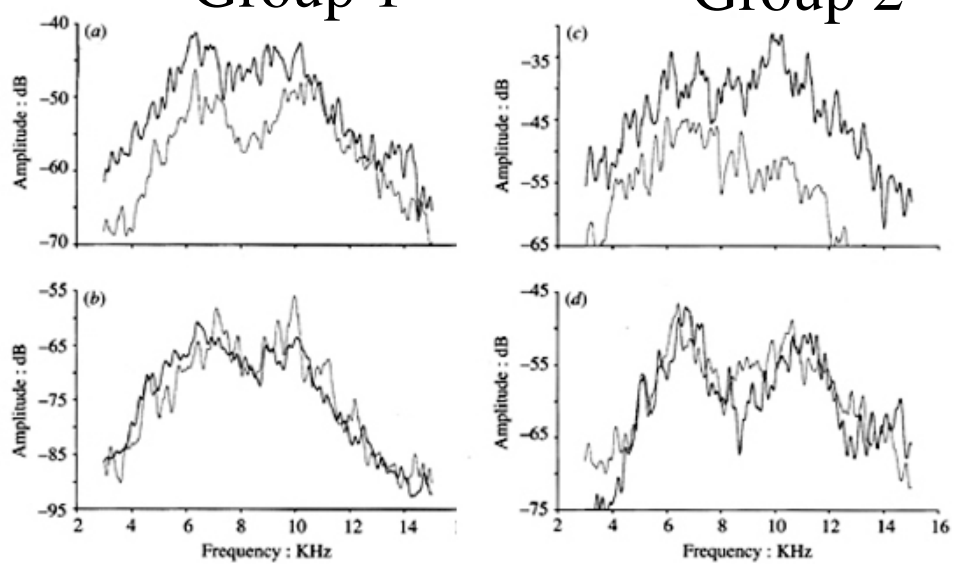
Greater spear-nosed bats

Wilkinson, G.S. and Boughman, J. W. (1998) Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour* 55:337-350

Boughman, J.W. and Wilkinson, G.S. (1998) Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour* 55:1717-173

Boughman, J.W. (1998) Vocal learning by greater spear-nosed bats. *Proceedings Royal Society B* 265: 227-233.

Group 1 Group 2



Before

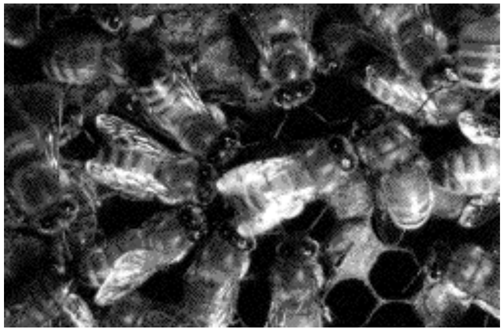
5 months after move

Food location signals

Discoverer broadcasts signal from the resource and receivers recruit to the site

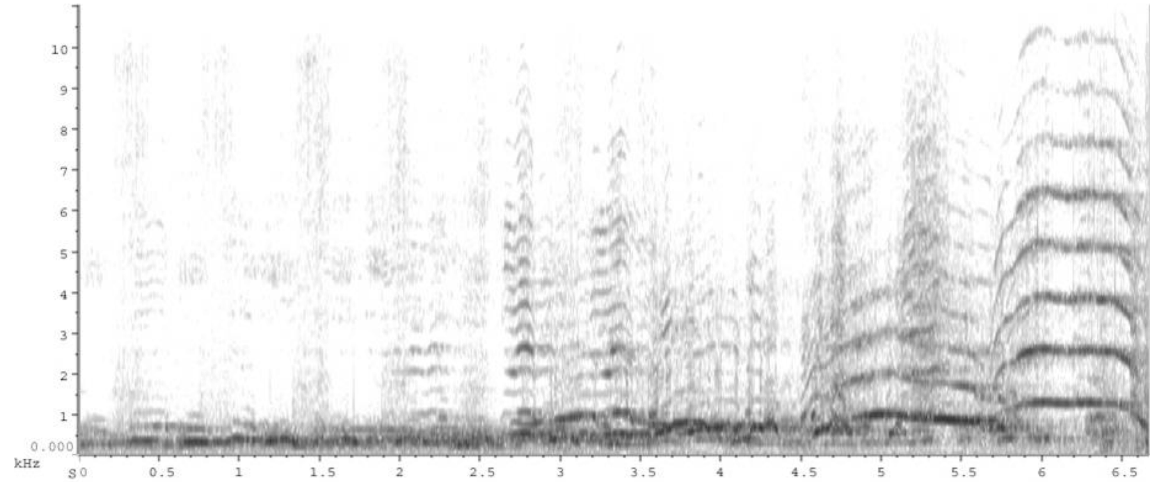
Discoverer goes to receivers (often at nest or colony), communicates discovery, and then leads receivers to site

Discoverer goes to receivers and provides directional information about site



Chimpanzee pant hoots

Notman, H. & Rendall, D. 2005 Contexual variation in chimpanzee pant hoots and its implications for referential communication. Animal Behaviour 70: 177-190.



- Found acoustic differences among individuals in Uganda
- Also found pant hoot variants in different contexts: e.g. party size, food abundance, and movement
- Argue that these differences are not likely to be intentional modifications to convey information
- Rather, they may be due to differences in arousal, locomotor activity or calling effort.

Why signal food location?

- Costs
  - Increases competition
  - Signal production takes time and energy
- Potential Benefits
  - Increasing number of foragers improves foraging success and/or decreases predation risk
  - Increases reproduction of relatives
  - Food may allow long-term survival of group which increases chance of discovering sites in future

Summary of food-associated signals

Table 6.5
Synthesis of Some of the Primary Studies of Food-Associated Signaling

Species	Signal Info	Signal Context	Function	References*
Leptothorax Solenopsis Atta Pogonomyrmex	Location of food (chemical signal)	Following immobilization of prey that are too large for transport by a single individual	To recruit workers to prey and obtain aid in transport	1
Apis spp.	Location and quality of food (visual and auditory signal)	Return to the hive following successful foraging trip	To provide information to nest members about location of food	2
Passer domesticus	Location of food (acoustic signal)	Following discovery of divisible food item	Recruit conspecifics to divisible food items	3
Corvus corax	Location of food (acoustic signal)	Following discovery of carcass	Recruit others to food; carcass defense	4
Gallus gallus	Food quality (acoustic signal)	Discovery of food by rooster	Announce discovery and attract mates	5
Hirundo pyrrhonota	??Shareable food (acoustic signal)	Foraging	?Recruit others to food	6
Saguinus oedipus	Food preference Food quality (acoustic signal)	Foraging	?Recruit others to food	7
Leontopithecus rosalia	Food preference Food quality (acoustic signal)	Foraging	?Recruit others to food	8
Ateles geoffroyi	Location of food (acoustic signal)	Food discovery	Recruit group members	9
Macaca fuscata	?Location of food (acoustic signal)	Food discovery	?Recruit group members	10
Macaca mulatta	Caller's hunger level and food quality (acoustic signal)	Forager anticipates access to food, discovery, and/or possession of food	Recruit group (?kin) members to food	11
Macaca sinica	Location of high-quality/rare food (acoustic signal)	Forager discovers high quality food	Recruit group members to food	12
Pan troglodytes	Arousal, food quantity, and divisibility (acoustic signal)	Food discovery and possession	Recruit community members to food source	13

Vertebrates:

- Food signaling is rare
- Most signals occur at food (except mole-rats)

Social insects:

- Food signaling is common
- Signals to food from hive using trail pheromones or bee dances

Alarm calls:
Belding's ground squirrels

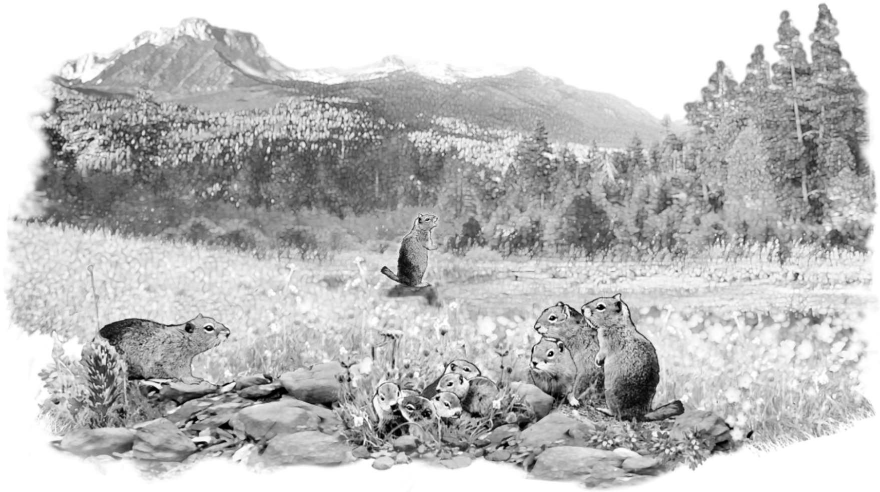


FIGURE 8.4: Kin selection and ground squirrels

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High risk Low risk

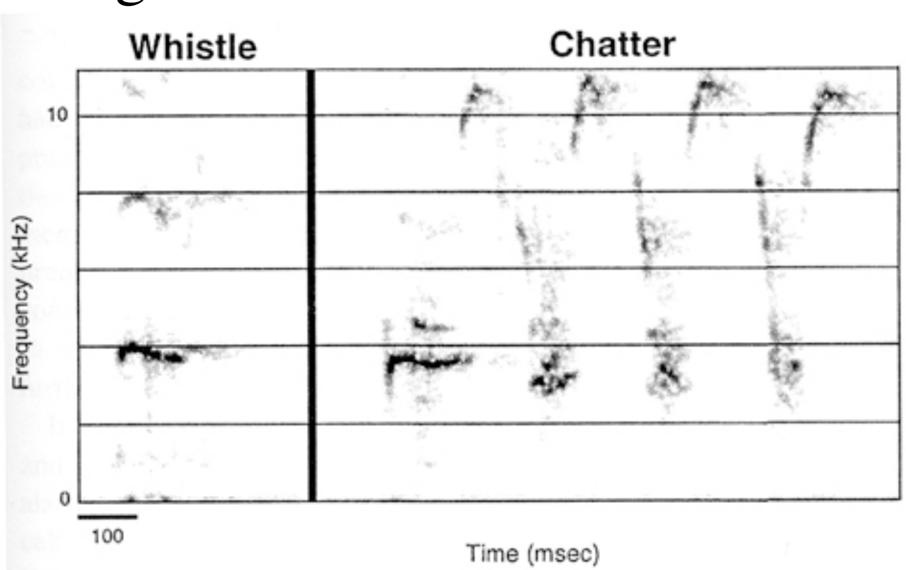


TABLE 17.1 Alarm Calling and Survival in Belding's Ground Squirrels at Tioga Pass, California.[a]

	Number of Ground Squirrels			
Category	Captured	Escaped	Percent Captured	$P(x^2$ Test)
Aerial predators				
Callers	1	41	2%	
Noncallers	11	28	28%	<0.01
Total	12	69	15%	
Terrestrial predators				
Callers	12	141	8%	
Noncallers	6	143	4%	<0.05
Total	18	284	6%	

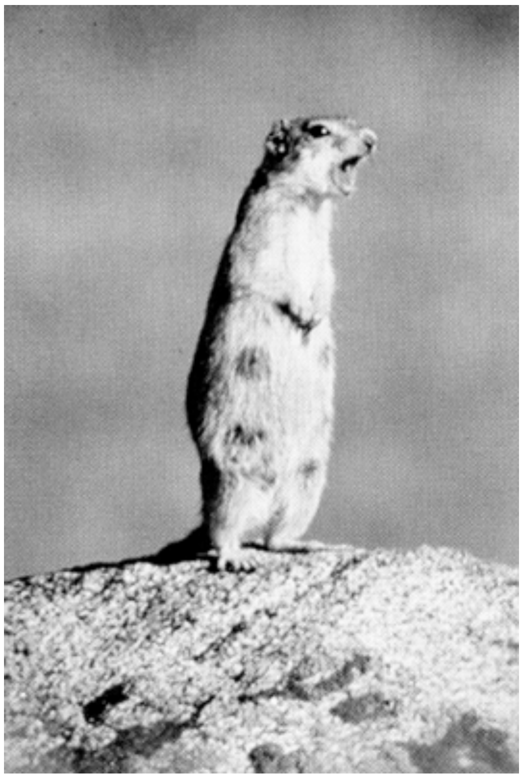
[a]All data are from observations made during attacks by hawks (n = 58) and predatory mammals (n = 198) that occurred naturally during 1974–1982.

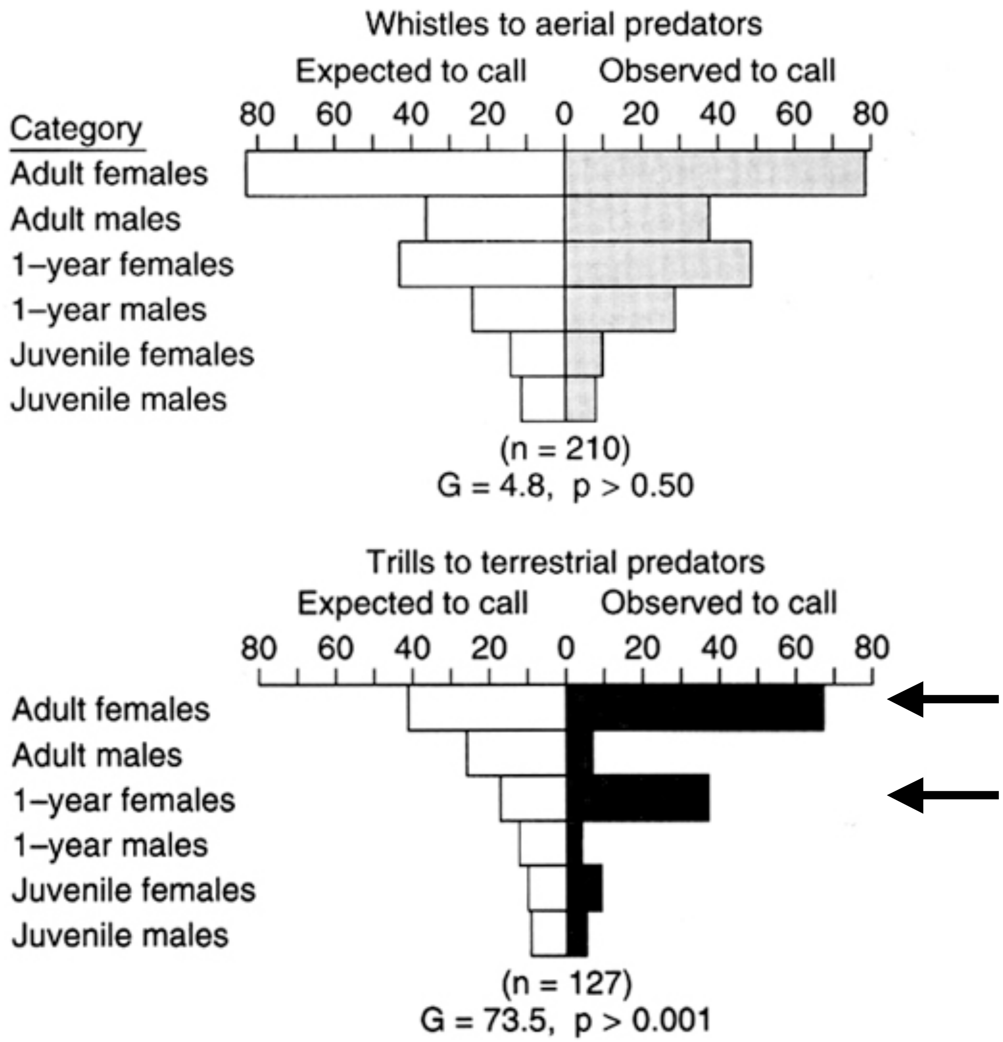
Source: P. W. Sherman (1985).

Why give alarm calls?

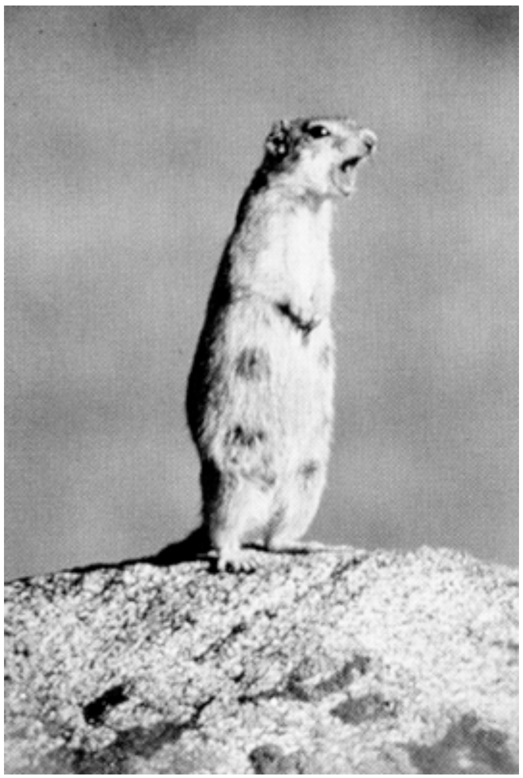
- Costs
  - Increase risk of capture
  - Signal production takes time and energy
- Possible benefits
  - Direct: signal to predator
    - Deter future attack by predator
  - Direct: signal to conspecifics
    - Manipulate fellow prey into capture
    - Improve own escape through synchronized response
    - Protect mate
    - Maintain optimal group size
  - Indirect: signal to conspecifics
    - Increase survival of relatives

Alarm trills differ by age and sex





Alarm calls and kinship



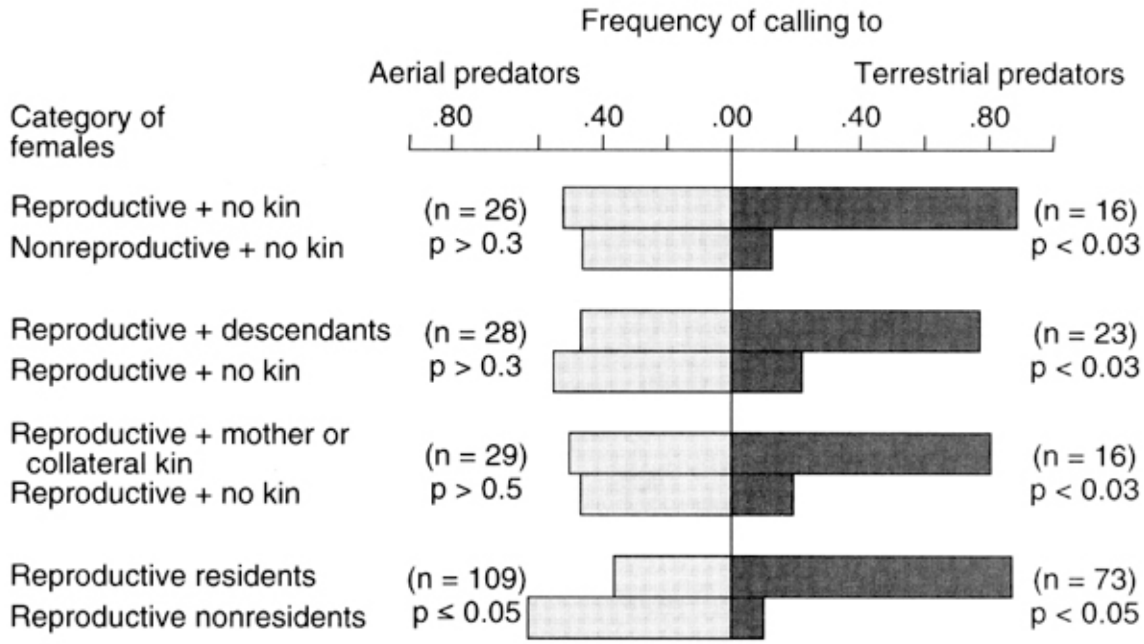
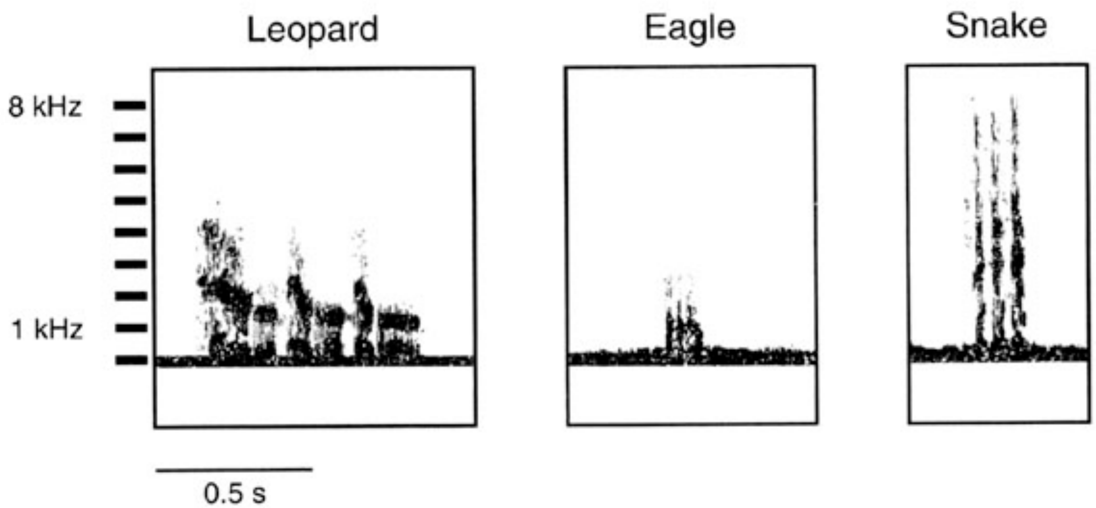


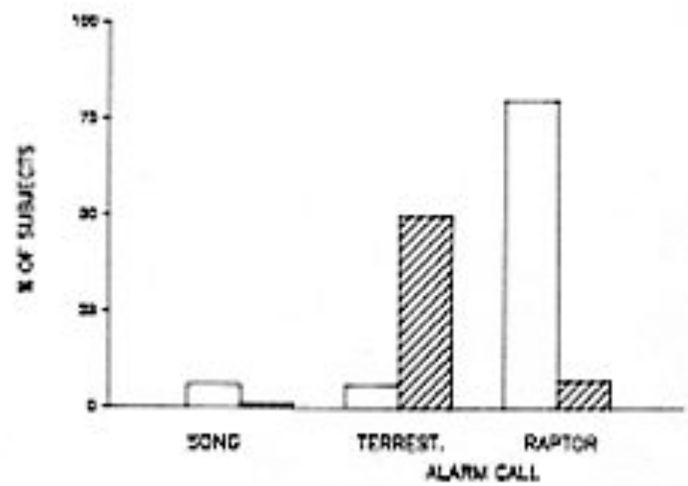
FIGURE 17.12 The effects of residency and genetic relatedness on the frequency of alarm calling for terrestrial and aerial predators in Belding's ground squirrels. Notice that when a terrestrial predator approached, reproductive females called more frequently than nonreproductive females. Furthermore, reproductive females with kin nearby called more than reproductive females with no kin, and residents called more frequently than nonresidents. Kinship and residency did not affect the frequency of calling when an aerial predator approached. (From P. W. Sherman 1985.)

Referential signaling

- Do alarm calls convey information about predator type or just urgency associated with potential attack?

Vervet alarm calls





Hatched = run up trees
Open = run down to shelter

Alarm calls refer to predators

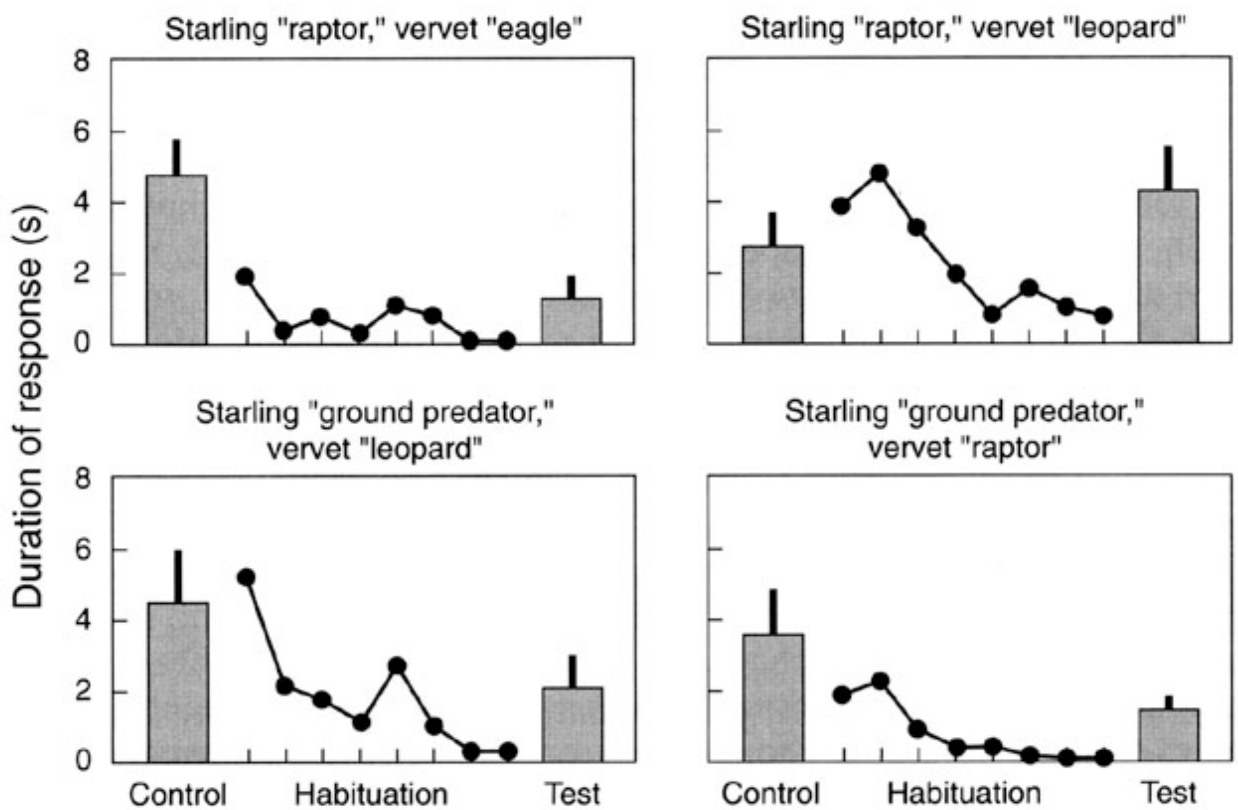


Figure 12.13. Duration of looking toward a speaker in vervets exposed to the indicated alarm calls recorded from vervets and starlings, demonstrating cross-habituation between calls with the same meaning. The call listed first above each panel was the habituating call; the second call was played in the control and test trials. Redrawn from Seyfarth and Cheney (1990) with permission.

Development of vervet eagle alarm calls

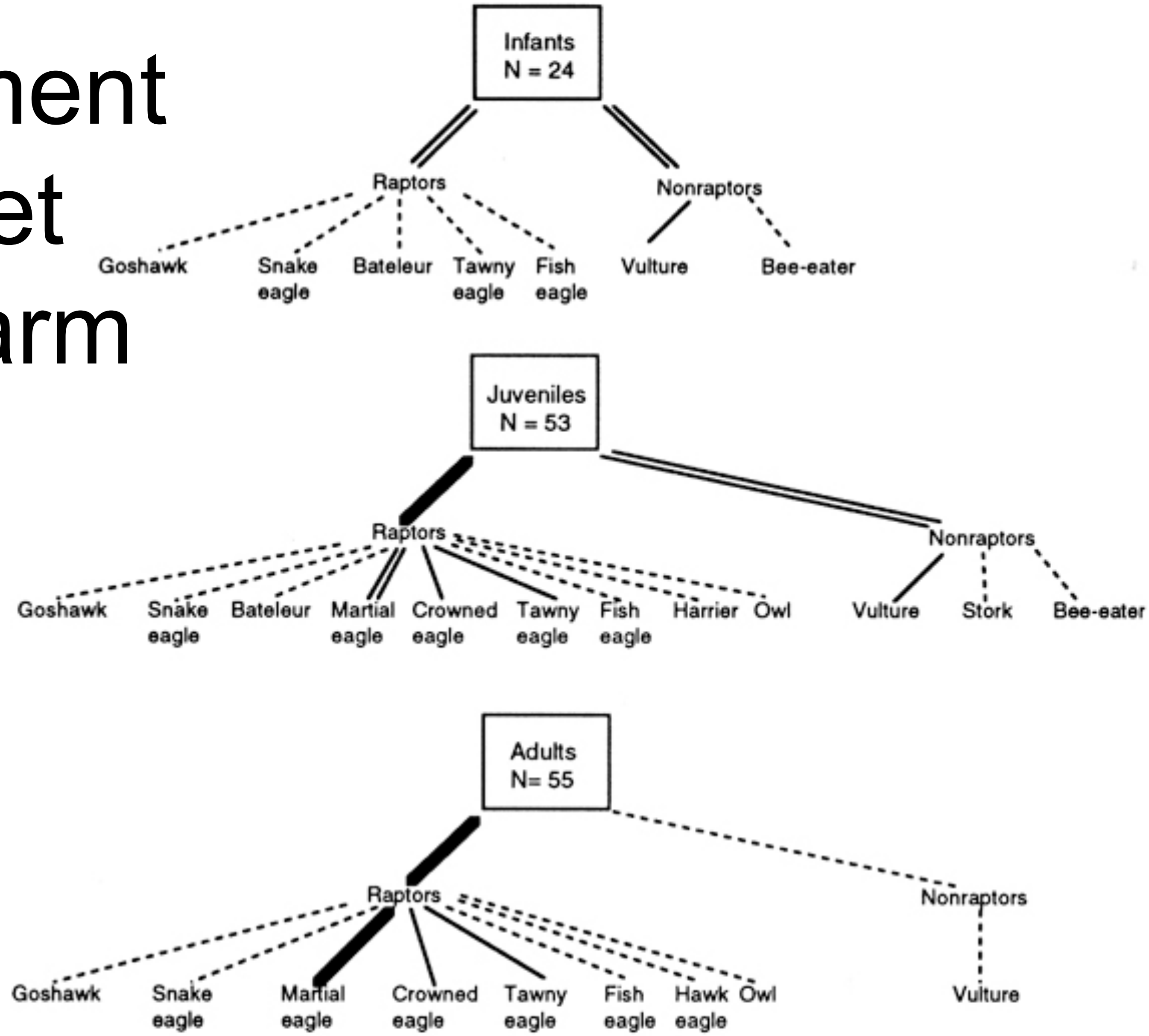


Figure 5.19
Developmental changes in the target of vervet monkey eagle alarm calls. Infants: <1 year old; Juveniles: 1–4 years old; Adults: >4 years old. Dashed lines: <5 alarms; thin solid lines: 6–10 alarms; double lines: 11–15 alarms; thick solid lines: >15 alarms (redrawn from Seyfarth and Cheney 1986).



Meerkat alarm calls signal predator class and urgency

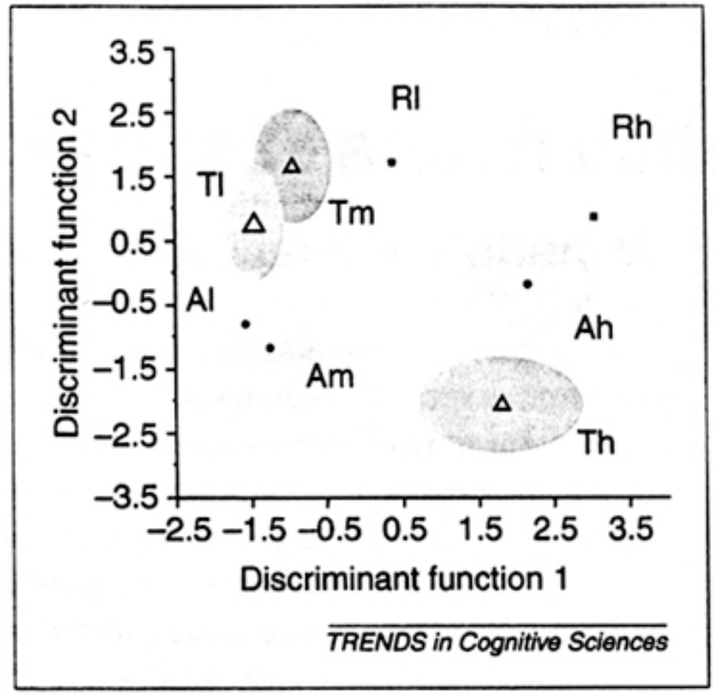


Fig. 2. Arrangement of the alarm calls given in different predator contexts according to their values as established by discriminant function analysis (DFA) of the calls' acoustic properties. Circles are spanned by the mean ± SD of the first two discriminant functions, with data drawn from 10 runs of the DFA. T, A and R stand for terrestrial predator alarms, aerial predator alarms and recruitment alarms, respectively; l, m and h stand for low-, medium- and high-urgency calls, respectively.

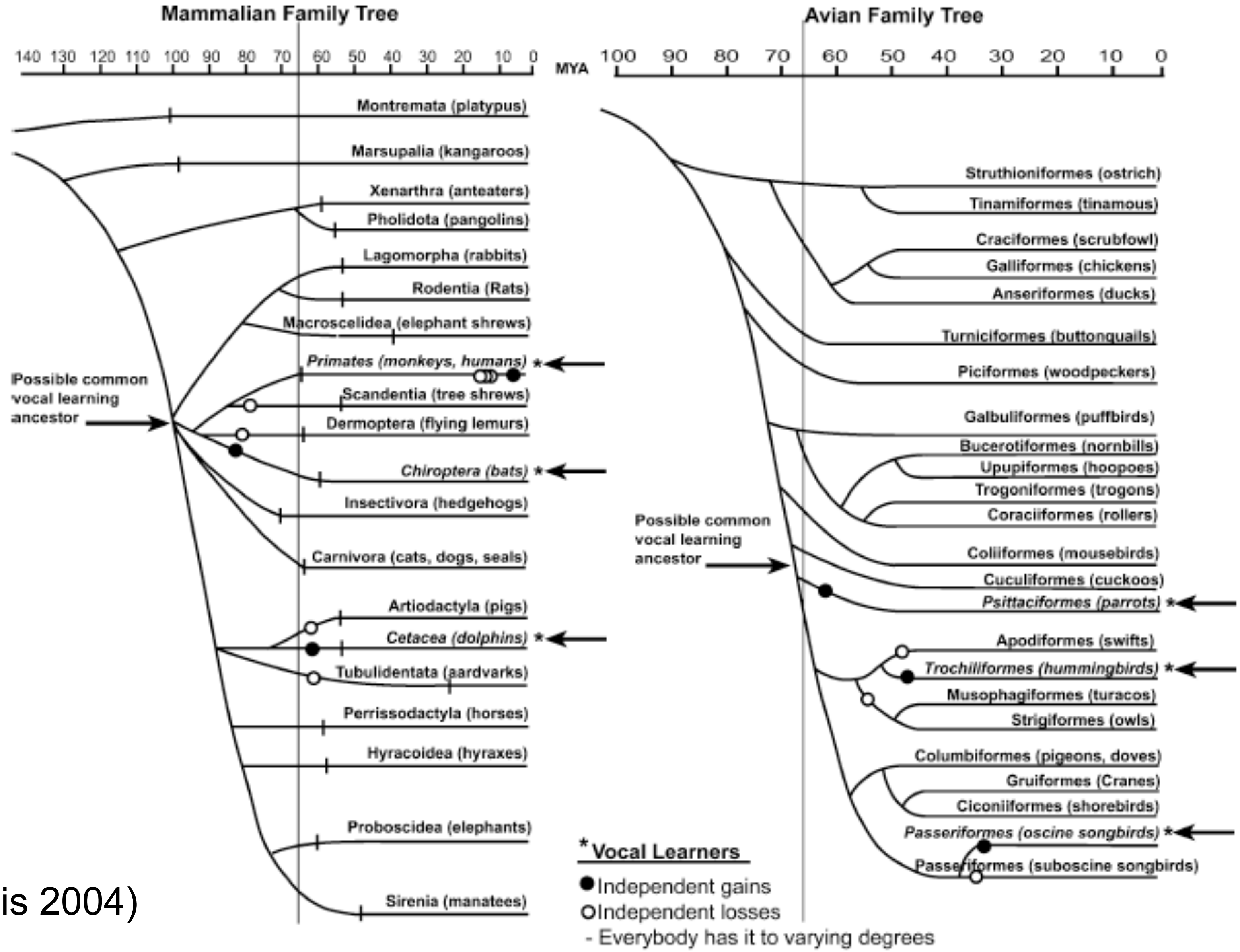
and young animals acquire urgency context before predator context

Hollen, L.I. and Manser, M.B. 2007 Motivation before Meaning: Motivational Information Encoded in Meerkat Alarm Calls Develops Earlier than Referential Information. Am Nat 169: 758-767.

Vocal learning conclusions

- Mammals
  - Young animals learn call context, not call type
  - Examples of vocal learning typically involve call convergence for group recognition
- Birds
  - Vocal mimicry is widespread and male-limited in oscines
  - Repertoires function in sexual advertisement and territorial encounters
    - Why species differ in repertoire size is unclear
  - Parrots exhibit call convergence of group calls
  - We know little about hummingbird vocal learning

Is vocal learning a single trait?



(Jarvis 2004)