Social Integration

- Recognition
  - Process
  - Mechanisms
- Male-female integration
- Parent-offspring integration
- Group integration

Recognition Process

- Sender provides information
- Receiver perceives signal above background
- Receiver compares information in signal to a model of target stored in memory
- Receiver decides whether sender is target or not
- Receiver takes action in response to target
  - Feed offspring or not
  - Flee from predator or not

Recognition issues

- Difficulty of discrimination task depends on the number of classes that must be distinguished
  - Number of classes depends on identification level, i.e. sex, species, group, or individual
- Recognition is never perfect
- Sender and receiver need not agree on amount of information to transfer
- Mistakes happen

1

2

3

4

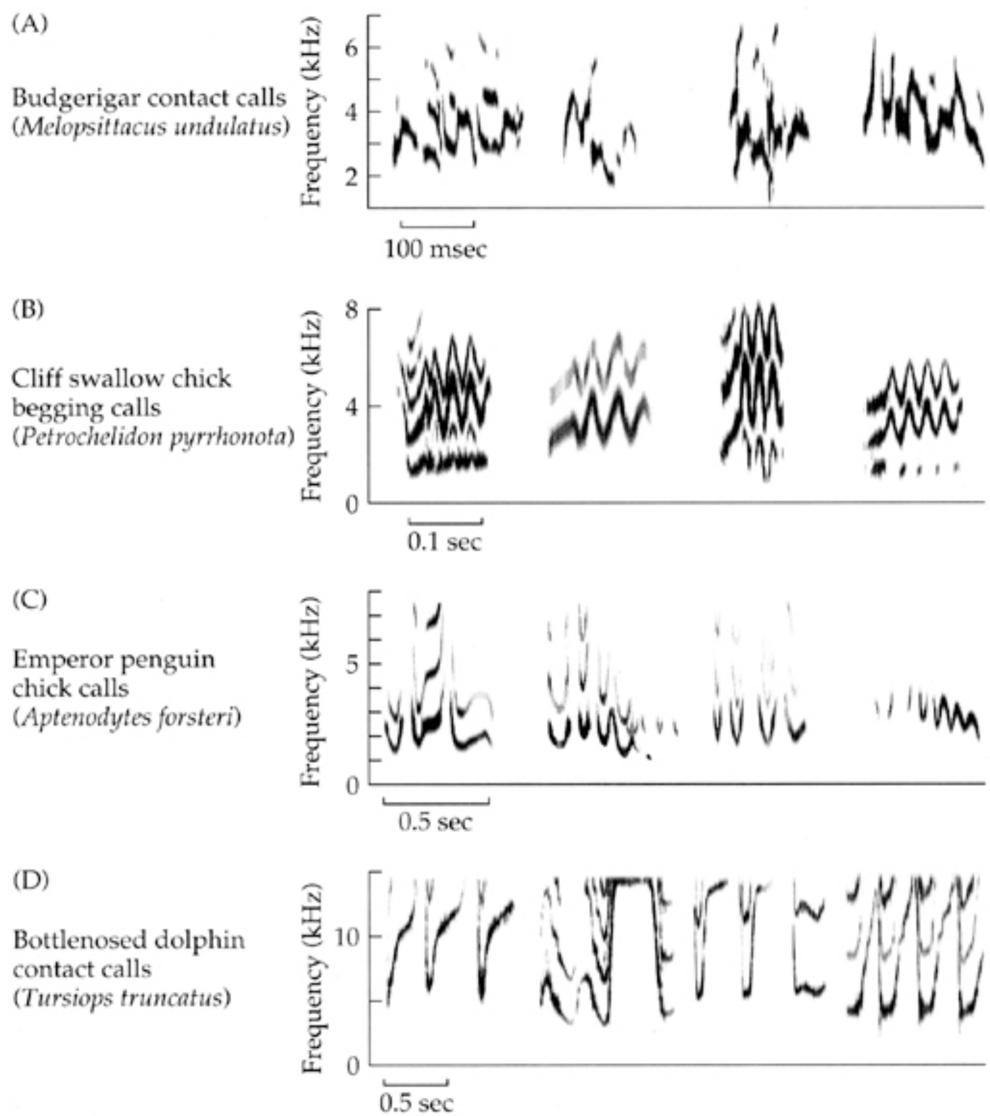
1. Larvae of the blister beetle (*Meloe franciscanus*) aggregate to mimic the appearance of female bees (*Habropoda pallida*)
2. Male *H. pallida* attemps to copulate with the aggregate (pseudocopulation)
3. Male deposits beetles on female during authentic copulation (venereal transmission)
4. Adult *M. franciscanus*

Hafernik, J. and Saul-Gershenz, L. 2000. Beetle larvae cooperate to mimic bees. Nature. Vol. 405. 4 May: 35

Recognition mechanisms

- Spatial location
  - e.g. treat offspring in nest as own
- Familiarity
  - Individual level recognition requires learned familiarity and requires complex signature signals
- Phenotype matching
  - Ability to assign stimuli to classes of relatedness relative to the receiver
  - Referent can be a known relative or oneself
- Allele matching
  - Requires hypervariable locus with olfactory signal

Vocal signatures



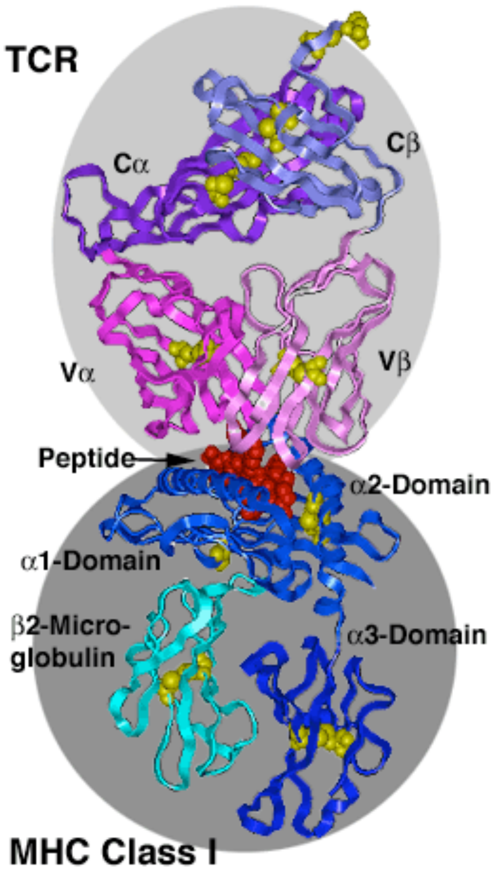
Phenotype matching in salamanders?

TABLE 1 The effect of genetic relatedness on the development of cannibal forms of the tiger salamander in aquaria with equal larval densities

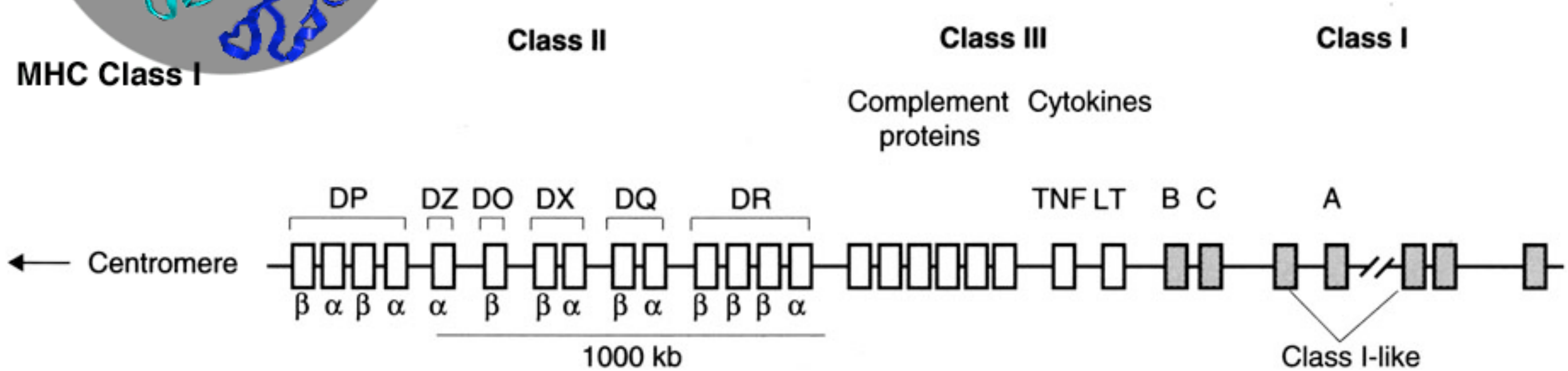
Composition of aquarium population	Cannibal develops	No cannibal develops	Total experiments
Siblings only	31 (40%)	46 (60%)	77
Nonsiblings present	67 (84%)	12 (16%)	79

Source: Pfennig and Collins [894]

Multiple Histocompatibility Complex



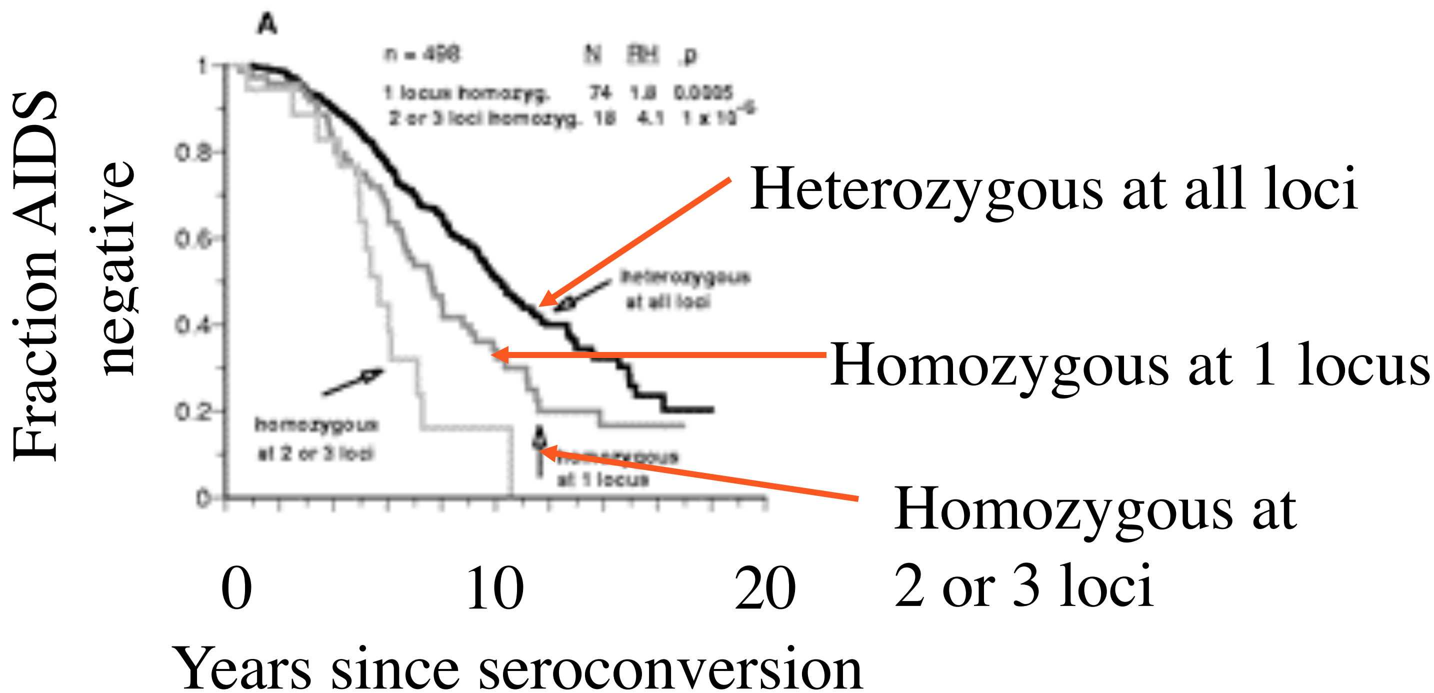
- T-cell receptor (TCR) occurs on T lymphocytes and detects antigens that bind to to MHC, formed by cellular recombination
- MHC is involved in cell-cell recognition
- = Human leukocyte antigen (HLA), chr 6
- Many loci exhibit high levels of heterozygosity with >100 alleles in humans
- Permits kin recognition in many vertebrates



Why is the MHC so diverse?

Heterozygote advantage

A study of humans infected with HIV showed that MHC heterozygotes showed a significantly slower progression to AIDS than homozygotes (Carrington et al. 1999)



MHC odors are expressed

- Sebaceous glands
  - Located all over the body
  - Secrete an odorless, oily liquid that is broken down by bacteria into volatile molecules
- Apocrine (sweat) glands in the axillae (e.g. armpits)
  - Protein carriers bind and transport odorants to the axillae
  - They are metabolized and made volatile by bacteria

Is MHC used for recognition?

(Potts et al., 1991, Manning et al. 1992, Penn and Potts 1998)

1. Create semi-outbred stocks of mice with multiple, known MHC types

2. Stock replicate populations in a barn, allow to interact freely.

3. Monitor interactions

4. Test MHC type of pups

MHC mate choice in humans

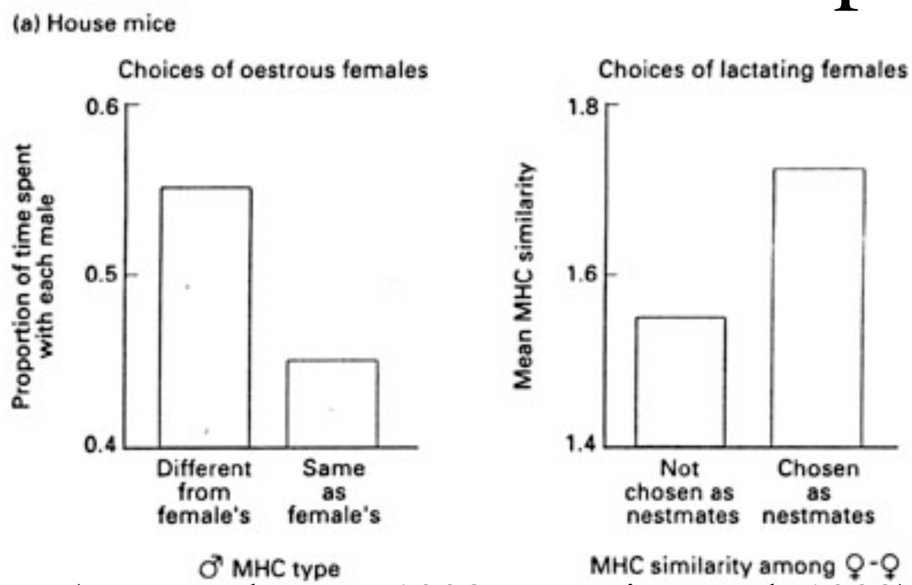
Odor Donators (Typed for MHC)

- 4 men, 2 women
- Between 21 and 25 yrs
- Armpits unshaved
- Wore plain cotton T shirt 2 nights in a row
- Bagged T shirt

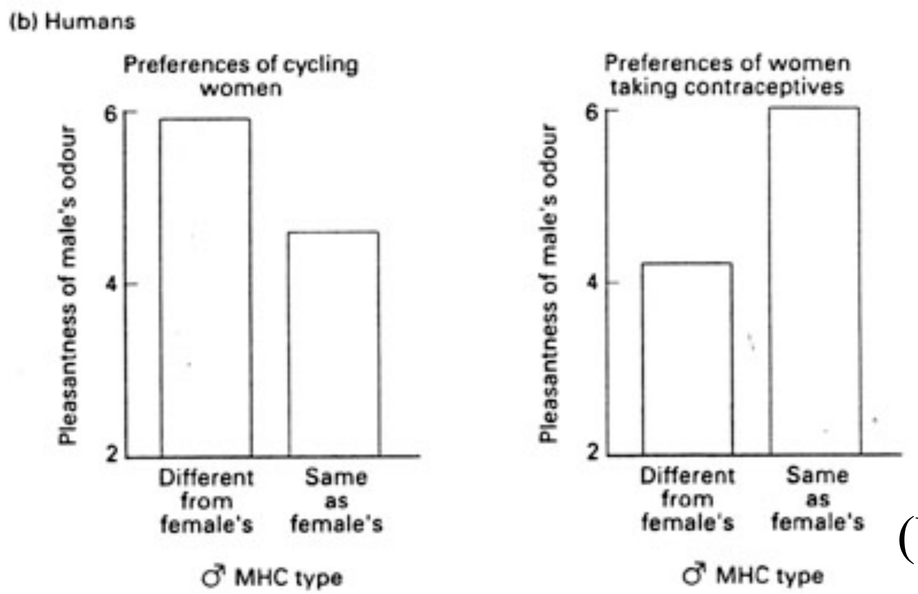
Smellers (Typed for MHC)

- 121 males and females
- Females in second week post menstruation
- Mean age 26 yrs
- Asked to smell T-shirt (no knowledge of odor donator) held inside of opaque box.
- Asked to rank pleasantness (1-10)
- Asked to rank memory association (like a previous lover? Family member?)

Mice and humans prefer alternate MHC



(Penn and Potts, 1998; Manning et al. 1992)



(Wedekind and Furi 1997)

MHC and mate choice in American Hutterites
(Ober et al. 1997)

Hutterites:

- Anabaptist sect
- In 1800's, 400 individuals immigrated to US to avoid persecution
- Have increased to 35,000 individuals today
- Most inbred US population of European descent
- Consequently, relatively few MHC types (more tractable for study)
- Contraception/abortion banned
- Communal living (equivalent nutrition)
- Use of alcohol/drugs banned

Deficit in MHC homozygotes at birth (relative to number expected based on random mating): Why?

Disassortative Mate Choice

Number of couples with:	Expected	Observed*
Matching MHC types	65	44
Different MHC types	346	367

Abortional (Miscarriage) Selection

Number of couples with:	Successful Pregnancy	Miscarried Pregnancy*	% Miscarried
Matching MHC types	20	10	33
Different MHC types	193	28	13

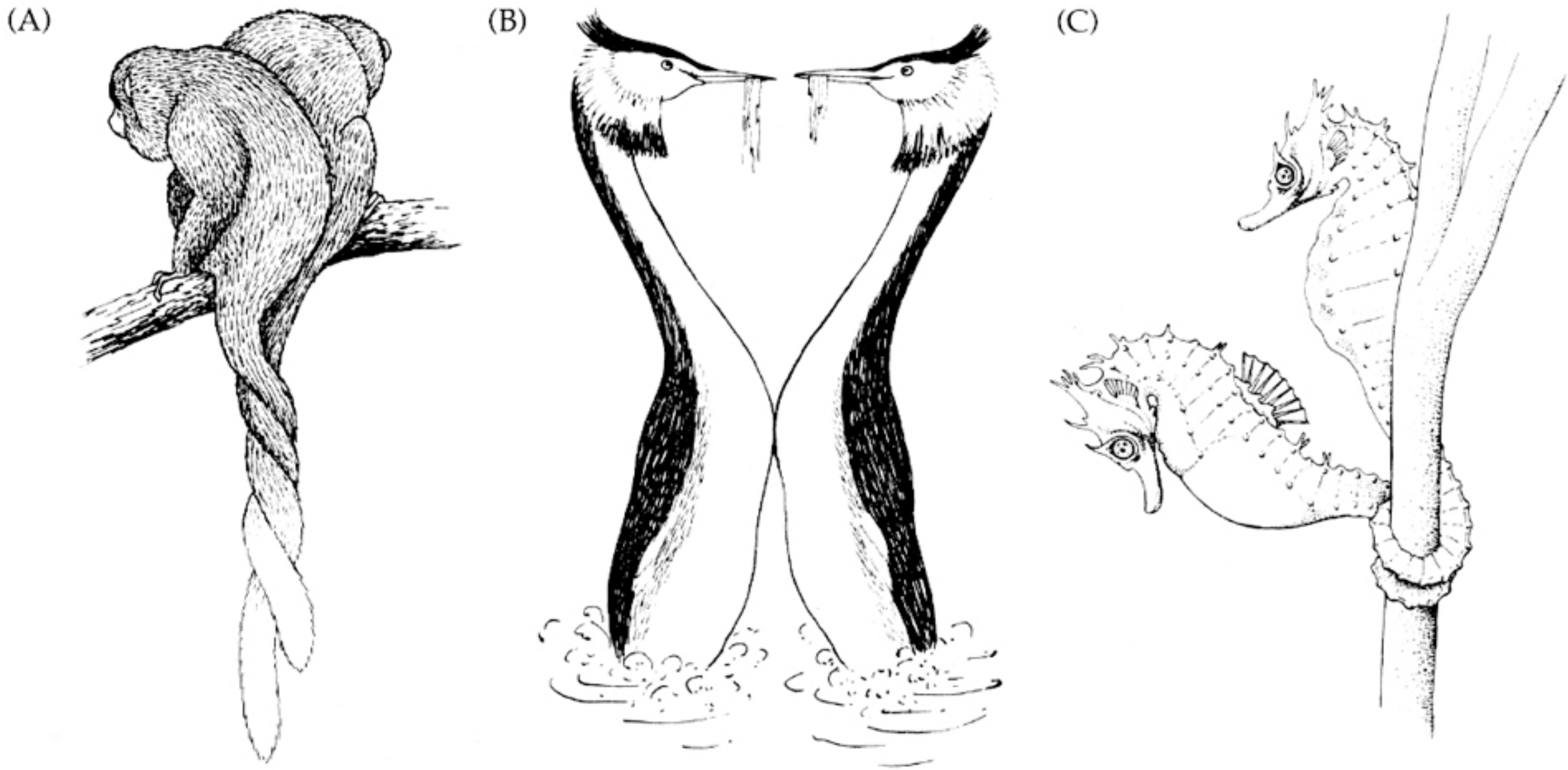
MHC recognition

- Advantages to MHC disassortative mating
  - Avoid inbreeding
  - Increase MHC diversity of offspring
- Advantages to MHC assortative nesting
  - Kin selection, e.g. increases inclusive fitness if there is cooperative care or defense of young

Male-female integration

- Species recognition
  - Can be hard-wired since only one signal variant needs to be recognized
    - Chemoreceptor sensitivity in some male moths
    - Color sensitive eyes of some fish and butterflies
    - Frequency sensitivity of some frogs
  - Parental care permits imprinting
- Coordination of reproduction
  - Female reproduction often needs stimulation by a species-specific male signal and vice versa
  - Provides opportunity for male exploitation

Pairbond behaviors



Pair-bonding in voles

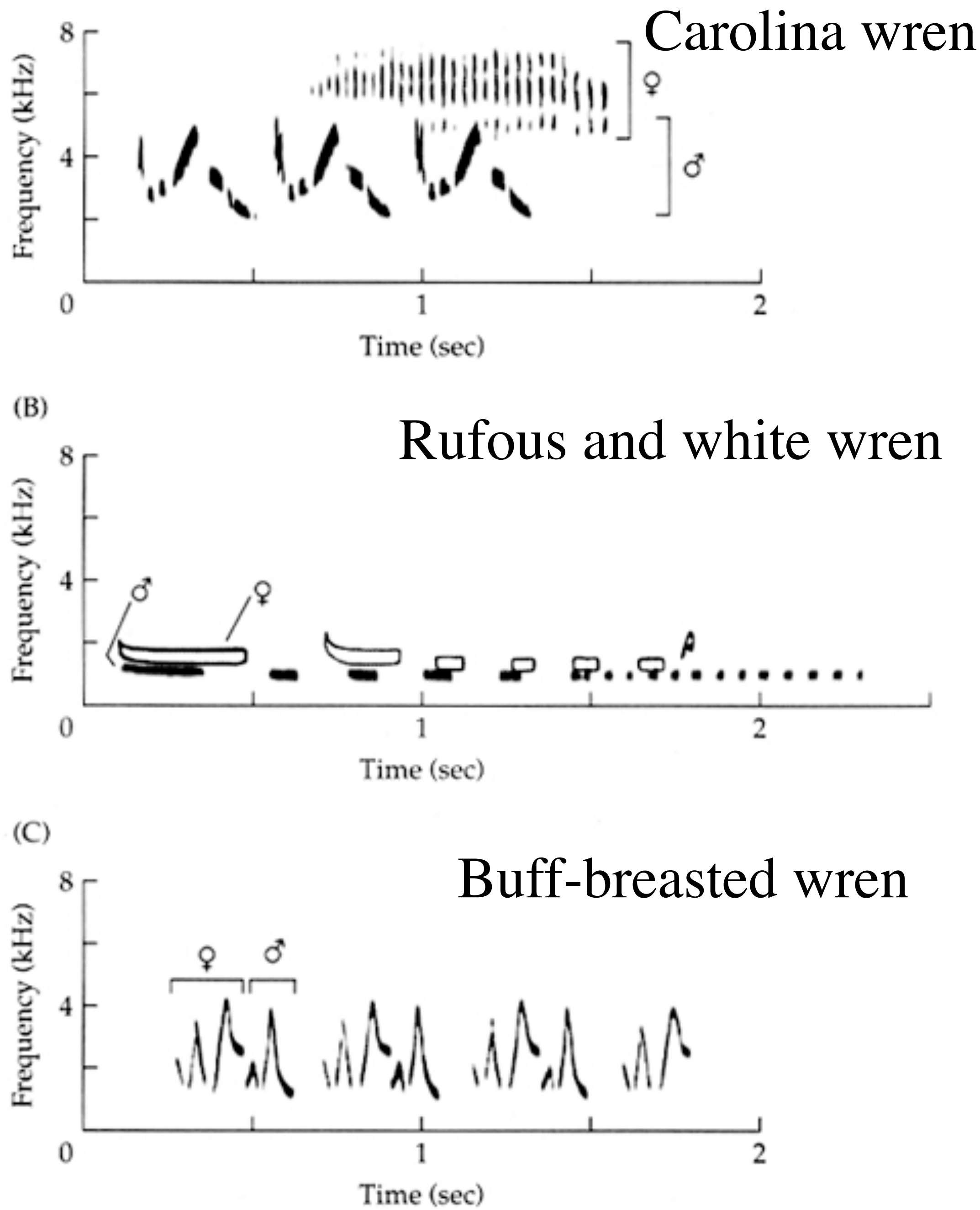
	Prairie Vole	Montane Vole
		
	Monogamous	Promiscuous
Duration of coitus (hrs)	30-40	0.5-3
Time to secretion of progesterone	> 2 hours	10 min.

Females must sniff males to enter estrous. Following mating, prairie vole pairs will show affiliation toward each other; hostility to strangers. Female response is due to oxytocin; male response to vasopressin

Duets

Found in

Monogamous species
In dense vegetation
Keeps pair together
Minimizes extra pair cops
Advertises territory

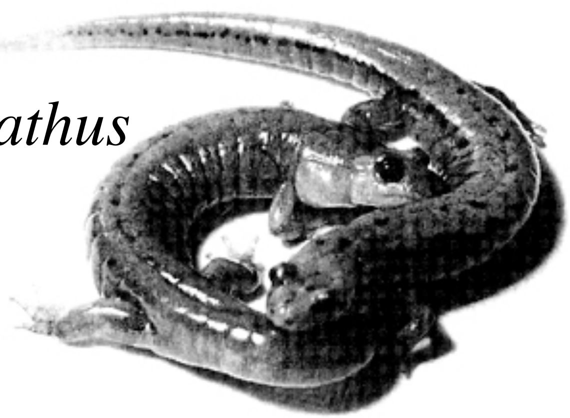


Pheromone delivery in salamanders

Pheromone wafting by male newt

Chin rubbing on female nares by male *Plethodon*

Chin rubbing on female back by male *Desmognathus*

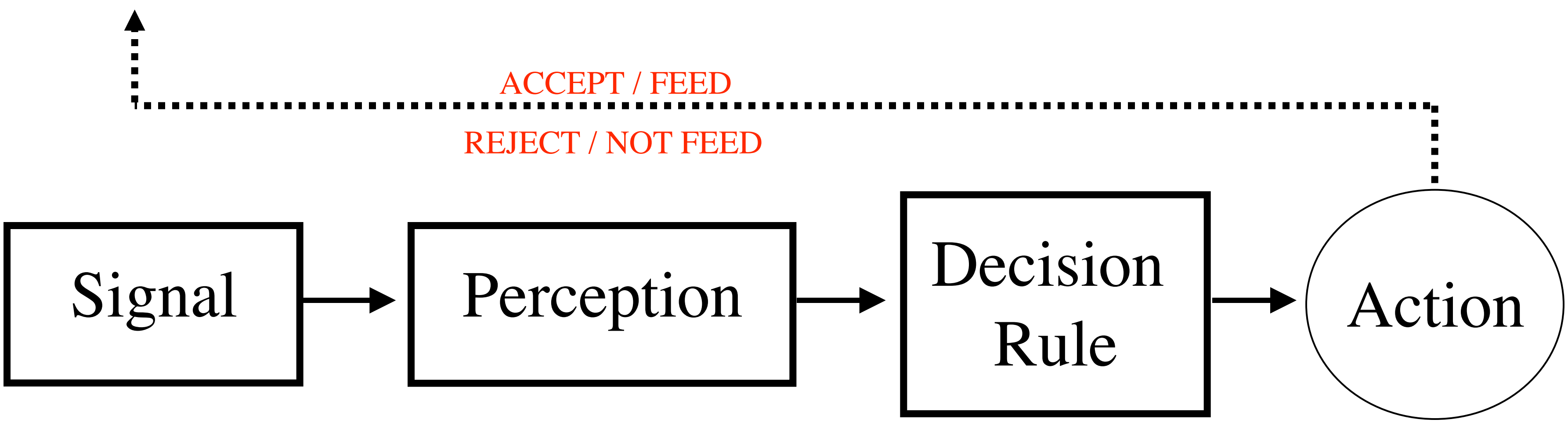


Forced copulation by male *Euproctis*

Parent-Offspring Recognition

Sender
Offspring

Receiver
Parent



- Signature

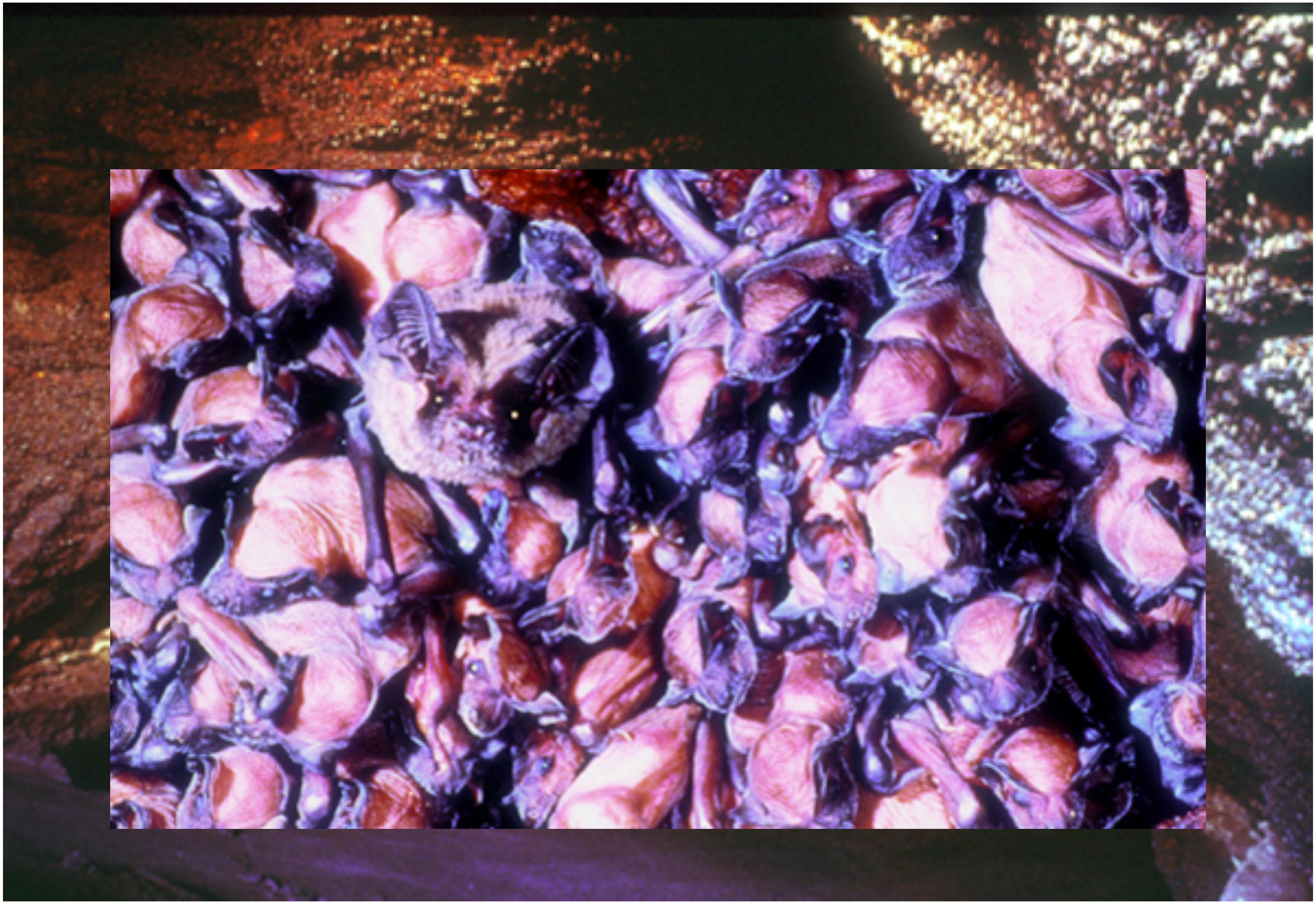
- Discrimination
- Template-Matching

- Depends on *a priori* probability (1/n)
- Costs and benefits likely differ between offspring and parent

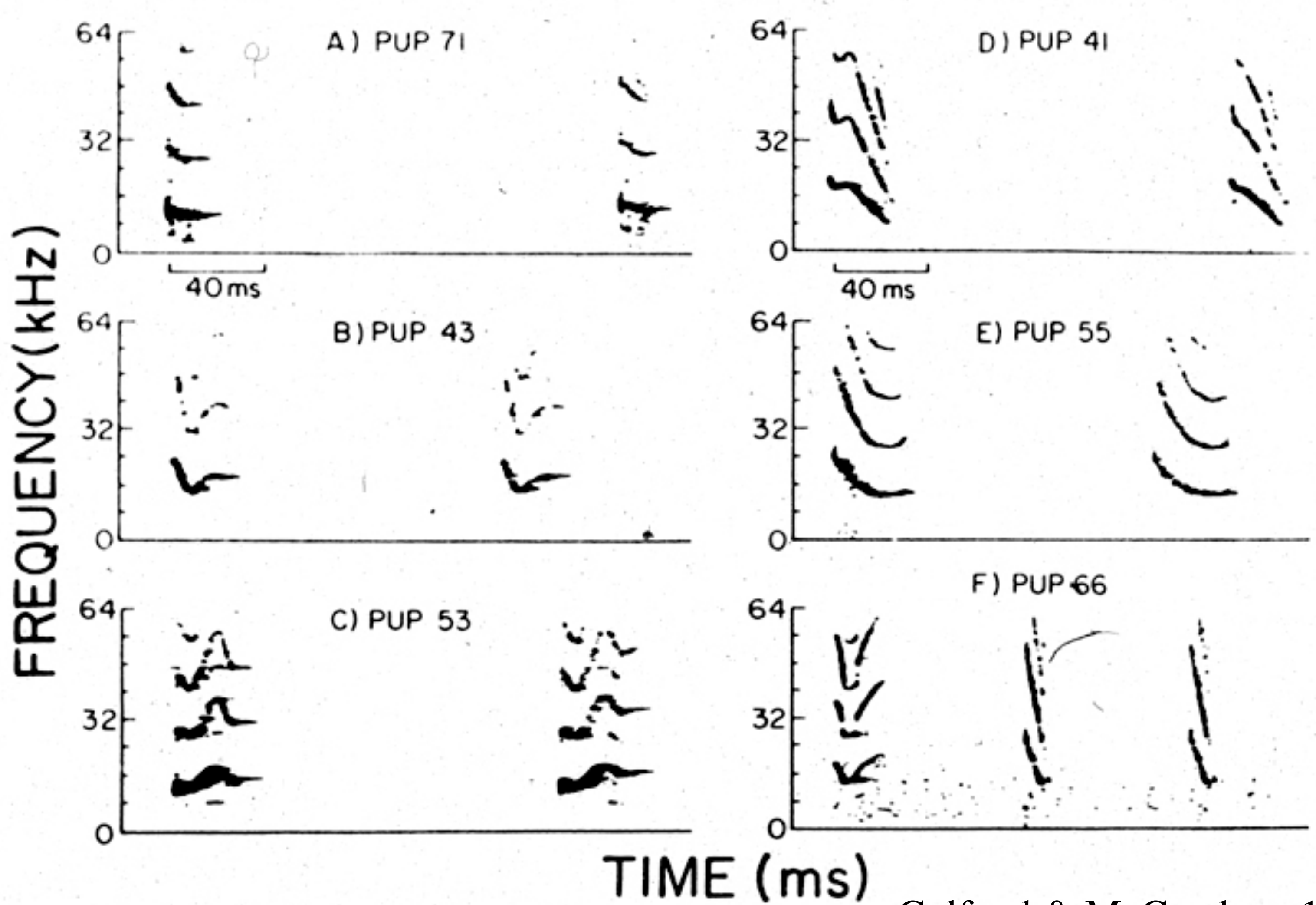
Parent-offspring recognition

- Predict recognition accuracy of parents should be high when cost of making mistake is high
- Recognition accuracy of pups may be low, unless there is punishment
- Signal complexity or enhanced receiver discrimination or both should increase with task difficulty

Pup recognition in Mexican free-tailed bats

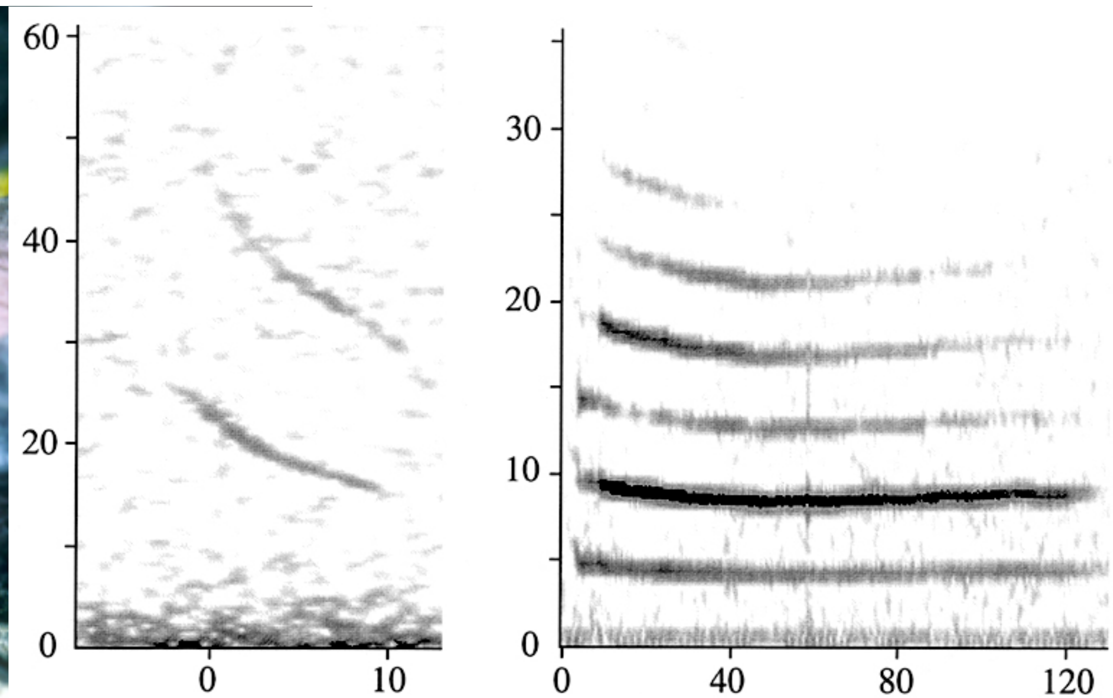


Tadarida brasiliensis
(Molossidae)



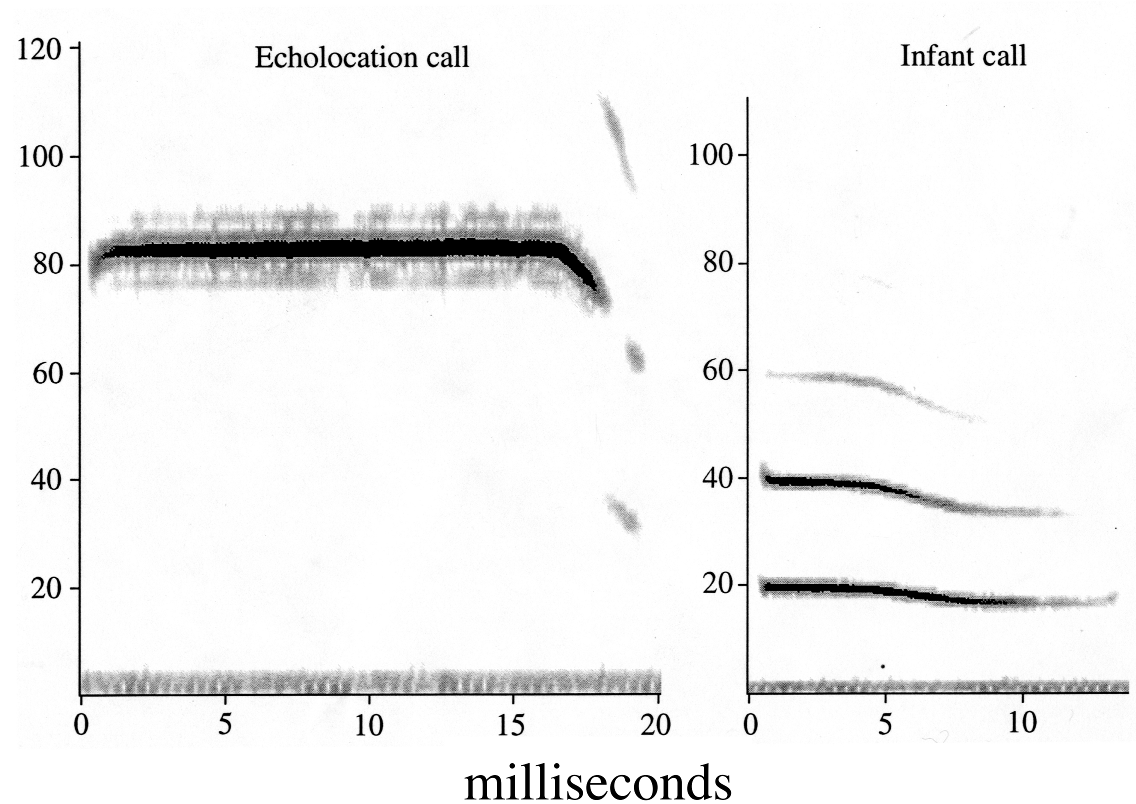
Gelfand & McCracken, 1986

Chaerophon pumila
(Molossidae)



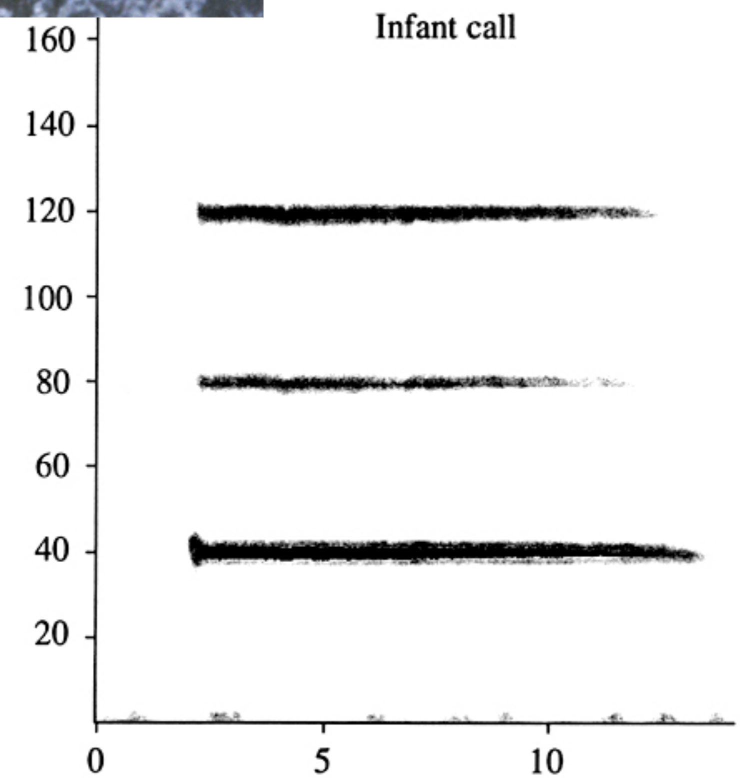
milliseconds

Rhinolophus simulator
(Rhinolophidae)

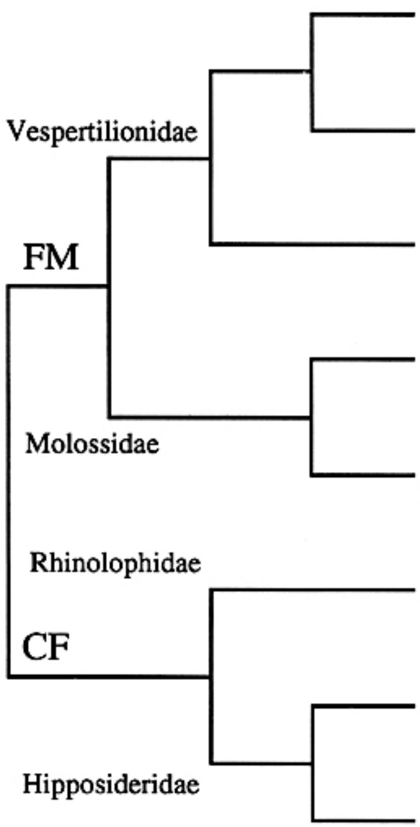


Cleotis percivalli

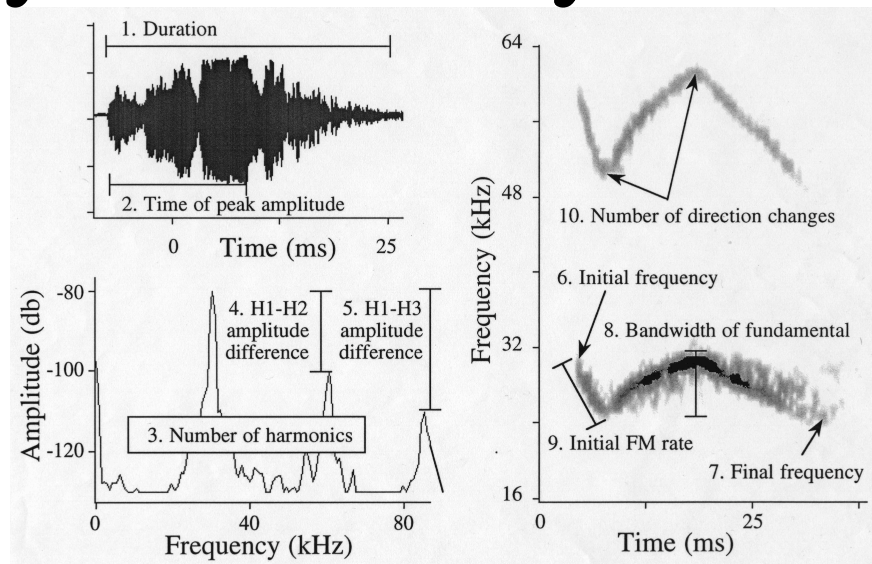
(Rhinolophidae)

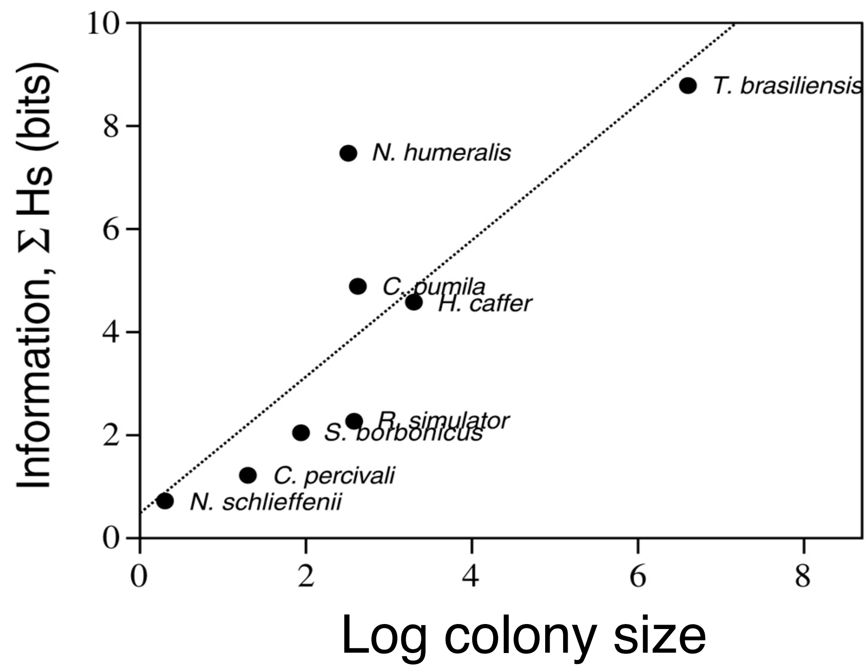


Pup call complexity and colony size



Species	Creche?	Colony Size
Nycticeius humeralis	yes	240
Nycticeinops schlieffenii	no	2
Scotophilus borbonicus	yes	87
Tadarida brasiliensis	yes	4,000,000
Chaerephon pumila	yes	422
Rhinolophus simulator	yes	380
Hipposideros caffer	no	211
Cleotis percivali	no	20

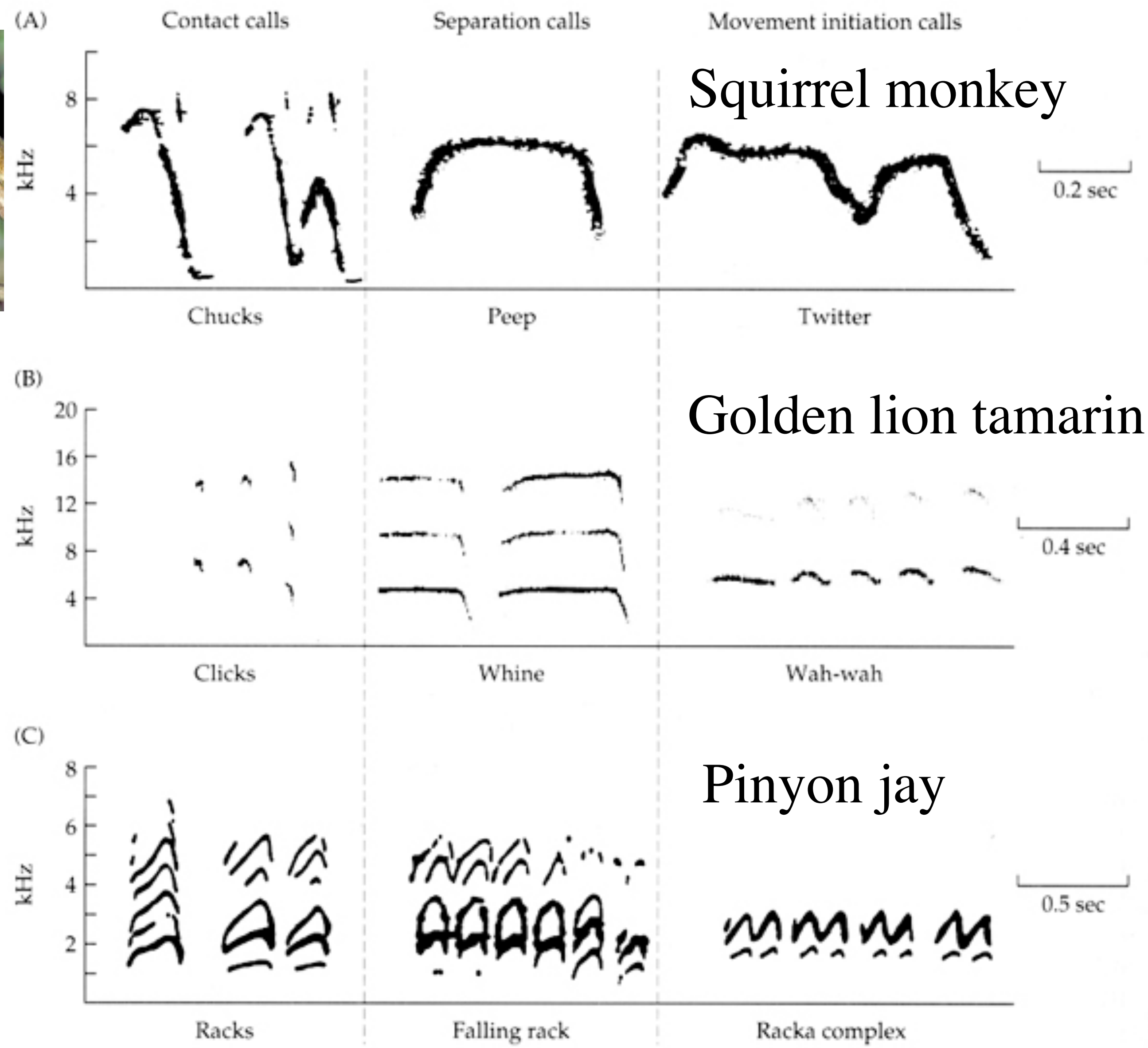




Group integration

- Social groups permit cooperation, but require mechanisms for recognition to prevent cheaters
- Group recognition and mimicry
- Coordination of group movements in bird flocks and fish schools
- Worker organization in social insects

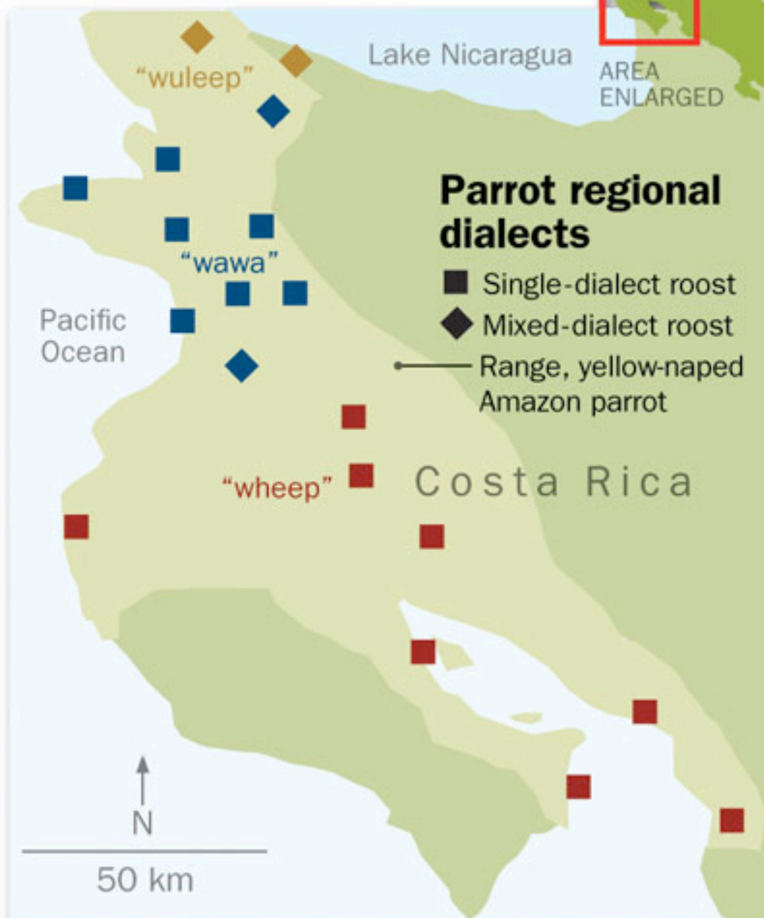
Group cohesion calls



Group recognition vocalizations can involve vocal mimicry

- Amazon parrots
- Bottlenose dolphins
- Killer whales
- Chimpanzees
- Spear-nosed bats

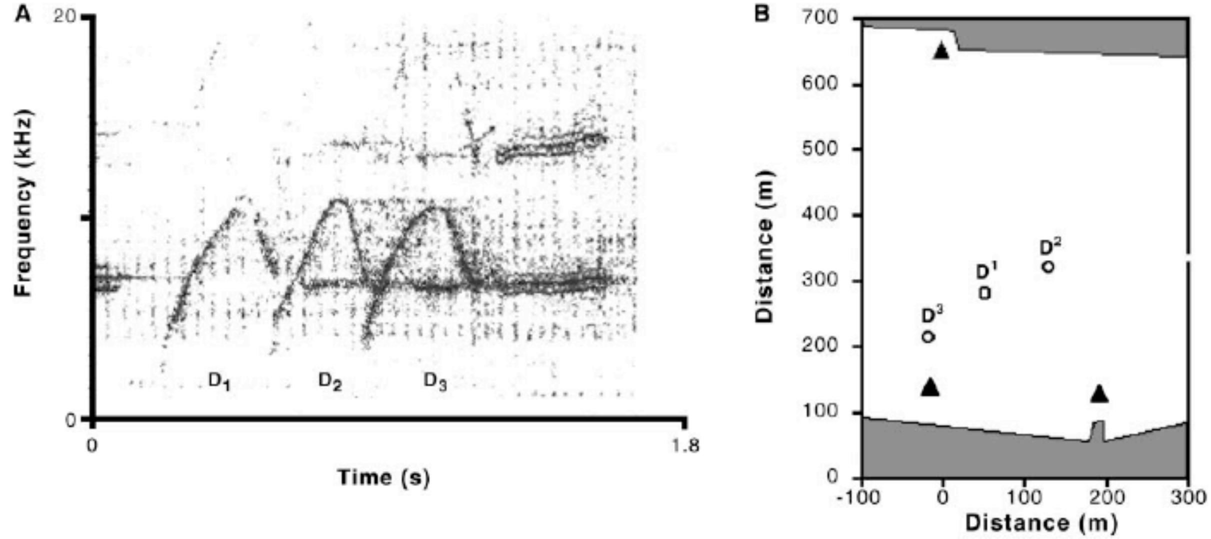
Amazon parrots



Wright, T.F., C.R. Dahlin, A. Salinas-Melgoza. 2008. Stability and change in vocal dialects of the yellow-naped amazon. *Animal Behaviour. 76:1017-1027*

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*).



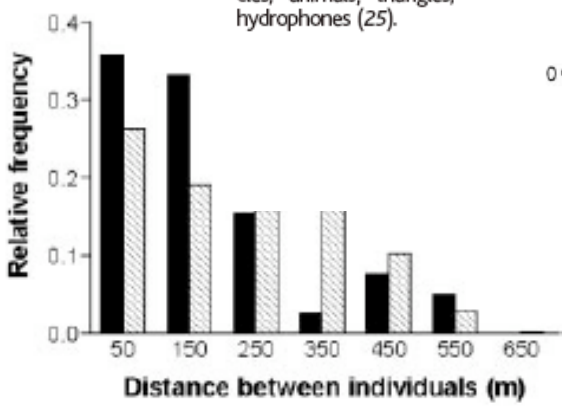
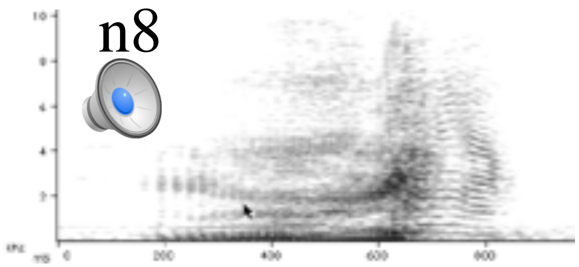


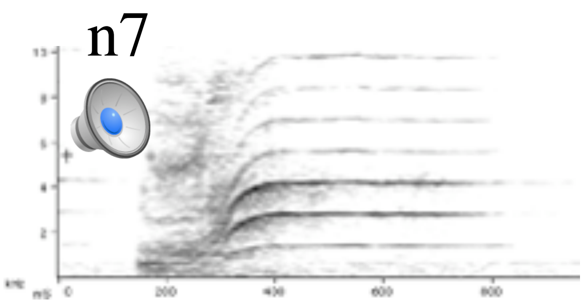
Fig. 2. Distributions of the distances between dolphins in matching (solid bars) and nonmatching (hatched bars) whistle interactions.

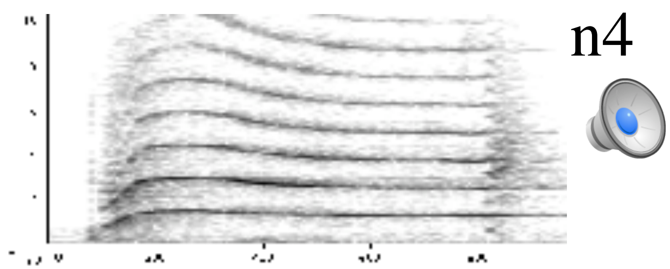
Janik VM 2000 Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289: 1355-1357.

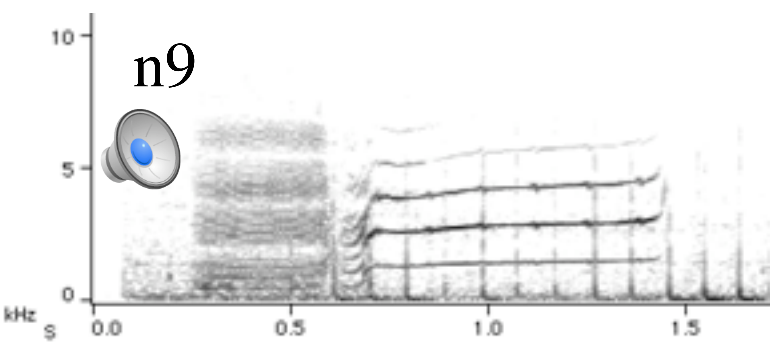
- Free-ranging animals produce matching whistles in response to nearby calls
- Propose that individuals are signaling to known individuals

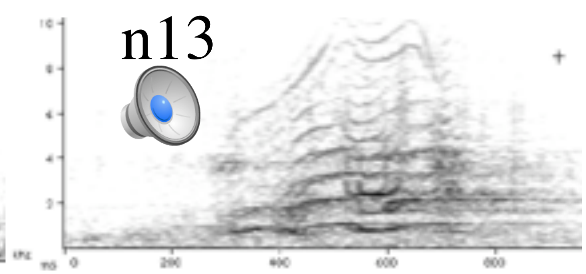
Killer whale dialects

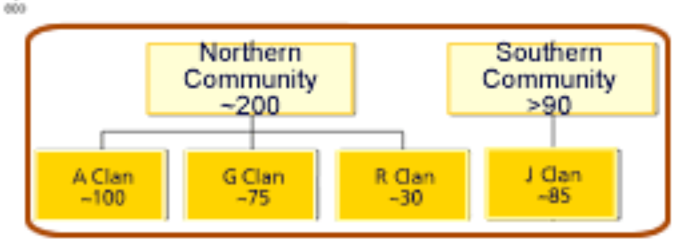










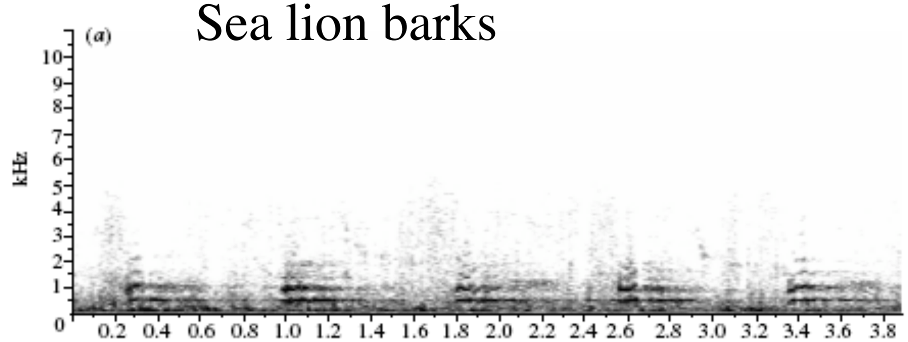


http://www.killerwhale.org/fieldnotes/chat.html

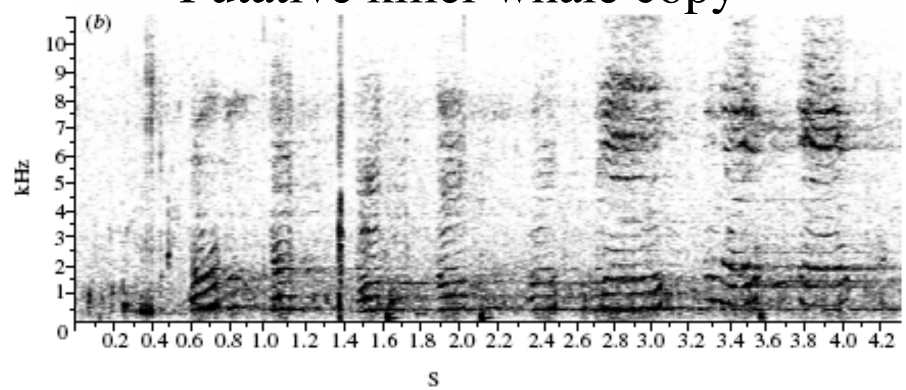
Vocal mimicry by a killer whale?

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

Sea lion barks

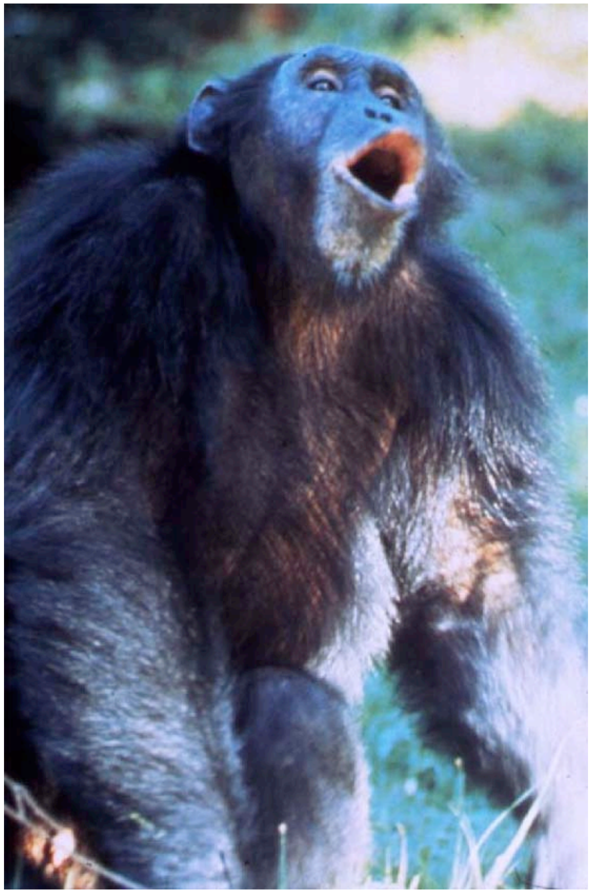


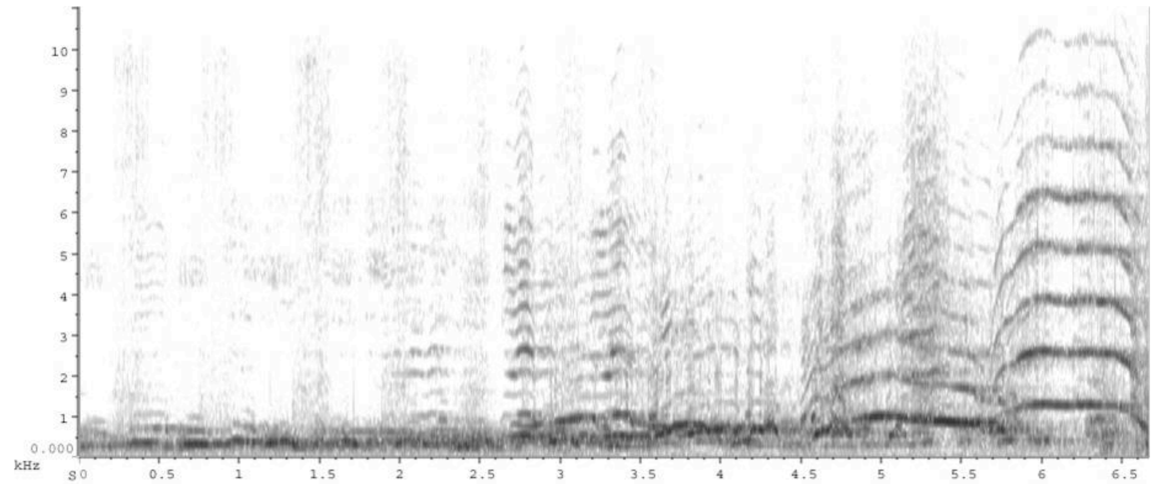
Putative killer whale copy



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.

Chimpanzee pant hoots

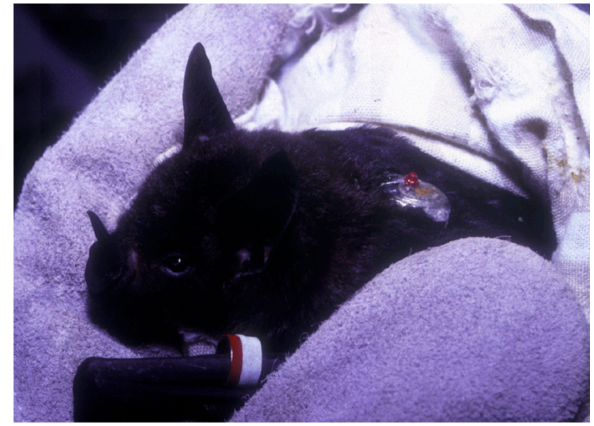




Crockford C, Herbinger I, Vigilant L, et al. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? Ethology 110: 221-243

- 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



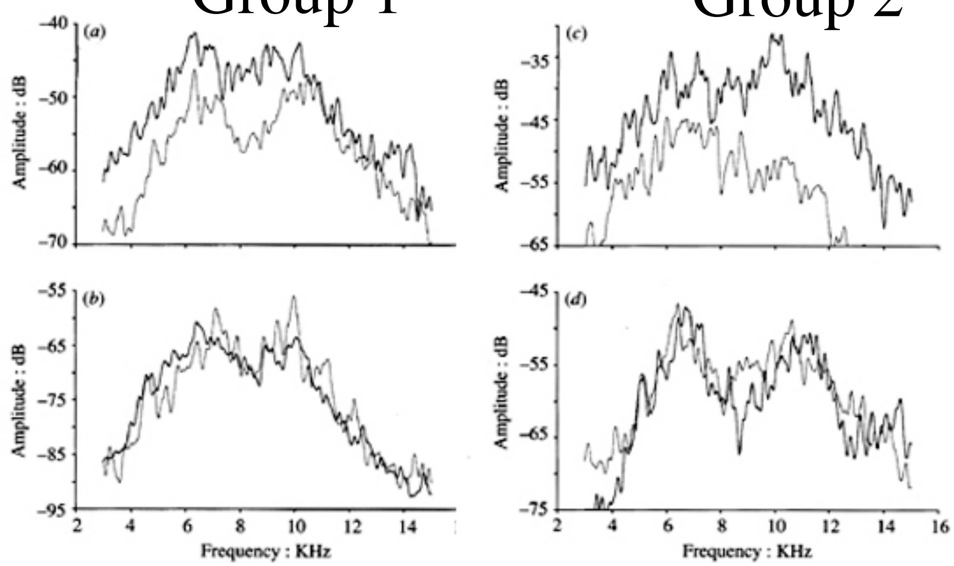
Wilkinson, G.S. and Boughman, J. W. (1998) Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour* 55:337-350

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

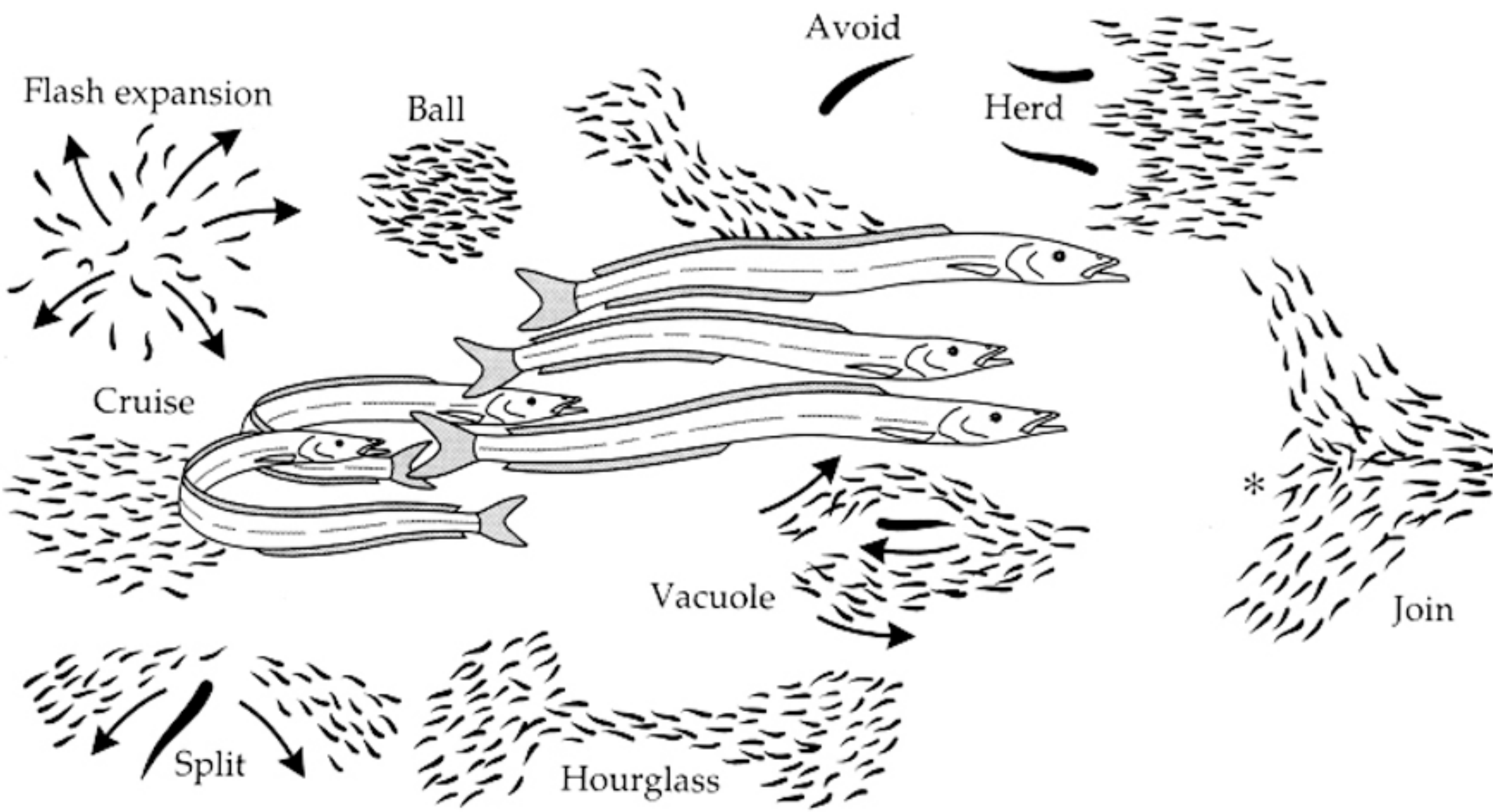
Group 2



Before

5 months after move

Coordination of group movement



Coordinated movement likely depends on simple rules

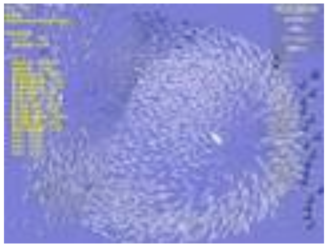
Bird flocks

Fish schools

http://www.princeton.edu/~icouzin/index.htm

http://www.youtube.com/watch?v=XH-groCeKbE&feature=related

Mormon cricket bands



Fish school simulation

http://biology.kent.edu/FacultyPages/Lorch/mormon.html

Nest construction by termites