Environmental signals

- Why are environmental signals rare?
  - Pp 632-635
- Resource recruitment signals
  - Costs and benefits
  - Vertebrates and social insects
- Predator detection signals
  - Types
  - Patterns of usage
- Intertrophic level signals

Give game

- Symmetric contest with two strategies
  - Passive: do not signal, accept benefits if offered
  - Donor: signal benefit, B, and pay costs, C
- Assume donors can discriminate between donors and passives, and offer passives benefit, b (< B), and pay costs, k (< C)

		Opponent: Passive	Opponent: Donor
Actor:	Passive	0	b/2
	Donor	-k/2	(B-C)/2

- If B < C and b > 0, then Passive is pure ESS
- If (B - C) > b, then either strategy is pure ESS

  Cooperation (pure donor) requires reciprocity, kin selection or immediate direct benefits

Why signal food location?

- Costs
  - Increases competition
  - Signal production takes time and energy
- Potential Benefits
  - Direct
    - foraging success increases with group size
    - predation risk decreases, more eyes and ears
  - Indirect
    - Kin selection: increases reproduction of relatives
    - Reciprocity: information sharing is reciprocated

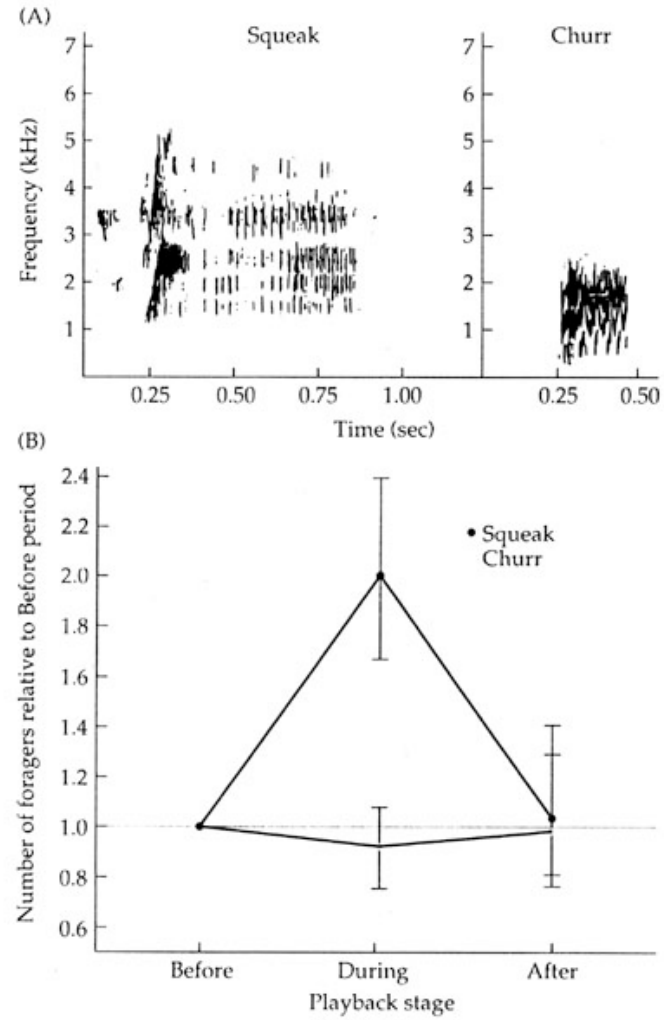
Types of location signals

- 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

Ravens "yell" at carcasses

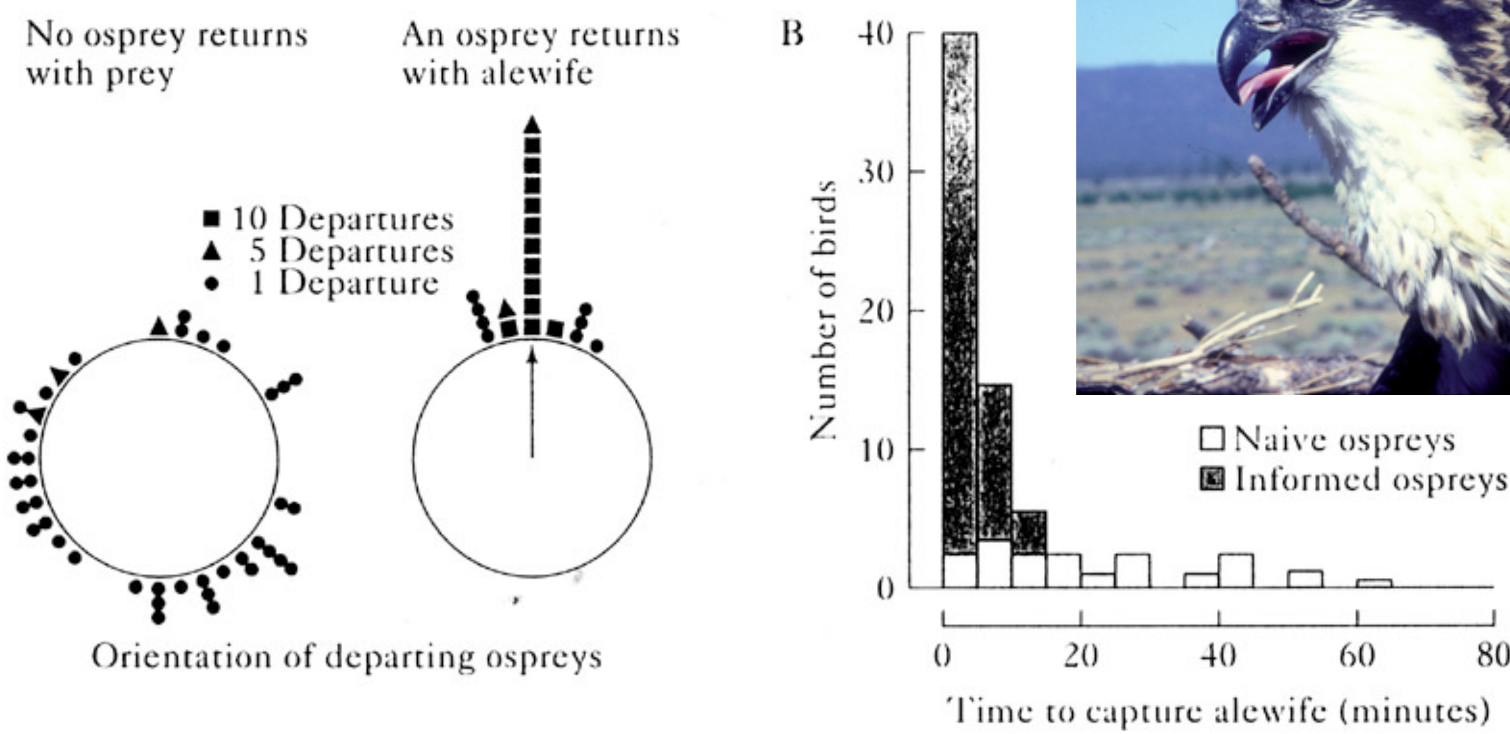
Nomadic juveniles recruit others to help defend carcasses from territorial pairs

Cliff swallow recruitment calls



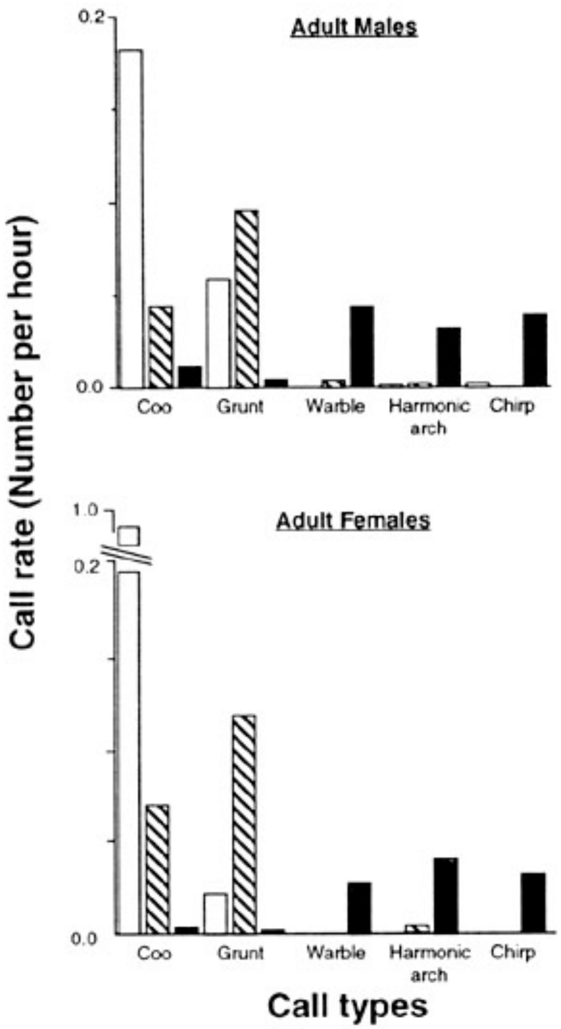
Squeaks recruit foragers; foraging success increases with group size

Food signalling by osprey



Males give display to females after catching preferred fish

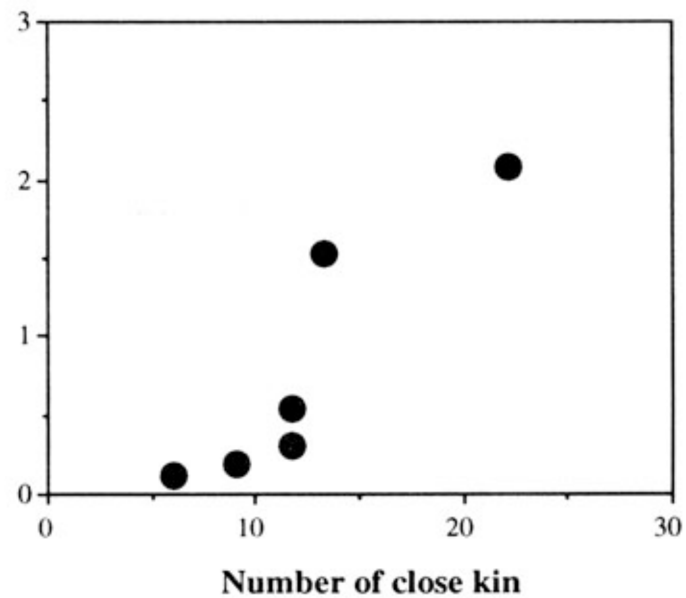
Rhesus macaque food calls



"coo" calls signal food discovery

Females call more than males

Juveniles that don't call at food are attacked



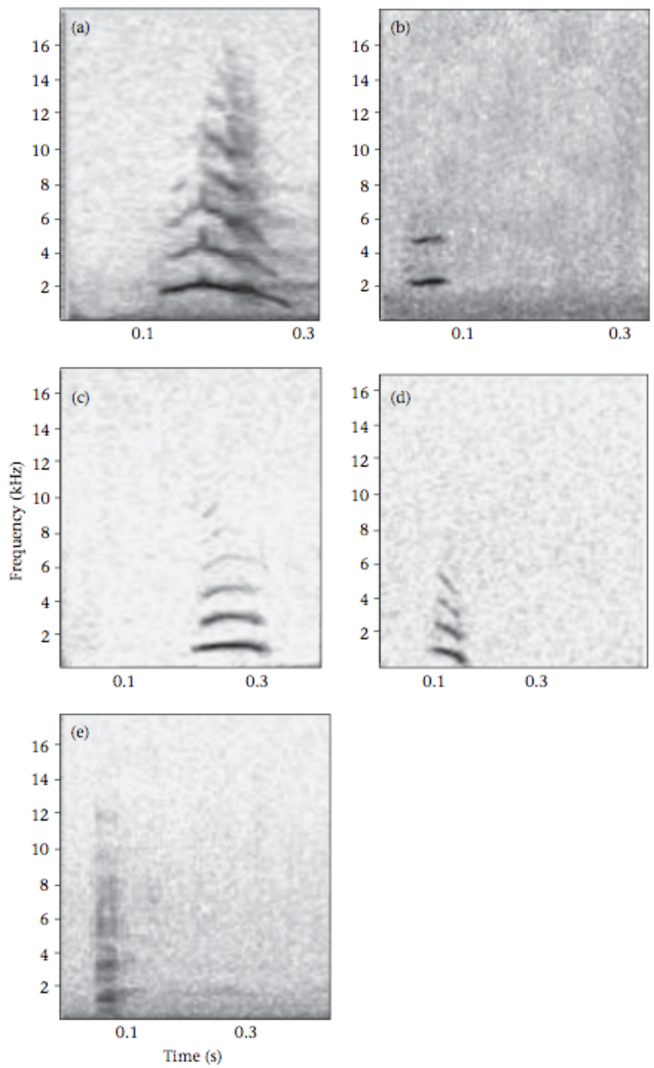
Chimpanzee food calls

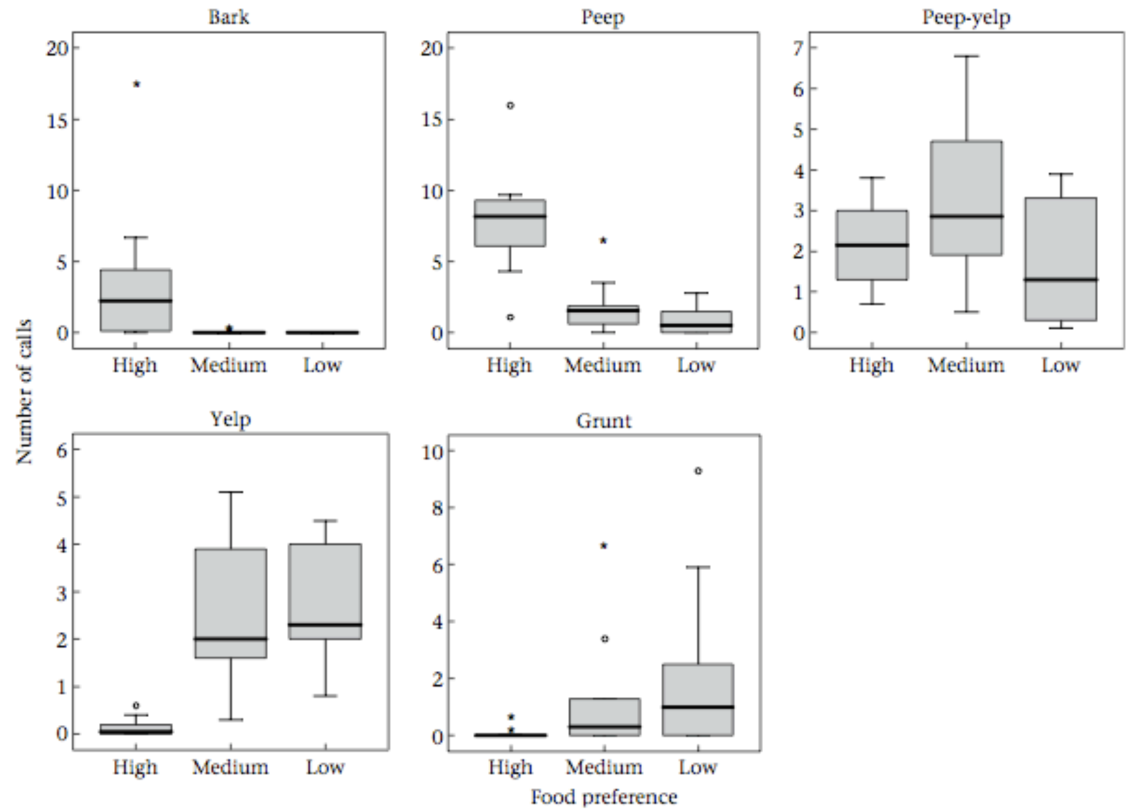
Pant-hoots advertise discovery of divisible food and are often given by males

Grunts are given for any amount of preferred food




Food calls in bonobos



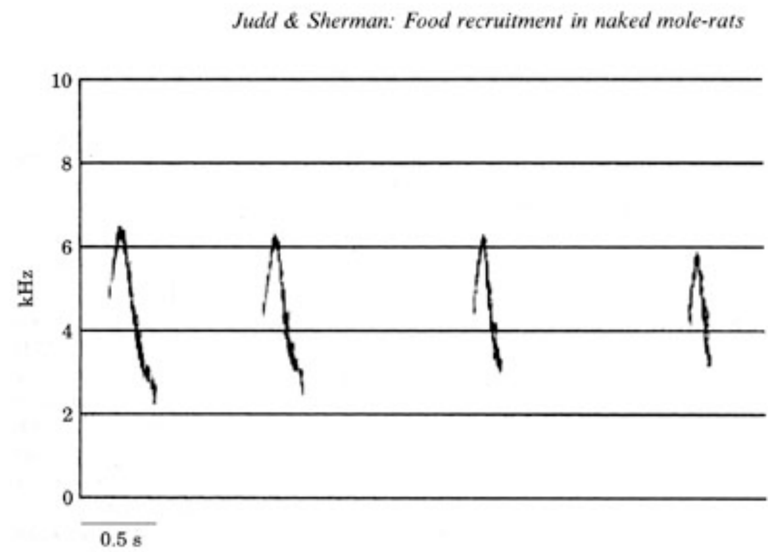


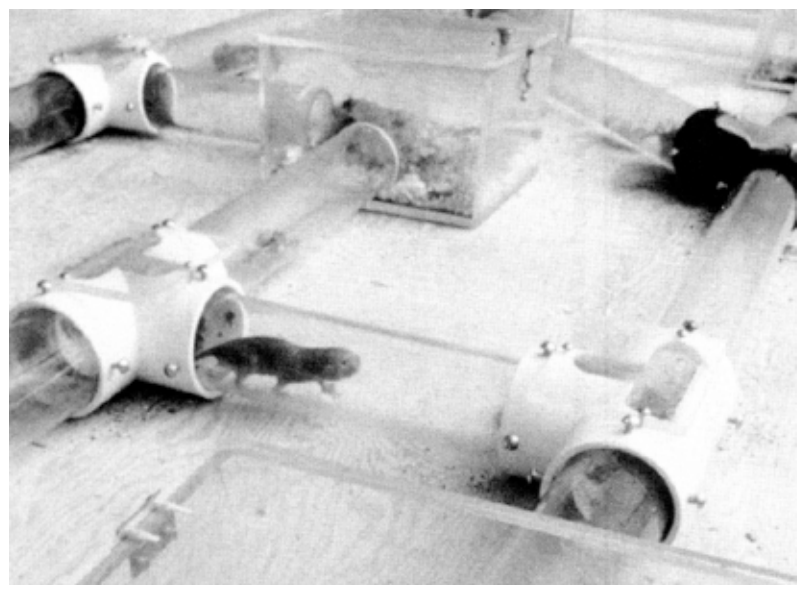
. Box plots showing the number of times each of the five call types was produced within food-associated call sequences. Thick black lines represent medians; l

Call type (and pitch) signal degree of food preference to group

Clay, Z., Zuberbuhler, K., Food-associated calling sequences in bonobos, Animal Behaviour (2009)

Mole rats recruit to roots

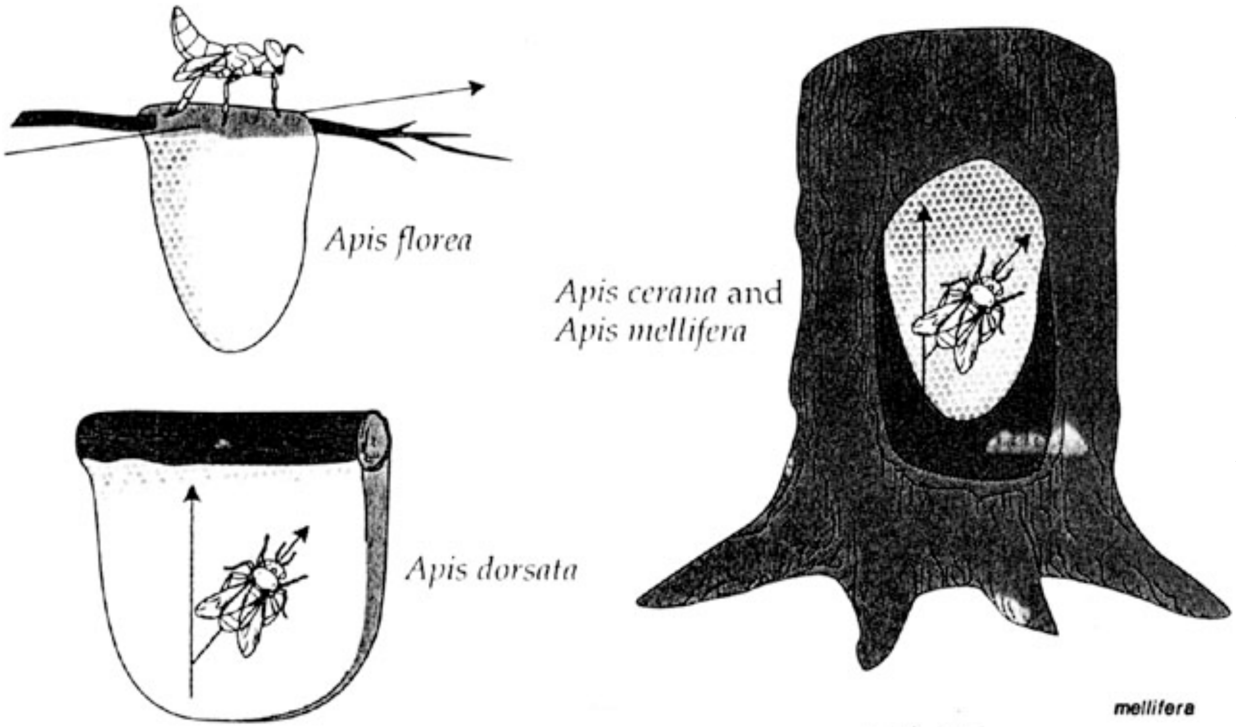




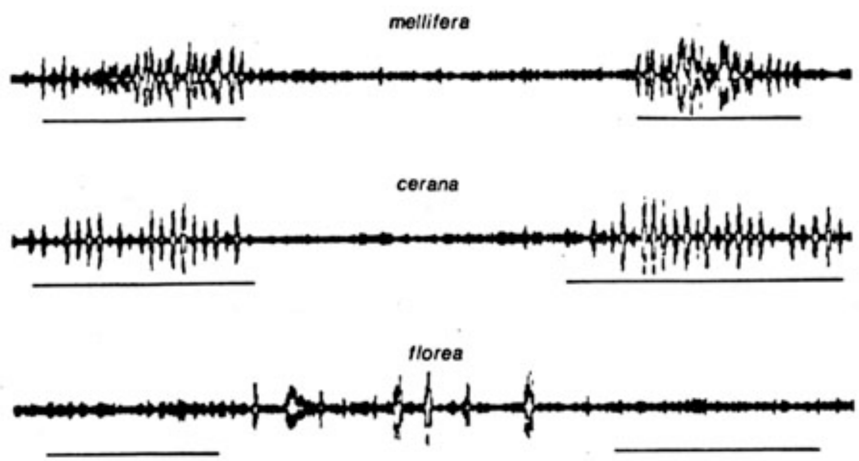
Food recruitment in ants

- Small colonies use tandem running
- Large colonies use group leading which involves a scout laying an odor trail from nest to food source
- If successful, subsequent foragers apply more pheromone which reinforces signal and leads to mass recruitment until food is exhausted

Bees encode direction to food

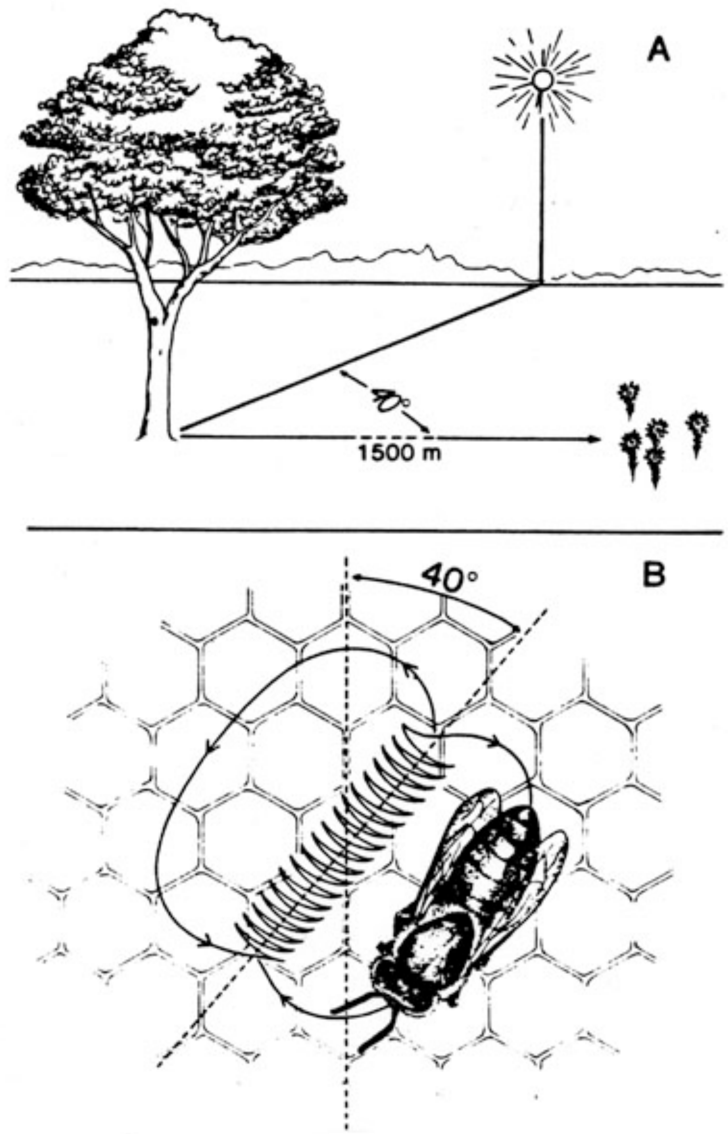


Azimuth is encoded by the angle from vertical in enclosed hives

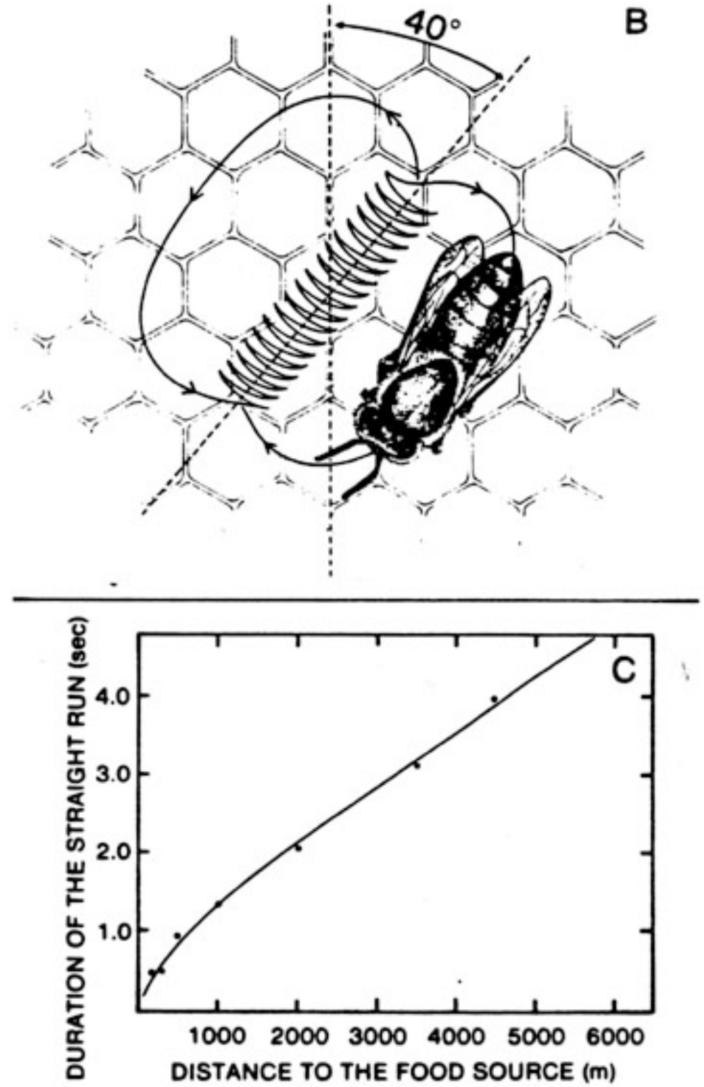


Waggle includes near-field sound in enclosed hives, visual signal (raised abdomen) in open hives

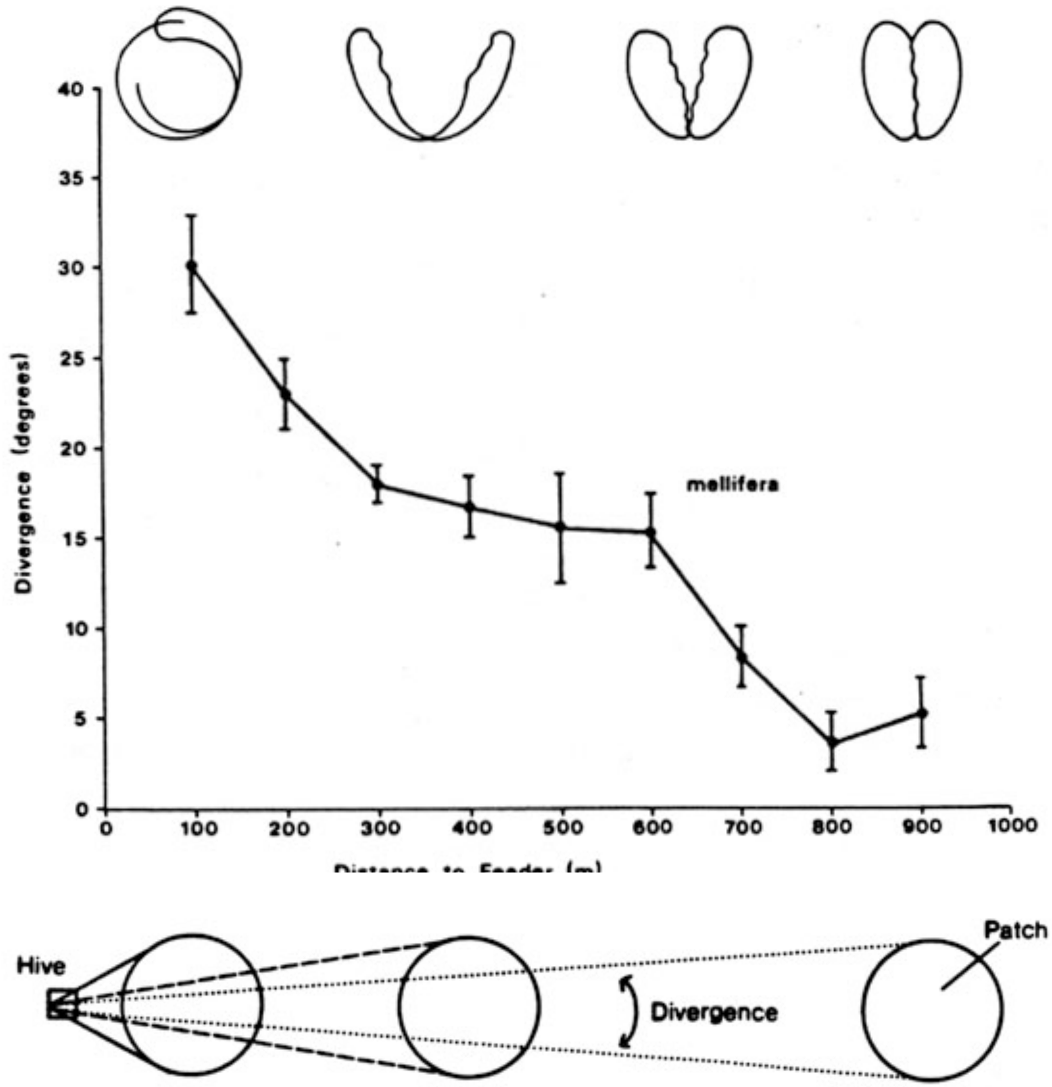
Food recruitment in honey bees: dance angle indicates direction



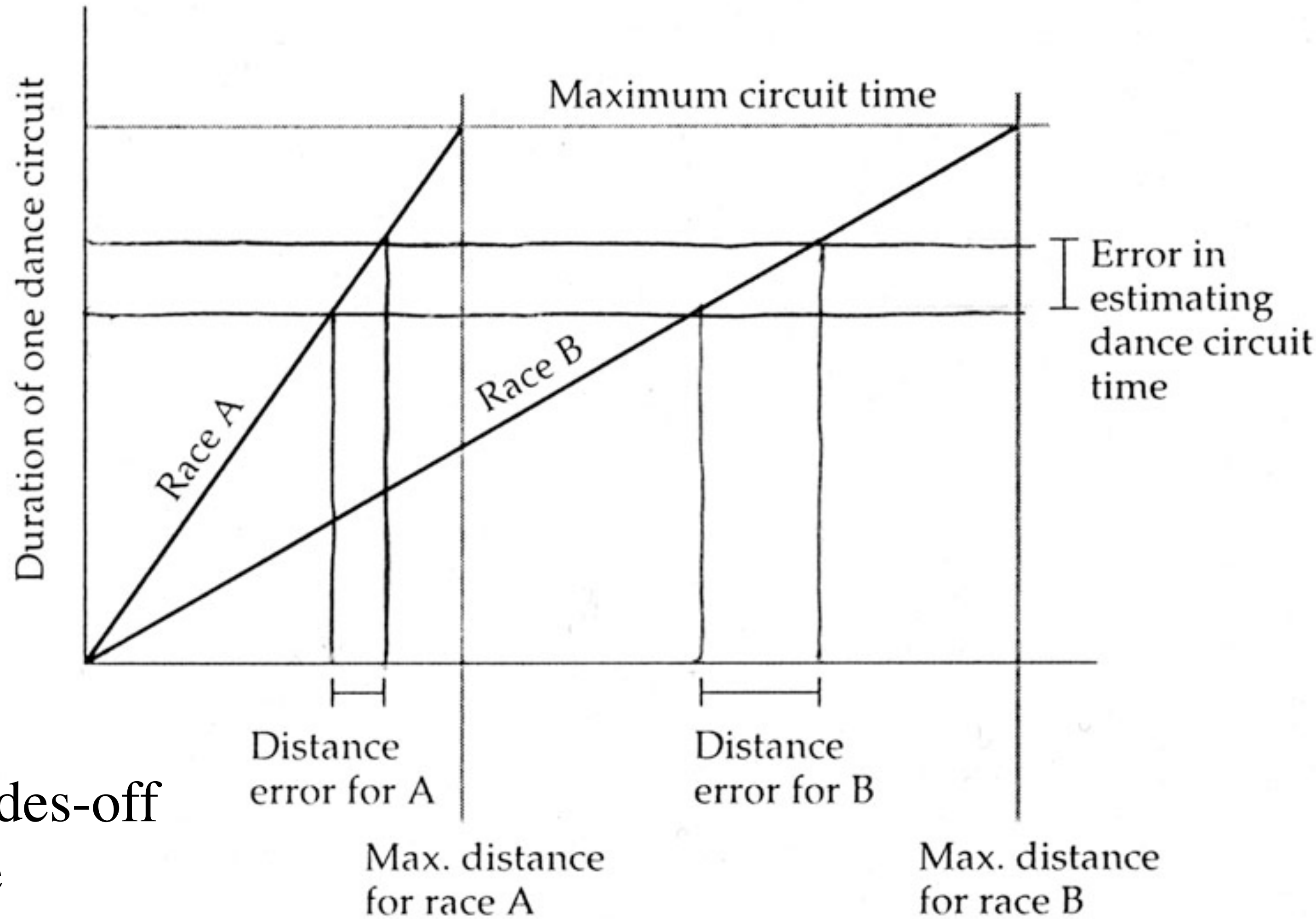
Dance duration indicates distance



Dance divergence indicates patch size



Advertisement distance is constrained by dance duration



Accuracy trades-off with distance

Bee dialects reflect foraging distances

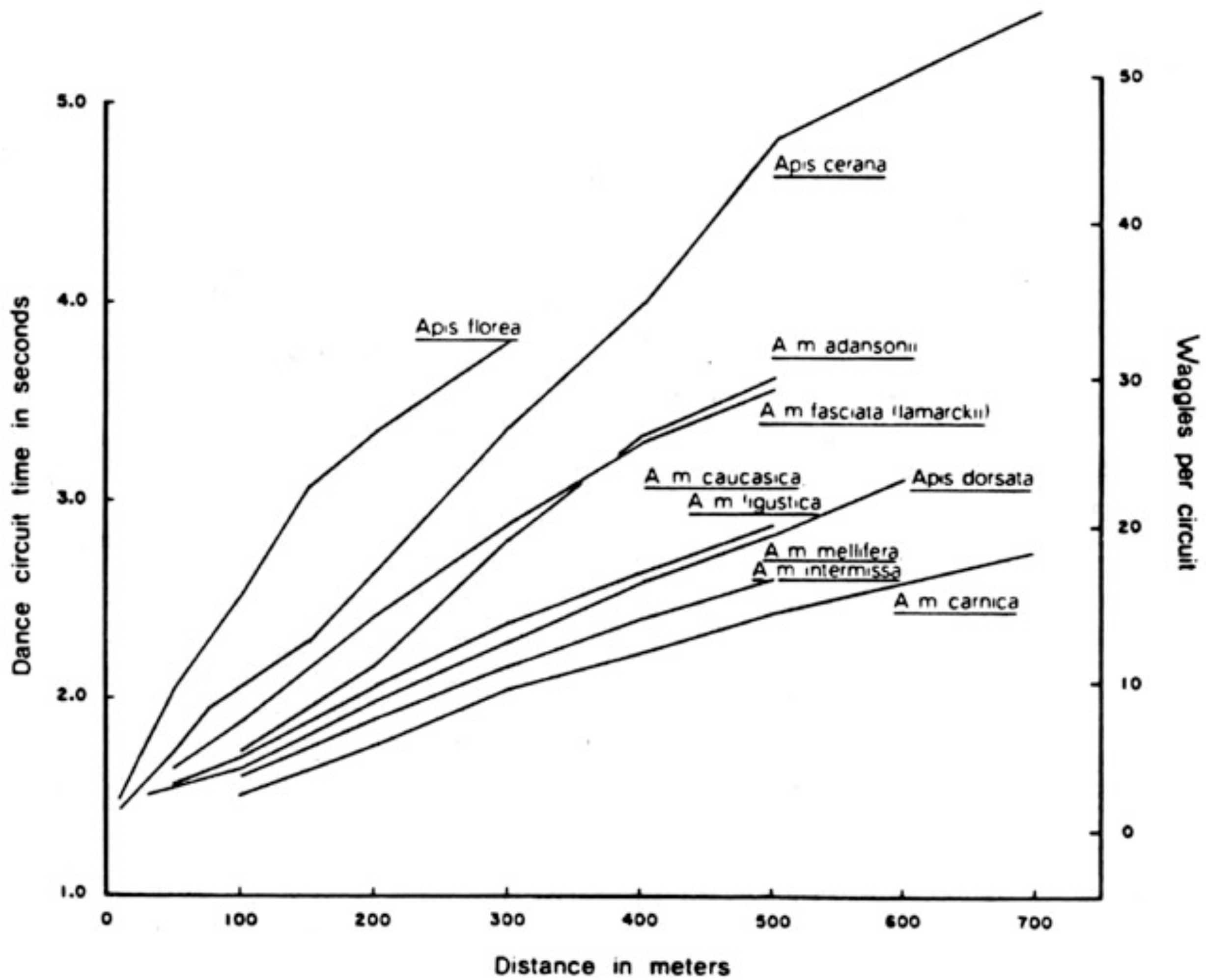


Table 6.5
Synthesis of Some of the Primary Studies of Food-Associated Signaling

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

Summary of food-associated signals

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

Social insects:
- Food signaling is common likely due to high relatedness
- Signals to food from hive using trail pheromones or "dance language"

Predator alarm signals

- Function
  - Alert conspecifics
  - Deter predator
- Types
  - Predator inspection and mobbing signals
    - Low risk - elicit scans or approach
  - Distress signals
    - High risk - prompts escape

Alarm signal design rules

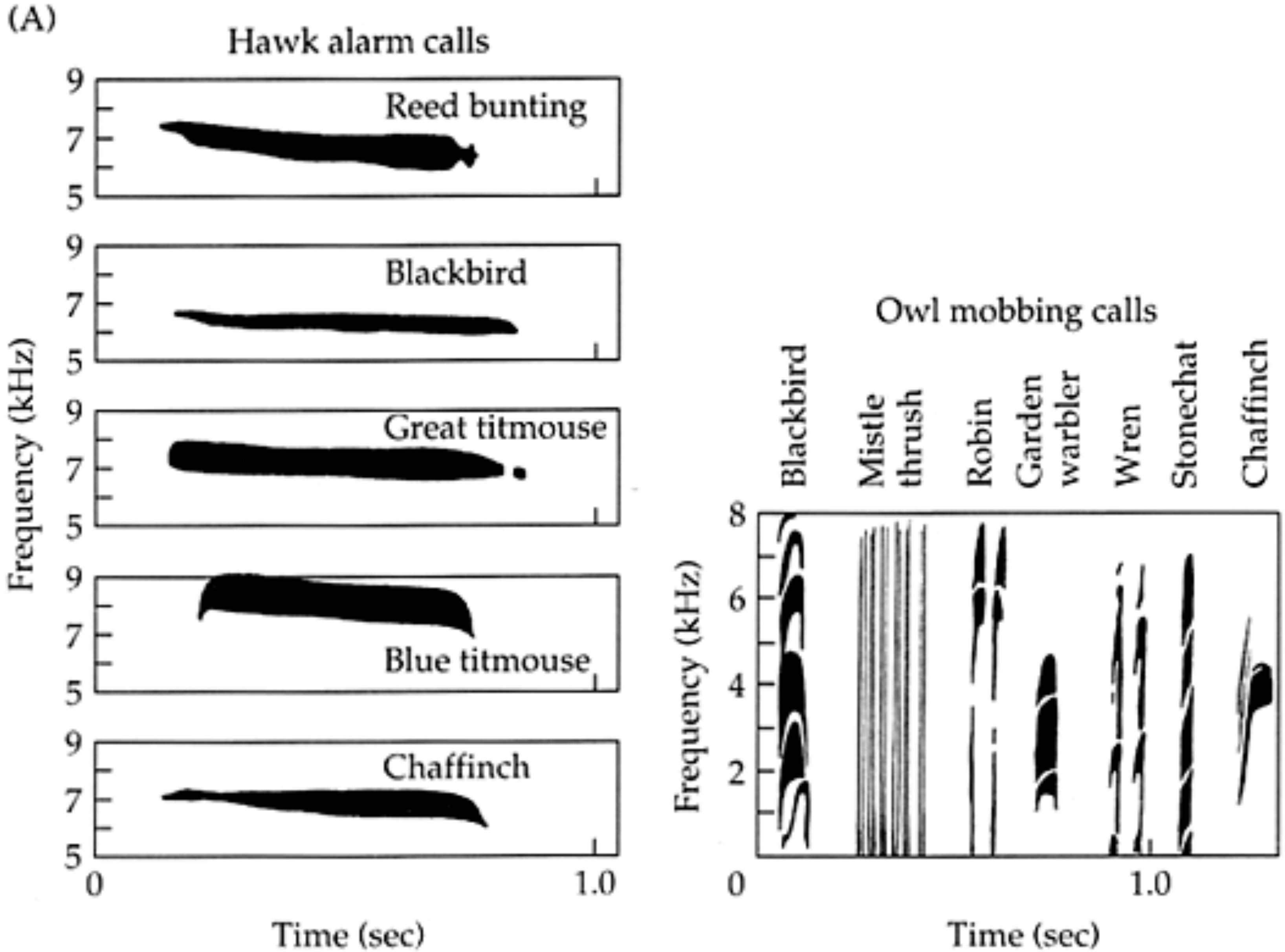
Table 18.6 Design rules and modality-specific mechanisms for alarm signals

Flee

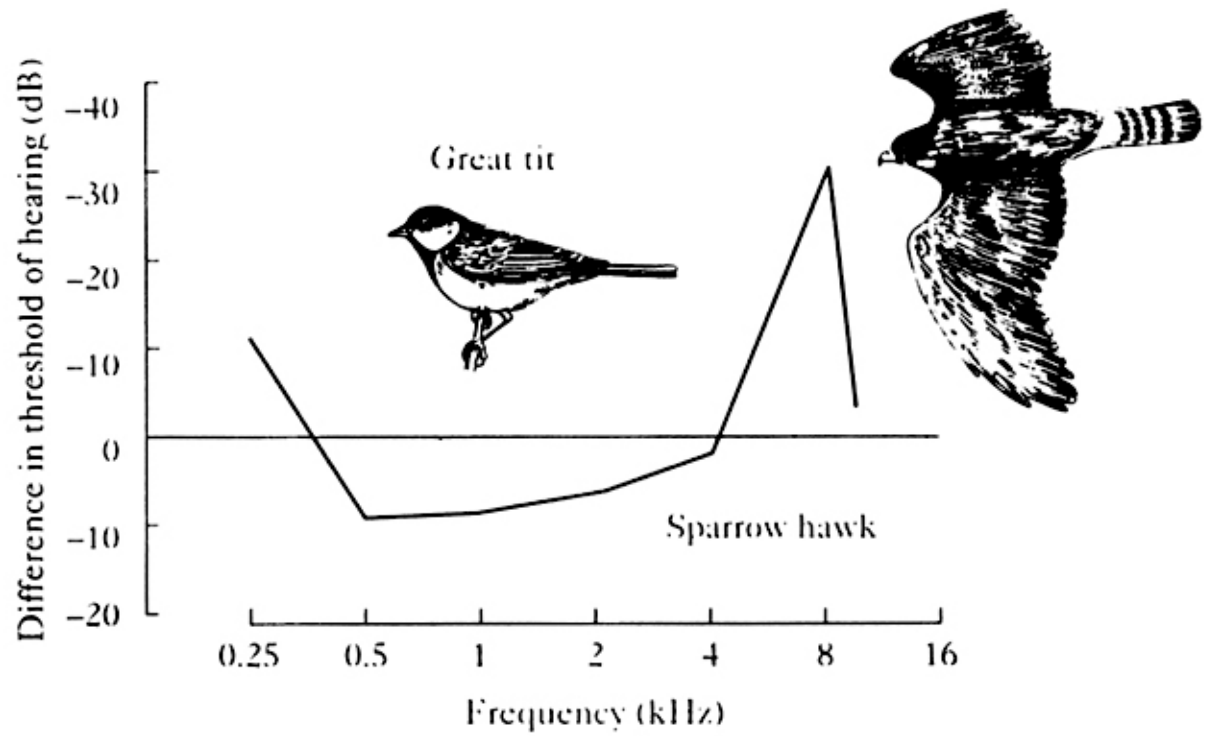
Assembly

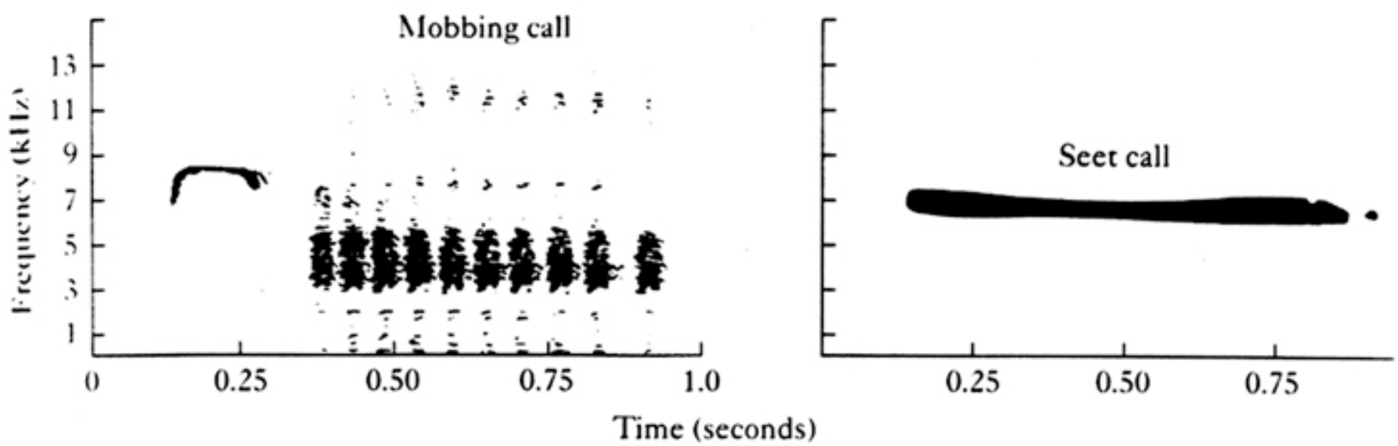
Design feature	Rule	Visual mechanisms	Auditory mechanisms	Olfactory mechanisms
		FLEE ALARM		
Range	Short–moderate	Color flash Appendage movement	Medium intensity call	Volatile, diffusable chemical
Locat-ability	Conceal sender location	Coverable patch	Pure tone Gradual onset	Diffusion gradient
Duty cycle	Short	Single flash Rapid movement	Single call	Single puff
ID level	None			
Modula-tion level	Stereotyped			
Form-content linkage	Linked: Fear, flight	Signal on tail or rear end	High frequency	Derive from defense chemical
		ASSEMBLY ALARM		
Range	Medium-large	Contrasting movement	Loud call	Increase Q
Locat-ability	Sender Enemy	Repeated jerky movement	Broadband note Trill	Diffusion gradient
Duty cycle	High while danger present	Regular repetition	Regular repetition	Repeated puffs
ID level	Species (Group)	Visual pattern	Note shape	Chemical mix
Modula-tion level	Graded	Repetition rate	Repetition rate	Concentration
Form-content linkage	Arbitrary	Maximize visual contrast	Maximize detection	Optimize fadeout

Avian alarm and assembly calls



Private alarm calls





Potential benefits of alarm calls

- Direct: signal conspecifics
  - Manipulate fellow prey into capture
  - Improve own escape through synchronized response
  - Protect mate
  - Maintain optimal group size
- Direct: signal predator
  - Deter future attack by predator
- Indirect: signal relatives
  - Increase survival of kin

Ground squirrel alarm calls

High risk Low risk

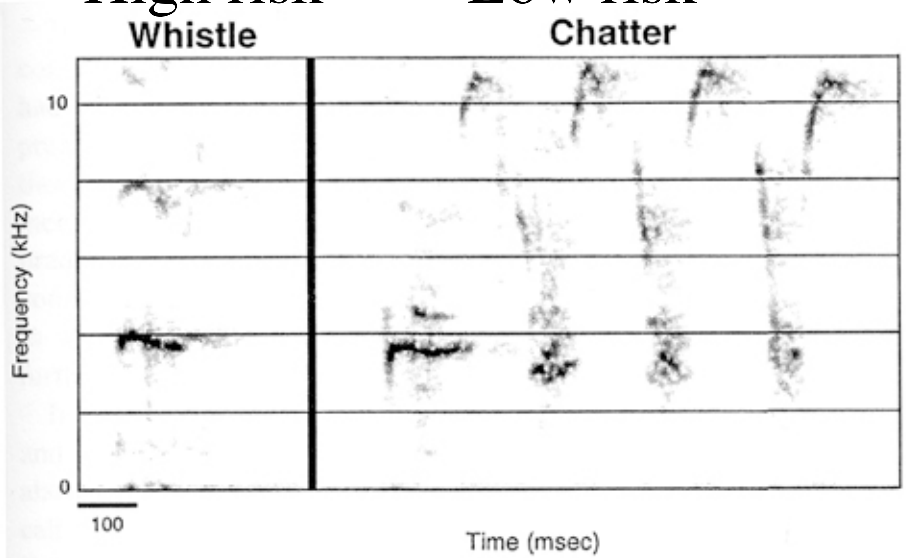


TABLE 17.1 Alarm Calling and Survival in Belding's Ground Squirrels at Tioga Pass, California.[a]

	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).

Alarm calls do not coordinate movements

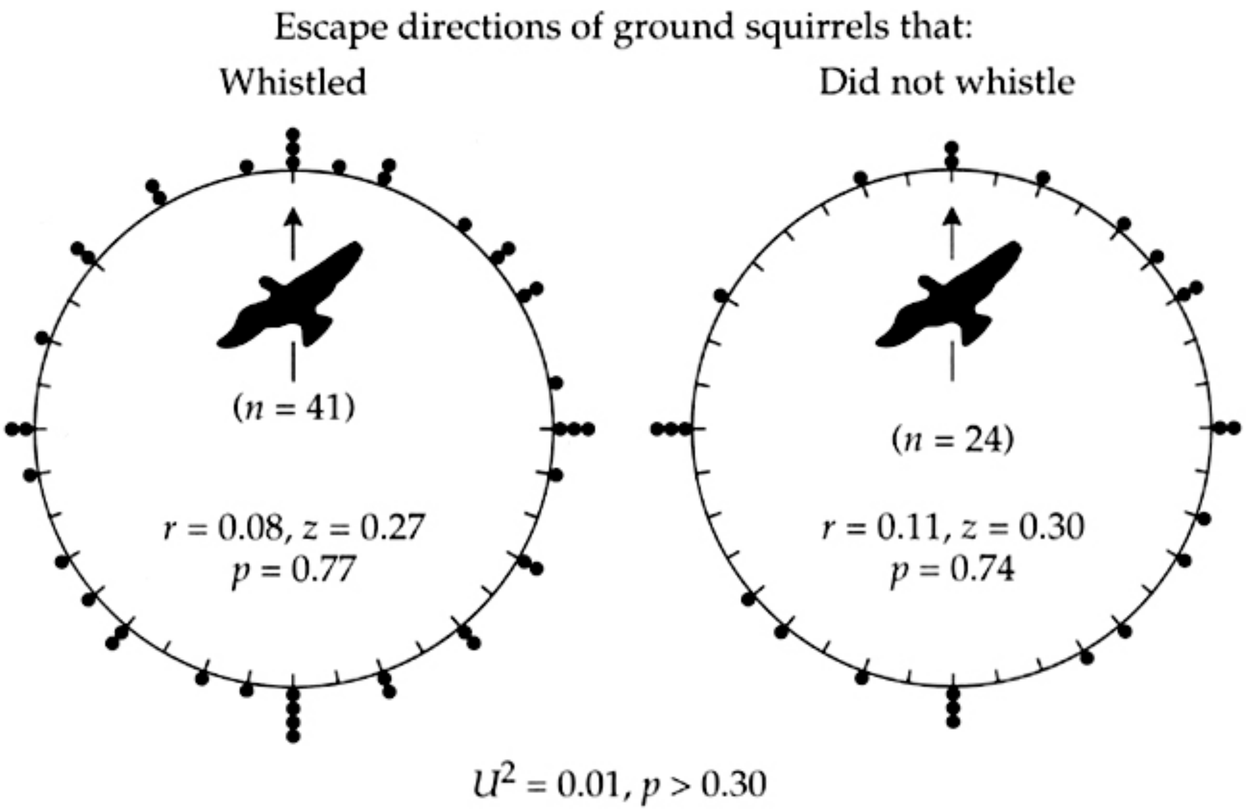
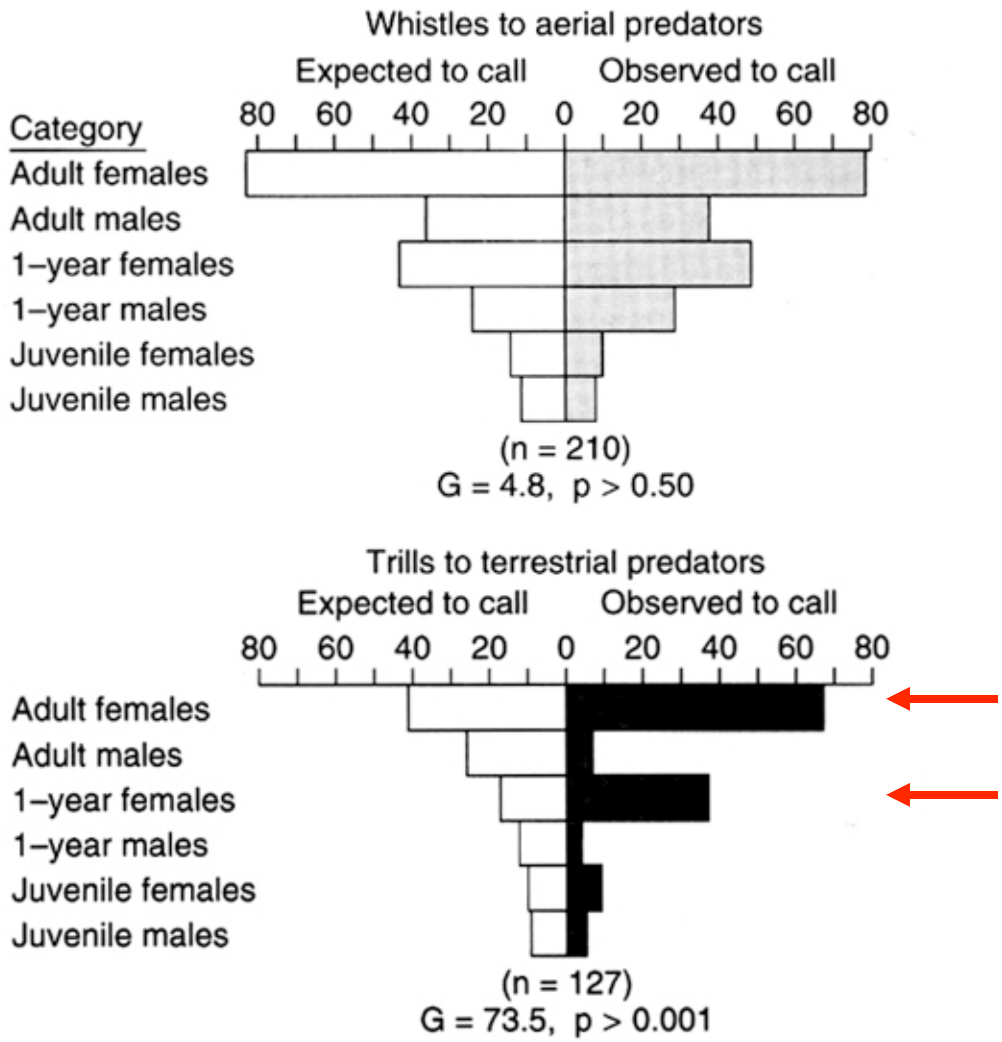


Figure 25.9 Direction of flight of senders and receivers after high-risk warning in Belding's ground squirrels (*Spermophilus beldingi*). Neither senders nor receivers show any directional pattern of flight relative to the location of the predator after emission of a high-risk warning. There is thus no indication that compensatory benefits of emitting high risk alarms is due to manipulation of fellow prey. (From Sherman 1985, © Springer–Verlag.)

But do synchronize timing of escape behavior

Alarm calls differ by age and sex



Alarm calls and kinship

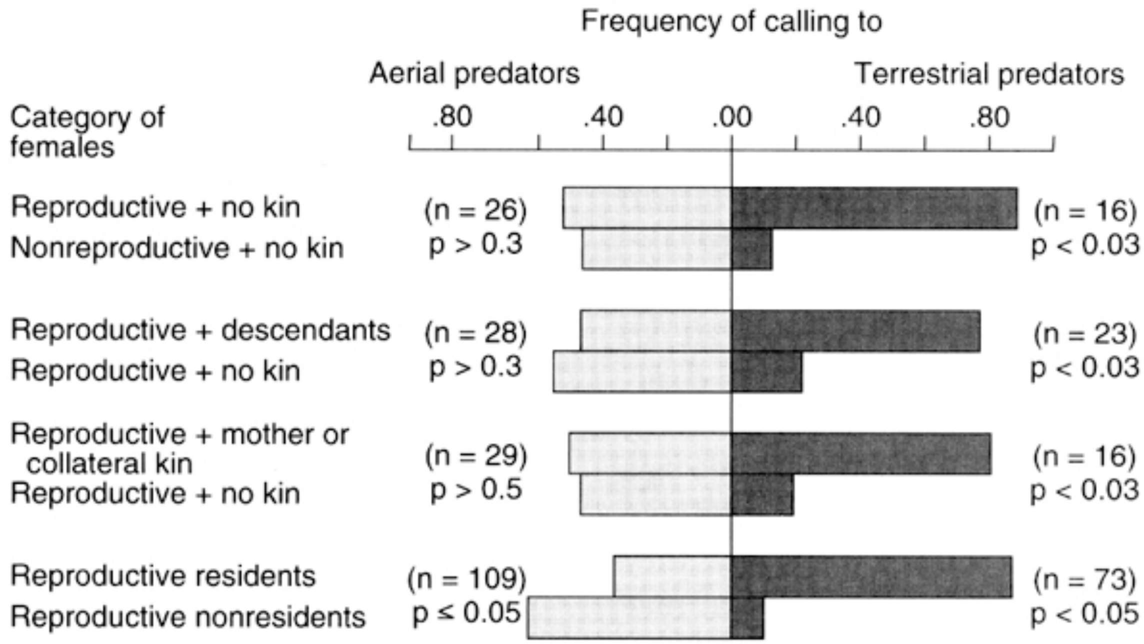
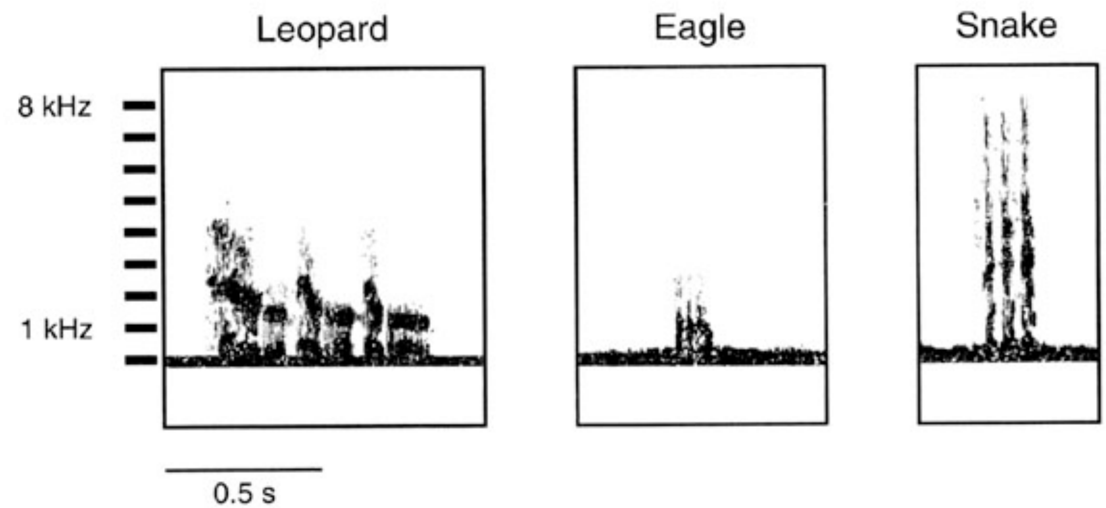


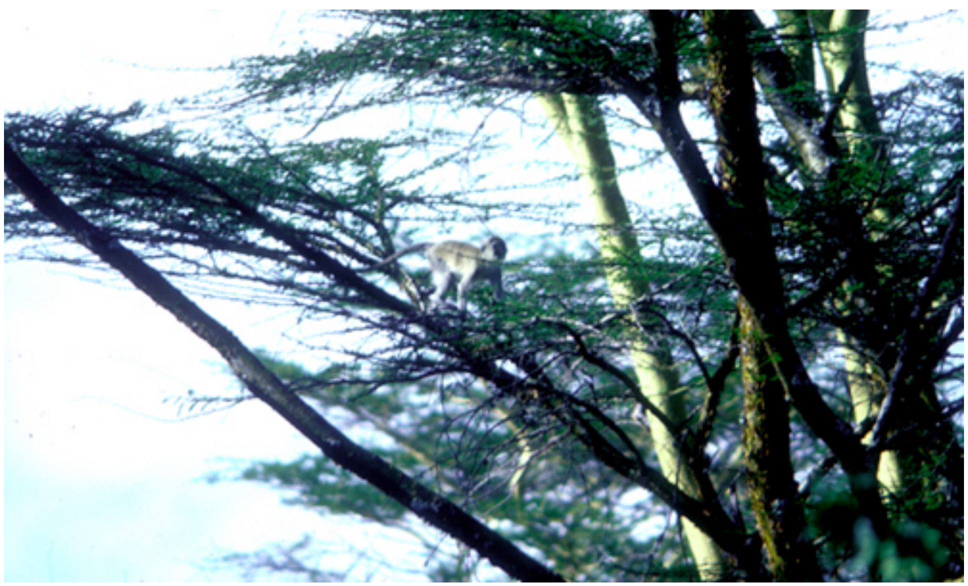
FIGURE 17.12 The effects of residency and genetic relatedness on the frequency of alarm calling for terrestrial and aerial predators in Belding's ground squirrels. Notice that when a terrestrial predator approached, reproductive females called more frequently than nonreproductive females. Furthermore, 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.)

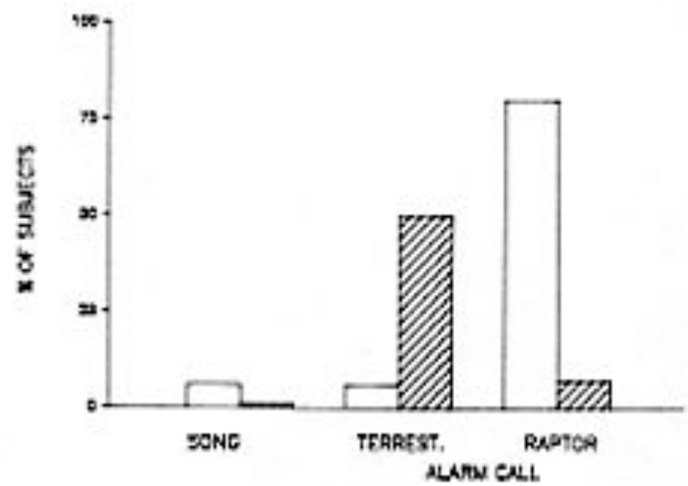
Referential signaling

- Do alarm calls convey information about predator type or just urgency associated with potential attack?
- Signals that carry information about categories of things, such as predators, are "referential"
- The presence of referential signaling among nonhuman animals interests philosophers

Vervet alarm calls







Hatched = run up trees
Open = run down to shelter

Alarm calls refer to predators

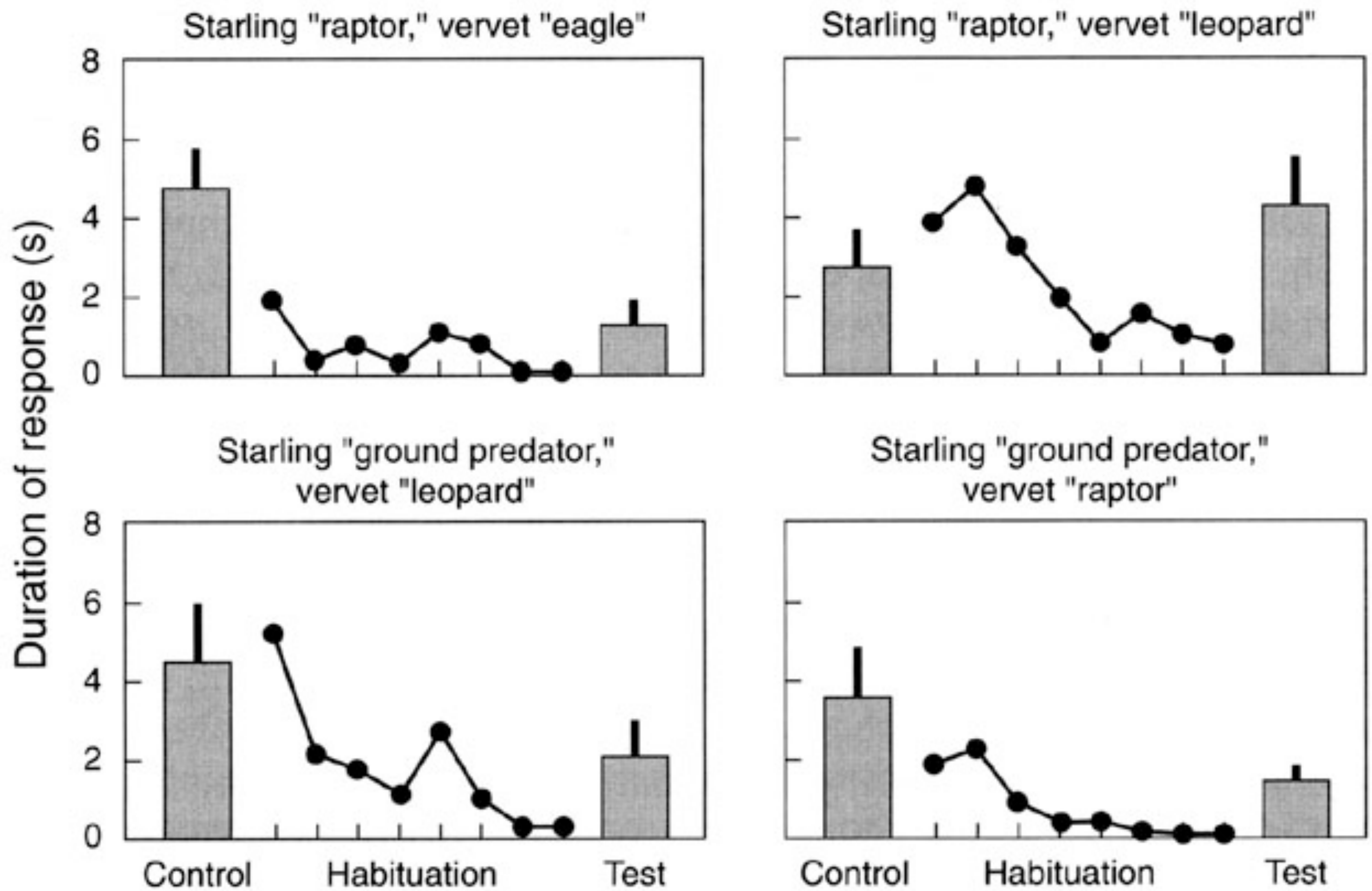


Figure 12.13. Duration of looking toward a speaker in vervets exposed to the indicated alarm calls recorded from vervets and starlings, demonstrating cross-habituation between calls with the same meaning. The call listed first above each panel was the habituating call; the second call was played in the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

Development of vervet alarm calls

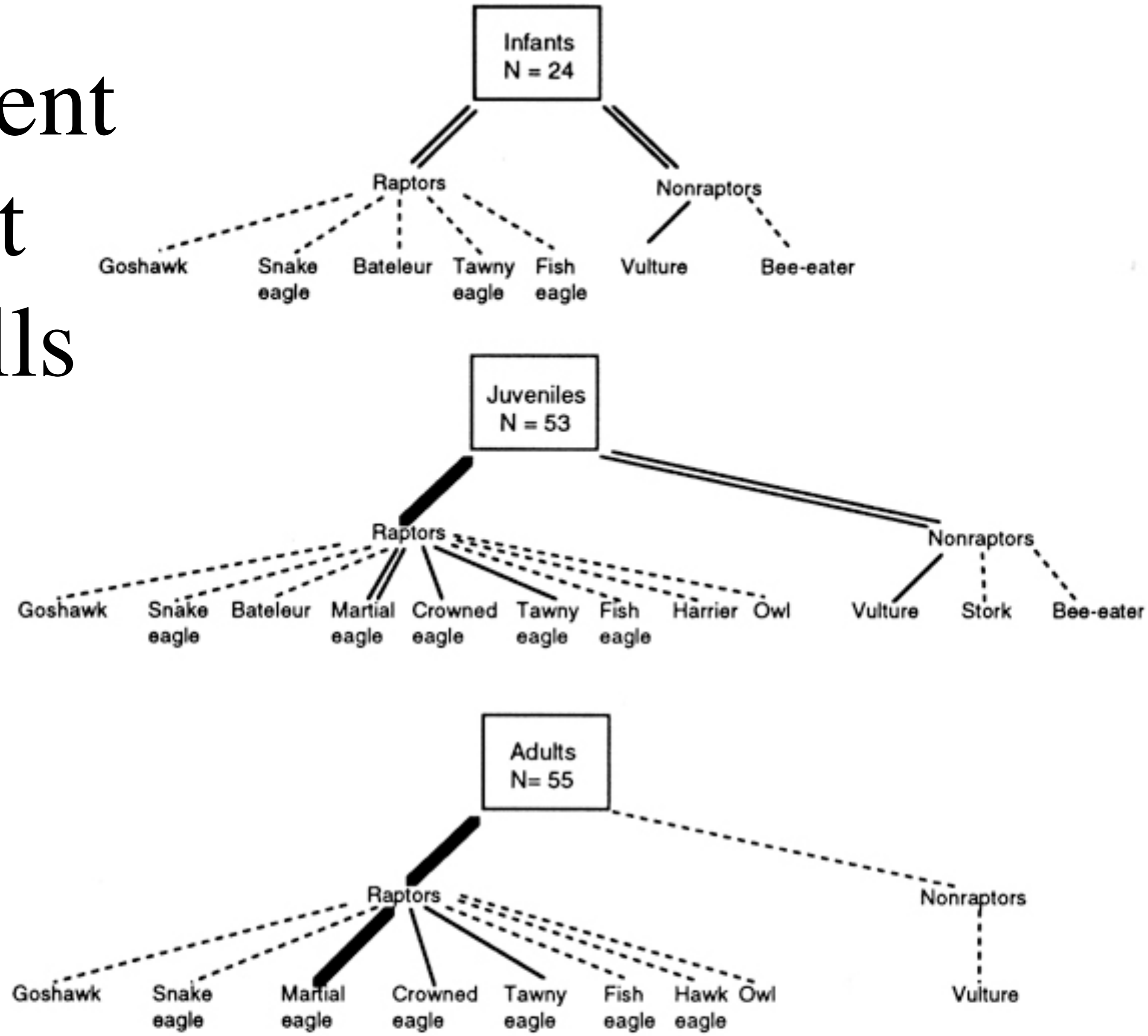
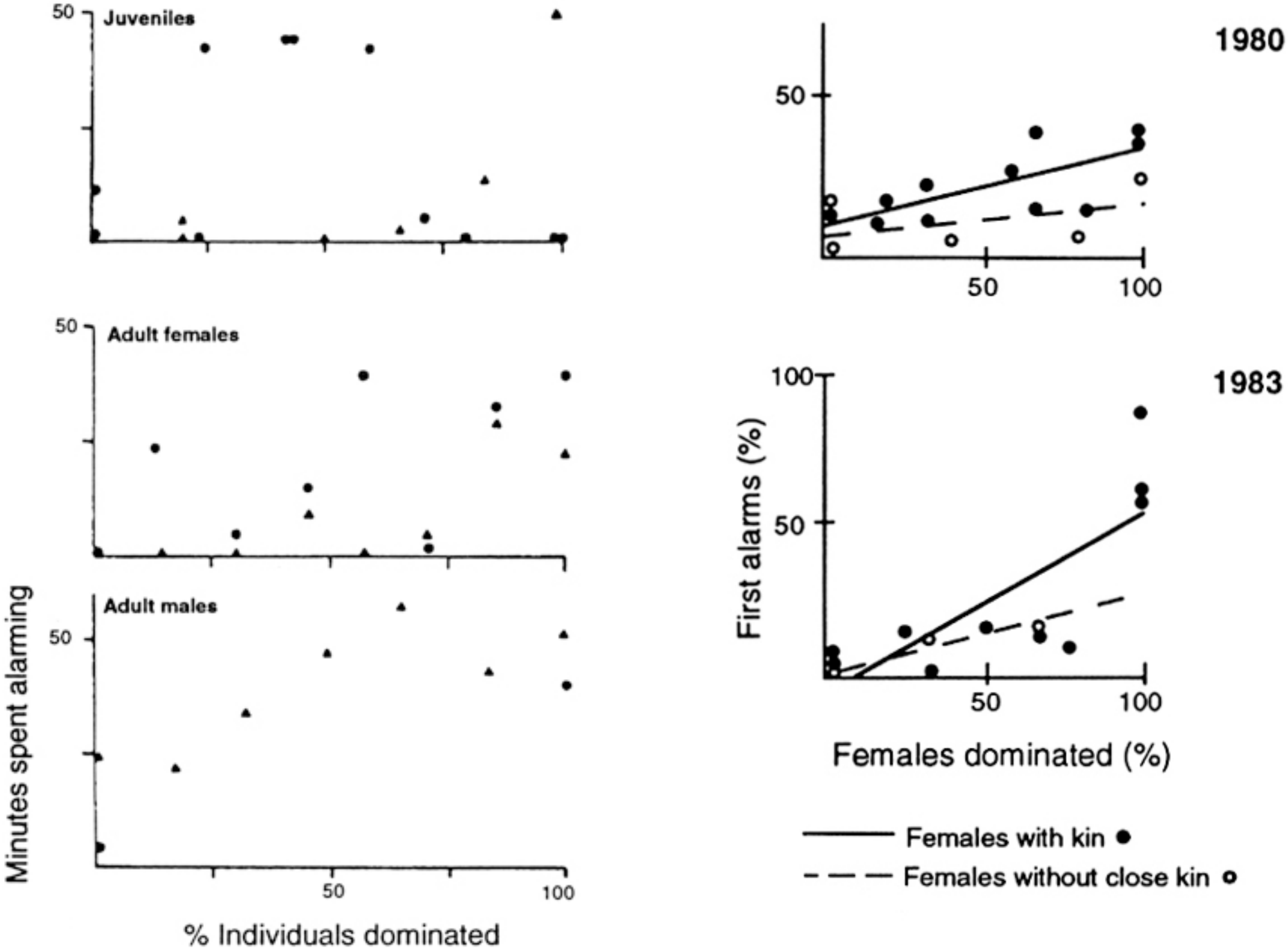


Figure 5.19
Developmental changes in the target of vervet monkey eagle alarm calls. Infants: <1 year old; Juveniles: 1–4 years old; Adults: >4 years old. Dashed lines: <5 alarms; thin solid lines: 6–10 alarms; double lines: 11–15 alarms; thick solid lines: >15 alarms (redrawn from Seyfarth and Cheney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

Vervet calls, relatedness and dominance





Meerkat alarm calls signal predator class and urgency

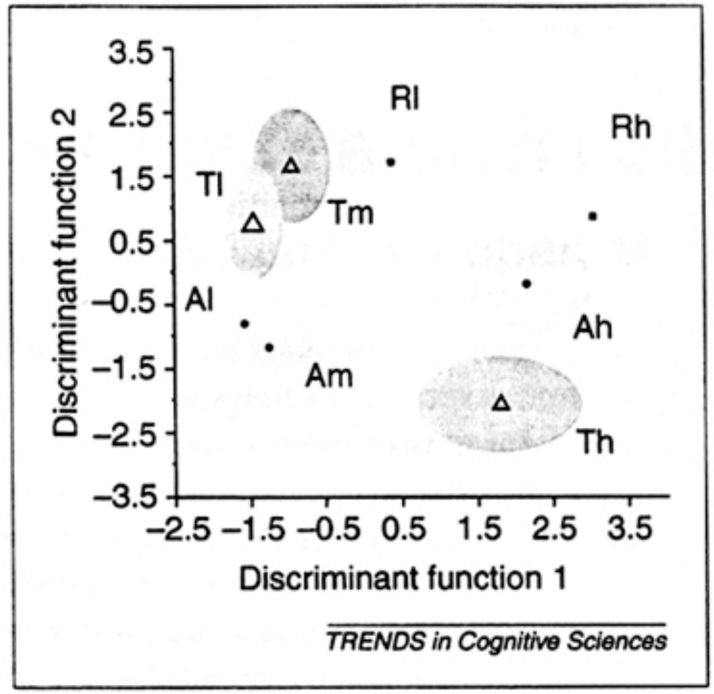


Fig. 2. Arrangement of the alarm calls given in different predator contexts according to their values as established by discriminant function analysis (DFA) of the calls' acoustic properties. Circles are spanned by the mean ± SD of the first two discriminant functions, with data drawn from 10 runs of 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.

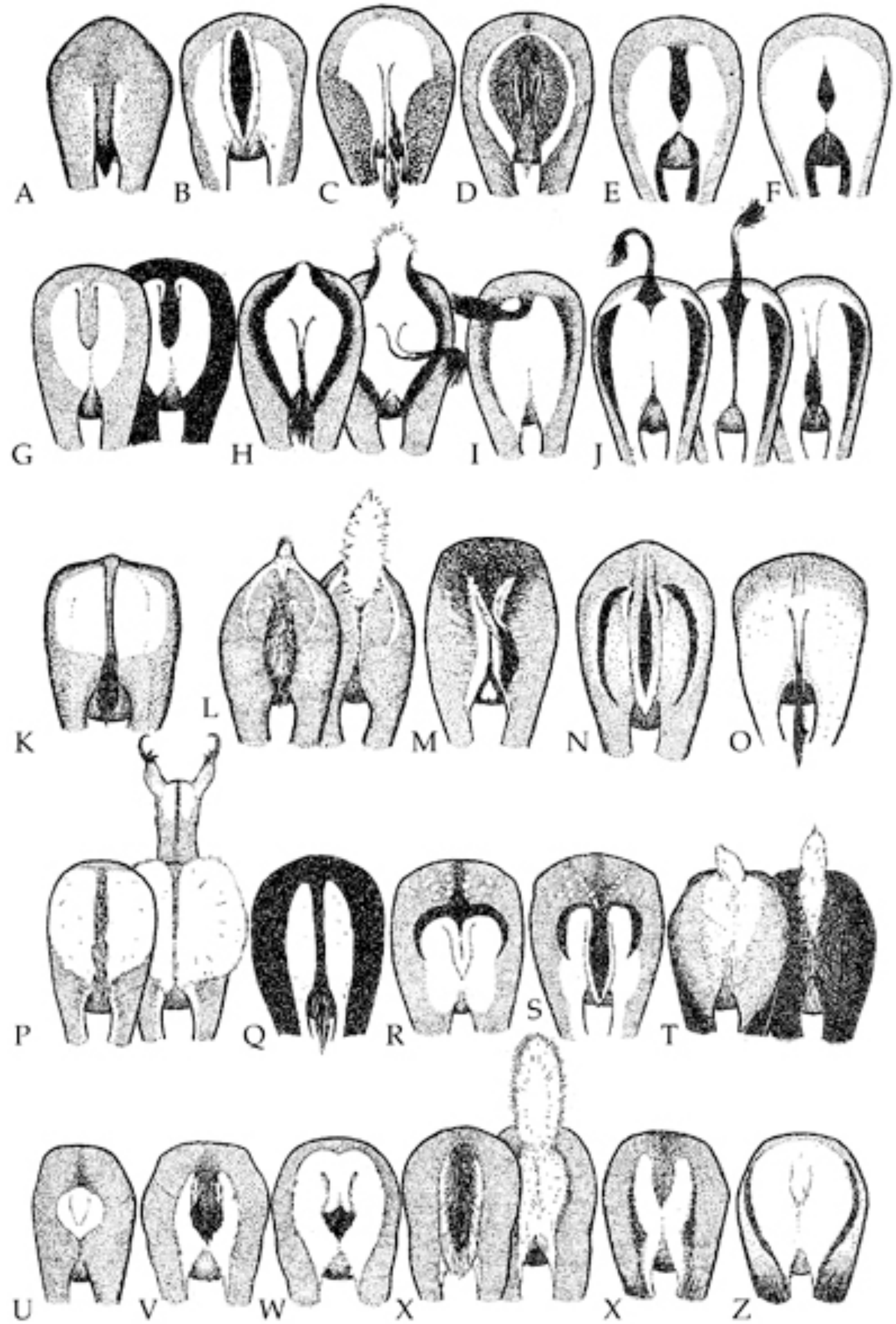
Meerkats give three types of calls
(terrestrial, aerial and recruitment)
with three levels of urgency (low, medium and high)
All 9 categories are acoustically distinct (M. Manser)

Intertrophic level signalling

- Prey - predator notification signals
  - Detection vs condition notification
  - Aposematic signals
    - Warning colors that signal poison or distaste. How can they evolve?
- Distress signals
  - Given by animals captured by predators

Predator notification displays

stotting



Aposematicism

Prey advertise taste to predators

Initial evolution requires
-kin groups
-receiver biases or
-improved survival after attack

Can be invaded by mimics, but must remain at low frequencies