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)

\[
\begin{array}{c|cc}
\text{Opponent:} & \text{Passive} & \text{Donor} \\
\hline
\text{Passive} & 0 & b/2 \\
\text{Donor} & -k/2 & (B-C)/2 \\
\end{array}
\]

- 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

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

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
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>
<thead>
<tr>
<th>Design feature</th>
<th>Rule</th>
<th>Visual mechanisms</th>
<th>Auditory mechanisms</th>
<th>Olfactory mechanisms</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FLEE ALARM</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>Short-moderate</td>
<td>Color flash Appendage movement</td>
<td>Medium intensity call</td>
<td>Volatile, diffusible chemical</td>
</tr>
<tr>
<td>Locatability</td>
<td>Conceal sender location</td>
<td>Coverable patch</td>
<td>Pure tone Gradual onset</td>
<td>Diffusion gradient</td>
</tr>
<tr>
<td>Duty cycle</td>
<td>Short</td>
<td>Single flash Rapid movement</td>
<td>Single call</td>
<td>Single puff</td>
</tr>
<tr>
<td>ID level</td>
<td>None</td>
<td>Stereotyped</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modulation level</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Form-content linkage</td>
<td>Linked: Fear, flight</td>
<td>Signal on tail or rear end</td>
<td>High frequency</td>
<td>Derive from defense chemical</td>
</tr>
</tbody>
</table>

| **ASSEMBLY ALARM** |      |                   |                     |                      |
| Range             | Medium-large | Contrasting movement | Loud call | Increase Q |
| Locatability     | 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 |
| Modulation level | Graded | Repetition rate | Repetition rate | Concentration |
| Form-content linkage | Arbitrary | Maximize visual contrast | Maximize detection | Optimize fadeout |
Avian alarm and assembly calls

(A) Hawk alarm calls

- Reed bunting
- Blackbird
- Great titmouse
- Blue titmouse
- Chaffinch

Frequency (kHz)

Time (sec)

0.0

1.0

(B) Owl mobbing calls

- Blackbird
- Mistle thrush
- Robin
- Garden warbler
- Wren
- Stonechat
- Chaffinch

Frequency (kHz)

Time (sec)

0.0

1.0
Private alarm calls

[Graphs showing frequency response and time series for different bird sounds]
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

TABLE 17.1 Alarm Calling and Survival in Belding’s Ground Squirrels at Tioga Pass, California.\(^{a}\)

<table>
<thead>
<tr>
<th>Category</th>
<th>Captured</th>
<th>Escaped</th>
<th>Percent Captured</th>
<th>(P(x^2) Test)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerial predators</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callers</td>
<td>1</td>
<td>41</td>
<td>2%</td>
<td></td>
</tr>
<tr>
<td>Noncallers</td>
<td>11</td>
<td>28</td>
<td>28%</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Total</td>
<td>12</td>
<td>69</td>
<td>15%</td>
<td></td>
</tr>
<tr>
<td>Terrestrial predators</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callers</td>
<td>12</td>
<td>141</td>
<td>8%</td>
<td></td>
</tr>
<tr>
<td>Noncallers</td>
<td>6</td>
<td>143</td>
<td>4%</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>284</td>
<td>6%</td>
<td></td>
</tr>
</tbody>
</table>

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

Alarm calls do not coordinate movements

But do synchronize timing of escape behavior

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.)
Alarm calls differ by age and sex

- Whistles to aerial predators
  - Expected to call: (n = 210)
  - Observed to call: \( G = 4.8, \ p > 0.50 \)

- Trills to terrestrial predators
  - Expected to call
  - Observed to call: \( G = 73.5, \ p > 0.001 \)
**Alarm calls and kinship**

![Image of a ground squirrel](image)

<table>
<thead>
<tr>
<th>Category of females</th>
<th>Aerial predators</th>
<th>Terrestrial predators</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Frequency of calling to</td>
<td></td>
</tr>
<tr>
<td></td>
<td>.80</td>
<td>.40</td>
</tr>
<tr>
<td>Reproductive + no kin</td>
<td>(n = 26)</td>
<td></td>
</tr>
<tr>
<td>Nonreproductive + no kin</td>
<td>p &gt; 0.3</td>
<td></td>
</tr>
<tr>
<td>Reproductive + descendants</td>
<td>(n = 28)</td>
<td></td>
</tr>
<tr>
<td>Reproductive + no kin</td>
<td>p &gt; 0.3</td>
<td></td>
</tr>
<tr>
<td>Reproductive + mother or collateral kin</td>
<td>(n = 29)</td>
<td></td>
</tr>
<tr>
<td>Reproductive + no kin</td>
<td>p &gt; 0.5</td>
<td></td>
</tr>
<tr>
<td>Reproductive residents</td>
<td>(n = 109)</td>
<td></td>
</tr>
<tr>
<td>Reproductive nonresidents</td>
<td>p ≤ 0.05</td>
<td></td>
</tr>
</tbody>
</table>

**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

% Individuals dominated

Minutes spent alarming

First alarms (%)

Females dominated (%)
Meerkat alarm calls signal predator class and urgency

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