Alarm Calls in Ground Squirrels

Sherman 1977

Natural History of Belding's Ground Squirrels

Female sedentism

- •Females remain near their natal nest throughout life
- •Males disperse after birth.
- •Brothers do not congregate elsewhere
- •**Females are thus surrounded by kin!**

Foraging and daily behavior habits

Natural predators

Alarm calling

Hypotheses for Evolution of Alarm Calls

1. Predator attention diversion
   - •Pandemonium! or ventriloquism
2. Predator discouragement
   - •The "I see you!" hypothesis
3. Alerting relatives
   - •This is the **kin-selection** hypothesis
4. The Group-selection hypothesis
5. Reduction of probability of later attack
   - •Depriving predators of experience
6. The reciprocal altruism hypothesis

The method of competing, alternative, hypotheses...

Observations Made

Audaciously large observation programme since 1969

- •Tagging and Kinship studies---pedigrees available

Summers of 1974–1976: 3082 hours of observation

9 ground squirrels observed to be killed in that time

6 adults and 3 juveniles

102 alarm calls heard when a predator was also observed

- •Females give alarm calls more often than "expected"
  - •Especially females with kin nearby
- •Males give alarm calls less often than "expected"
  - •"Expected" means "expected at random"

Alarm callers were stalked by predators significantly more often than non-alarm callers

3 of the 6 adults killed were alarm callers (NS)

Confronting the Hypotheses

1 and **2** not supported:

- •No pandemonium and predators stalk alarm callers
- •Alarm caller not always the closest one to predator

Would not be possible to reject **3** (kin-selection) in favor of **4** (group selection), also

- •Anecdotally, no between group differences

5 does not hold water

- •Predators don't preferentially return to particular areas
- •Older females call more often

6 Reciprocity not supported

- •Females don't call as often when they have no living kin. If reciprocity existed beyond kin relationships, this should not be the case
- •Presence of non-callers does not deter callers

Left with Hypothesis **3** (kin-selection) being far more intact than the others.

The Reality of Diversity

Kin-selection is not necessarily *the* explanation for all instances of alarm-calling.

Generalizing from one species or study to another is a risky business in ecology

Sentinel Behavior:

Somewhat different than ground squirrel alarm-calling

•Sentinels are self-appointed "lookouts" who take the job of watching out for "the group" while the others forage.

•The "rota" may seem like a highly organized, complex, social behavior.

•An extra tradeoff: sentinels can't forage simultaneously

•But, sentinels may be better at avoiding predators

Bednekoff's Model

The question: Can a simple model (i.e. direct fitness considerations alone) account for the rota.

A discrete time, stochastic model with many individuals

Consider a single individual

- •Choice made at *each time step*:
  - •Forage or
  - •Be a sentinel

•If you forage, you have a certain probability of finding a certain amount of food in that time step

•If you are a sentinel, you have zero probability of finding food in that time step

•However, the probability of being killed by a predator is *lower* if you are a sentinel or a forager **AND** those probabilities depend on how many others in the group are already sentinels

•An individual may die by

- •Starvation
- •Predation

Optimization

Assume: evolution has given animals optimal decision rules
- •i.e. Given hunger level and number of other sentinels in the current time step, an animal may choose to forage with probability *p* or become a sentinel with probability 1-*p*.
  - •There is some *p* that maximizes the individual's probability of long-term survival

Finding that p, (mathematically)

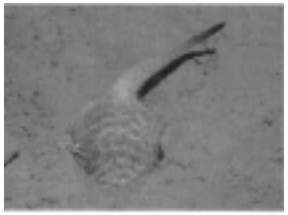
Simulating groups of animls behaving optimally
- •This yields very organized-looking rota behavior!

THE VALUE OF MODELLING:
- •Demonstrated that direct fitness arguments could explain sentinel behavior
- •Generated testable predictions:
  - •Sentinels have reduced predation risk
  - •Better-fed individuals are more likely to become sentinels

Clutton-Brock et al. 1999

Checking Bednekoff's predictions in meerkats
- •Group Structure of Meerkats
  - •One dominant female (75% of litters are hers)
  - •One dominant male (fathers most of the litters)
  - •Note that the close kinship *is* there
- •Foraging: can't watch out for predators while digging
- •Sentinels watch for predators and give alarm calls
  - •Seldom will an individual take two successive guarding bouts, but there is not a clearly defined rotation pattern

Nonetheless, because there is some alternation in sentinel behavior; it appears "organized"



Clutton-Brock et al. cont'd

Key Observations:
- •No sentinels were killed by predators in 2000 hours of observation (did they see *any* meerkats get killed?)
  - • (0.68/year mortality rate amongst adults)
  - • More adults killed in small groups than large groups
- •Recent babysitters spend less time as sentinels
  - •(They ate less the day before)
- •Meerkats were more likely to go on sentinel duty if there was currently no sentinel on duty

Manipulation of hunger status:
- •Fed some individuals 25g of hard-boiled egg
  - •They subsequently spent more time on sentinel duty

All this may be explained by Bednekoff's model

Not necessary to invoke kin-selection.

An application of Occam's Razor:
- "one should not increase, beyond what is necessary, the number of entities required to explain anything"