Lecture 9: Group Size - Eat or be Eaten.

Outline

Costs and benefits of living in groups

- Costs
  - Competition for food
  - Disease transmission
  - Social competition
- Benefits
  - Anti-predator
    - Detection
    - Defense
    - Confusion
    - Dilution (saturation)
  - Foraging efficiency
    - Hunting success (kills per hunt)
    - Prey size
    - Multiple kills
    - Hunting effort
    - Information - the “me too” effect
  - Group territoriality/defense of resources
  - Mating success

Why do many species of animals live in groups?

There are clear ***costs of grouping***:

1. Diseases are more easily transmitted.
2. Resources (food) must be shared w/group mates.
3. Social competition for dominance & mating opportunities.
4. More conspicuous to predators

For social species, there must be benefits greater than these costs, or solitary living would be favored. Rest of lecture discusses processes that favor group living, but keep in mind:

1. There are also *costs* of grouping.
2. Different types of benefits are seen in species with different ecologies.
3. The processes that favor grouping are not mutually exclusive - several are likely to operate simultaneously.

Benefits of Grouping

A. Reduced risk of predation

1. ***Detecting*** attacks: the ‘many eyes’ hypothesis.

Pulliam’s study of ground-foraging birds (finches and sparrows). Vulnerable to many predators (especially hawks) that rely on surprise - only succeed if finches don’t detect approach. Finches have no active defenses - early flight and avoidance only.

Finches cannot eat and scan for predators simultaneously. “Head-cock” periodically to scan for predators. Rate can be measured easily.

Model:

c = time required for predator to attack successfully
r = rate of head cocking
n = flock size
P_n = probability of detecting predator, which is a function of finch flock size (n)

Solitary finch: $P_1 = 1 - e^{-rc}$

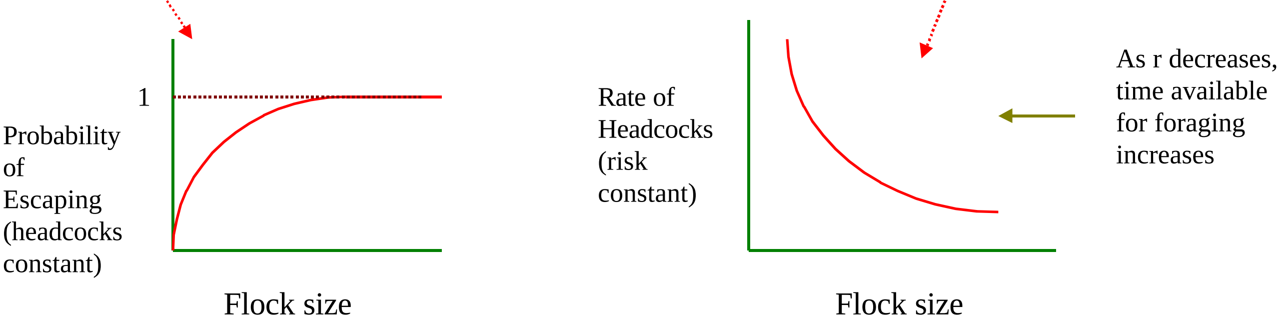
⇒ as rate of head cocking ↑, probability of detection↑
⇒ as time required for final approach ↑, probability of detection ↑

Flock of finches: $P_n = 1 - e^{-rcn}$

⇒ as before, but probability of detection also ↑ as flock size ↑

As flock size increases, there are two possible responses:

1. Maintain constant foraging rate and increase predator detection
2. Maintain risk of predation and increase foraging rate.



Pulliam's model is supported by data:

A. Kenward (1978), Goshawk trained to prey on wood pigeons:
   Detection distance increased as pigeon flock size increased
   Probability of goshawk making kill decreases as flock size increased

   (Fig. 6.2 Krebs & Davies)

B. Bertram (1980) Ostriches vulnerable to lion predation:
   Individual ostriches scanned less (ate more) as flock size increased
   Percent of time with ≥ 1 ostrich vigilant also increased

   (Fig 6.3 Krebs & Davies)

C. Baboons in groups of 31 and 44 spent twice as much time eating as individuals in groups of 8. Small groups also restricted to areas near trees (to escape predation by big cats).

2. ***Defense*** against predators.

In the example above, success of predator relied on stealth. In other predator-prey interactions, the prey species can defend themselves once a predator is detected. The effectiveness of active defense may increase as group size increases.

Insect examples (in Alcock reading assignment)
   -'hand grenade' ants, Nasute termites
Ungulates form a ring, facing out, with young in the middle.
   - musk oxen/wolves
   - wildebeest/African wild dogs

(AWD overheads)

3. ***Confusion*** of predators

A predator must single out a target during its final approach. With solitary prey, this is straightforward. For groups of prey, unpredictable scattering of prey in many directions might confuse the predator and decrease its odds of success.

There are few clear-cut demonstrations that this actually occurs. Suggested to operate in shoals of brightly colored fish, which move in close synchronization at most times other than predator attacks.

Some evidence against this hypothesis — confusion can also operate in favor of the *predator*, rather than the prey. African wild dogs hunting impala: hunting success ↑ as impala herd size ↑, partly because impala scatter more slowly in large herds than in small herds, due to confusion.

4. ***Dilution*** of risk

Predator saturation: A predator can usually take only one prey individual in an attack. Even group hunters usually take just one prey, though up to seven has been recorded (African wild dogs hunting impala).

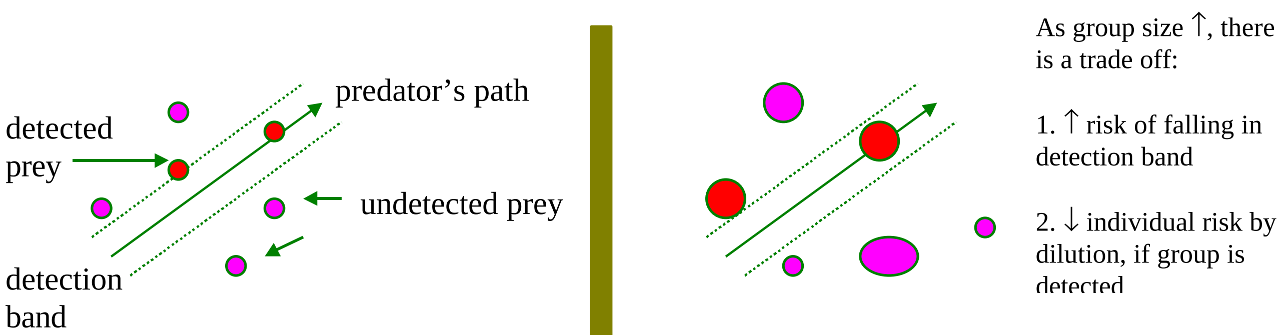
If

1. One or few prey killed per attack,
2. Single prey and groups of prey are equally detectable for predator,

then individuals can reduce their risk of being killed by grouping, even when the risk that *someone* in the group will be captured stays constant. ***Hamiltons' Selfish Herd: grouping to reduce the 'domain of danger'***

It is likely that prey groups are actually more detectable than solitary prey, but this usually does not negate the 'risk-dilution' benefit, when:

1. prey groups are tightly packed
2. predator has wide band of detection (raptors, open habitat mammals)
3. few prey killed per attack (solitary predators, prey large relative to predator)



Solitary prey

$$\text{risk} \propto r$$

Groups of Prey

$$\text{risk} \propto \frac{Nm}{n}\left[r + \sqrt{\frac{n-1}{\pi d}} \right]$$

r = predator's radius of detection
N = prey density (individuals/unit area)
n = group size
m = number of prey killed per detection
d = density of prey within group

Solitary Prey - risk simply proportional to radius of detection.

Groups of Prey

- risk still $\propto$ to radius of detection (r)
- risk $\propto$ (N/n) = # of groups. Group size ↑, fewer groups for pred. to detect
- but groups cover bigger area, so correction factor for easier detection:
  $\sqrt{(n-1)/(\pi d)}$ {d is in denominator ⇒ dense packing ↓ risk}
- risk $\propto$ number killed per attack; if predator can eat all group members in one attack, there is no benefit to grouping {m is in numerator}

Take home message:

$r > Nm/n[r + \sqrt{(n-1)/\pi d}]$ grouping is favored

$r < Nm/n[r + \sqrt{(n-1)/\pi d}]$ solitariness is favored

Many examples in which dilution/detection tradeoff favors grouping:

Penguins vs sea lions
Antelopes in open country vs. lions/hyenas/wild dogs

(AWD overhead)

Bottom line is that effects of grouping on detection, defense, confusion and dilution combine, and in some cases favor grouping, others not.

B. Foraging Efficiency

To now, mechanisms dealt with avoiding being eaten - are there also mechanisms that favor grouping to obtain food? Yes.

1. ***Hunting success***. For many predators, kills/hunt increases as hunting group size increases. In groups, one predator can cut off escape route while other predator pursues, or can join forces to pull prey to a halt, etc.
(Fig 4.2 Schaller) lion example

But no increase in hunting success for other predators - e.g. Kalahari hyenas.
(Fig 3.28 Mills)

2. ***Prey Size*** increases with hunting group size for most carnivores that hunt in groups
Spotted hyena hunt gazelle (small) in small groups, hunt wildebeest (large) in bigger groups.
(Figs. 35b and 49b Kruuk)
(AWD example)

3. ***Multiple kills*** may be more likely as hunting group size increases
(AWD example)

4. Kills may be made with ***lower individual effort*** with more hunters.
(AWD example)

5. Groups may allow transfer of ***information*** about location of food
Important in colonially nesting birds
- feed on ephemeral patches of food that are hard to locate (e.g. schools of fish for shorebirds, insect hatches for bank swallows, or carcasses for vulture)
- but the food patches are rich enough that many birds can feed on them without reducing others' intake
Roosts are ***"information centers"*** in vultures (Parker)
- at roost, those that did not find food observe the full crop of those that did, and follow them the next day
"Me-too effect" in herons (solitary feeders in most places but group feeders in Pacific NW salt marshes) (Krebs)
- herons likely to join other herons in pond, b/c a pond with no heron has no information while flying over, but a pond with a heron in it probably has enough fish to make hunting worthwhile. Leads to build-up of groups at good feeding locations, even with no direct benefit of feeding together.

Bottom line is that effects on hunting success, prey size, multiple kills, information and effort combine to determine ***net rate of energy intake*** (Kcal eaten - Kcal burned in hunts). Group size that maximizes net energy intake is favored.

(AWD example).

Note that Bednarz paper on Harris' hawks uses ***gross*** rate of energy intake - he is (implicitly) relying on the (untested) assumption that hunting costs are equal across hunting group sizes.

(Fig. 2 Bednarz)

C. Group territoriality

Grouping favored in some species as a means of defending territories or resources.
'Arms race'. If solitary initially, perhaps two decide to join. If two compete with conspecifics well enough to obtain more than double the resources as one acting alone, pairing is favored. Once established, then three may displace two, etc, until some factor other than intraspecific competition sets a limit (e.g. social competition within groups).

This argument has been made for female lions (Packer 1986).

D. Mating success

In cheetahs, some males live in groups, though there is no hunting benefit. Females live alone (consistent with no hunting benefit of grouping) and wander widely. Coalitions of males attract more females to their territories than solitary males do, so that males in groups mate more frequently than solitary males (Caro 1994).