The Problem of Where to Live

Physical and biotic environment critically affects fitness

- An animal's needs may be met only in certain habitats, which should select for the ability to recognize these habitats
- Within the range of habitats where it is possible to live, some living situations that are better than others
- Choosing where to live (and how to compete for space) is potentially an optimality problem

Components of the problem

- Dispersal (and migration, which is related to dispersal)
  - Whether to leave
  - When to leave
  - Where to go
  - Whether to return
- Competition for space
  - Competition by exploitation (scramble competition)
  - Competition by exclusion (territoriality)
Dispersal

Dispersal has costs; what are the benefits?

- H1: Avoid competition for food with parents
- H2: Avoid competition for mates with parents
- H3: Inbreeding avoidance

Some evidence: Belding’s Ground Squirrel

- Provisioning with extra food actually speeds up dispersal (Exclude H1)
- Postbreeding dispersal is no more likely among males with lowest mating success (Exclude H2)
- Inbreeding lowers fitness (consistent with H3), but this hypothesis is hard to test directly because all males disperse and so inbreeding is rare
Dispersal--Sex biases?

Why does only one sex disperse?
- Mammals: males disperse
- Birds: females disperse

Hypotheses for ground squirrels:
- H1: inbreeding cost higher for males
- H2: dispersal cost higher for females (related to value of burrow and knowledge of home range)

Hypotheses for other mammals?
Hypotheses for birds?

Ground squirrel data: Holekamp and Sherman
Migration

What it is: seasonal cycle of dispersal, followed by return to original range

Historical question: did migration arise all at once or gradually?

Birds:
- In bird families with short-range migrants and long-range migrants, all of the short-range migrants have ranges confined to tropics
- Suggests that long-distance migration resulted from tropical birds gradually extending distance of migration

Sea Turtles:
- Did Green sea turtles have to extend their migration distance to Ascencion Island gradually because of continental drift?
  - DNA evidence
    - Ascension population is genetically distinct (implies long isolation)
    - But, it is not distinct enough--has been isolated only about 1 million years
Migration: Costs and Benefits

Costs: energy, time, risk of getting lost, risk of predation

What are the benefits?
- Find better source of resources during breeding season
- Escape harsh weather during non-breeding season

Interspecific and intraspecific comparisons
- Variation in tendency to migrate or distance of migration provides clues as to the factors that determine benefits and costs

Interspecific variation:
Related to body size, feeding ecology and other factors

Bryde’s whale (tropical only)

Blue whales

Winter Breeding Areas
Migration Routes
Intraspecific and interspecific variation in birds—a latitudinal trend

Intraspecific variation: simple optimality perspective
- For each individual, is \( B > C \)?
- Decision is independent of what other individuals do
- Variation in migratory tendency results from variation in benefits and costs that individuals experience
Intraspecific variation: game theoretical perspective (Alcock pp 404-406)

- Payoffs of alternative options depends on what everyone else is doing
- Variation in migratory tendency reflects evolutionary equilibrium, such that each option delivers same average benefit (and equilibrium is maintained by frequency dependent selection)

<table>
<thead>
<tr>
<th>Your payoff</th>
<th>Everyone else</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stay</td>
<td>Migrate</td>
</tr>
<tr>
<td>Stay</td>
<td>Low</td>
</tr>
<tr>
<td>Migrate</td>
<td>High</td>
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</tbody>
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Result: a mixture of strategies
Competition for Space

Scramble competition
- Patches vary in quality, and competitors have to figure out how to distribute themselves
- No interference or fighting is involved

Simple model: Ideal Free Distribution A group of equal competitors distribute themselves numerically according to relative quality of patches

At equilibrium, competitors in two patches will get equal payoffs

If patches are equal in quality, numbers of competitors will be equal
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If patches differ in quality, ratio of competitors will match ratio of quality
Do animals meet the predictions of the Ideal Free Distribution?

- YES

Patch 1 (X crumbs/min)

Patch 2 (2X crumbs/min)

...but they typically don’t fulfill the assumption of equal competitive ability
April 5: Habitat Selection: Territories (cont’d)

Territoriality

What it is

• Defense of an area of habitat or resource against intrusions by other animals (usually conspecifics)
• Defense involves combat but also “Keep Out” signals (odors, song, visual displays)

Does territorial defense really exclude some individuals from habitat where they would rather be?

• Remove great tits from territories in woods (A)
• “Floaters” from marginal habitat move in immediately (B)

Alcock Fig. 10.29

Costs: Time, energy, risk of injury, risk of predation

Benefits: Exclusive access to resources in the territory: food, mates, refugia
Decision-making by territorial animals

Whether to defend territory (or compete in a scramble)
- A richer, more concentrated resource may not be worth defending
- Pressure from intruders may elevate costs of defense
- One strategy is to take on helpers (e.g., satellites in pied wagtail)

How large a territory to defend?
- Depends on how costs and benefits scale with territory size
- In nectar-feeding birds, territories get smaller in good times

How hard to fight?
- Fights may be settled by asymmetries in fighting ability (resource-holding potential, or RHP)
- Sometimes the outcome seems to depend on arbitrary rule: e.g., “owner always wins”