Lecture 8: Resource dispersion and spacing patterns

Outline

Terminology
- dispersal
- dispersion
- home range
- territory - ecological and behavioral definitions

Patterns of dispersion
- clumped
- random
- regular
- spatial and temporal aspects

Horn & Orians' model of redwinged and tricolored blackbirds

Macdonalds' Resource Dispersion Hypothesis: carnivores
- range size $\propto$ patch distribution
- group size $\propto$ patch richness

Waser - resource renewal rate

Economic defensibility
- Graphical model
- Algebraic model

Animals show a huge range of spacing patterns:
Red squirrels have regular, non-overlapping ranges, not even shared with a member of opposite sex
Shorebirds nest in colonies of 1000's

Even within relatively narrow taxonomic groups, there is considerable variation: some spiders are solitary except for mating, others live permanently in communal webs with 100's of spiders.

Today discuss explanations of *animal spacing patterns* that are based on *dispersion of resources*.

First, some terminology:

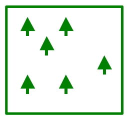
Dispersion and dispersal are not the same thing. ***Dispersal*** is movement of young animals away from site of birth. ***Dispersion*** is distribution of animals (plants, whatever) in space (and time).

Territory - (1) An exclusively used area (ecological). 2. A defended area (behavioral).

Home range - area an animal uses in normal activities. No qualifiers such as exclusive use or defense

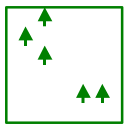
Dispersion of *resources* or of *animals* can show three basic patterns:

1. Random



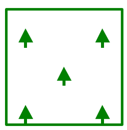
nearest neighbor is in some cases close, others cases far.
knowing location of one individual gives no information about whether others will be near or not.

2. Clumped



nearest neighbor *closer* than random, on average
knowing location of one individual predicts that others will be found nearby (patchy, underdispersed)

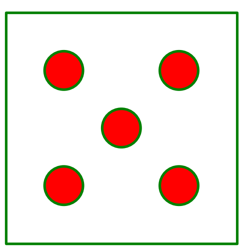
3. Regular



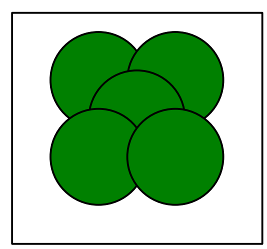
nearest neighbor *farther* than random, on average
knowing location of one individual predicts that others will *not* be found nearby (regular, overdispersed)

(**Fig. 11.1c & d Davies -** examples of regular dispersion , evidence of territoriality by ecol. defn)

With respect to *home ranges* of animals, can describe dispersion as above, but also need to describe *degree of overlap*



Regular, nonoverlapping



Regular, overlapping

Spatiotemporal distributions: For dispersion of resources or of animals, there is a ***temporal*** component, as well as a spatial one. Must be in the ***same place*** at the ***same time*** to be clumped in reality. If the central home range in the figure above right was never occupied at the same time as the four corner ranges, then the degree of real overlap in space use would go down substantially.

Several arguments or models for how spatiotemporal dispersion of resources (usually food, but could also be mates, dens) affect space use by animals.

1: Orians & Horn's blackbirds

Redwing blackbirds (cent. California): females nest singly, isolated from each other, little home range overlap, males defend home ranges that include the nest of their mates, so again little home range overlap

Tricolor blackbirds (cent. Calif.): females nest in huge colonies, home ranges of colony members virtually 100% overlap, males also virtually 100% range overlap.

Orians & Horn distinguished **two patterns of spatiotemporal distribution of food**:

1. **Regular dispersion**, **continuously available:** e.g. grass

2. **Spatiotemporally clumped**: e.g. emerging insect swarms from temporary ponds. Spatially patchy, with a lot available within a patch for a short time, but location and timing of patches is variable.

O&H's model predicted spacing of nests (clumped, random, regular) and of home ranges (clumped, random, regular, also overlapping/nonoverlapping)

Assumptions:

1. Model applies to species are **central place foragers** - any animal that must return to a fixed nest, den, roosting site between foraging trips.

2. Animals locate nests/ranges so as to **minimize energy expenditure while foraging.** (Note that there are other possibilities, e.g. maximize rate of energy intake, maximize intake - expenditure).

Graphical model:

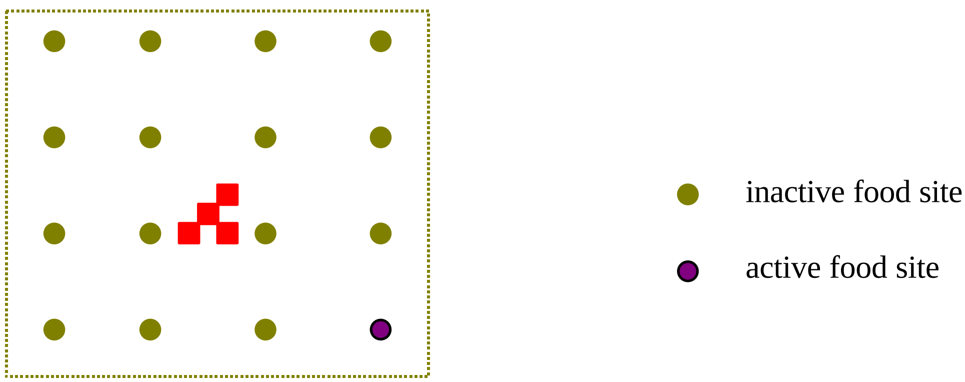
A. What spacing minimizes energy expenditure if food is regularly distributed & continuous? Suppose there are 16 small, regularly distributed, continuously available feeding sites in a marsh, and a RWBB requires 4 such sites to raise a clutch.

Where should the first pair to arrive put its nest? Right in the middle of 4 food sites.
Where should the next pair put its nest? If it uses any locations used by pair 1, it will get less food out of those locations — best solution is to put nest in middle 4 sites not used by pair one.
Same logic for subsequent pairs.

Result: If food is regularly distributed and continuously available, selection will favor animals that **disperse nest sites regularly, with nonoverlapping ranges**.

There is no territorial defense involved here - each pair maximizes efficiency by avoiding home range overlap.

B. What if resources are spatiotemporally clumped, so that only one of the 16 sites produces food at once, but produces enough to support 4 pairs (note that the total availability of food has not changed) (also, it is not necessary that the sites still be regularly distributed - they could also be clumped or random)



First pair does best by placing nest directly in center of marsh.
Second pair - same place. They do not lose anything by overlapping, because active patch is rich enough for 4 pairs.
Same logic for subsequent pairs.

Result: If food is spatiotemporally clumped, minimum foraging costs come with **clumped nests, overlapping ranges.**

These predictions apply well to California blackbirds:

Redwings fed in permanent marshes on solitary insects that emerge and crawl up cattails, so they are continuously and regularly dispersed.

Tricolors fed on lacewings - huge swarms emerge at unpredictable locations, at variable times determined by rainfall.

2: Macdonald's Resource Dispersion Hypothesis (carnivores)

Most carnivores (85%) are solitary. Traditional explanation for group-living in large carnivores is that communal hunting improves hunting success (more on this next time).

Macdonald points out that many small/medium carnivores hunt alone, but live in 'spatial groups'. They share a home range, perhaps even defend it cooperatively, and interact at den sites, but forage alone.

E.g. **red foxes**. Where food is sparse and uniform (e.g. N.American prairies), pairs share a home range, offspring disperse. Where food is rich and patchy (Oxford), they form spatial groups when female offspring don't disperse. Share a range, but only associate for a few minutes a night.

Macdonald's explanation for this difference is very much like Orians & Horns' explanation for RWBB. Foxes (like RWBB) are central place foragers. In N. American prairies they rely mainly on rodents, which are uniform and continuously available. In Oxford they rely on earthworms (patchy, ephemeral = spatiotemporally clumped) and garbage (also spatiotemporally clumped, though more predictable).

Macdonald's general argument is that:

1. Many carnivores rely on patchy food.
2. Home range size depends on distance between patches.

(Fig 11.2 Davies, golden-winged sunbirds)

3. Group size depends on richness (size & density) of patches.

(Coyotes - live in pairs where they are dependent on small prey such as rodents, live in packs (up to 6-7) where large carcasses are common , eg Natl. Elk Refuge)

4. This provides an explanation for 'spatial groups' of carnivores that live together but don't hunt together.

5. This explains why HR size is not necessarily related to group size, as you might expect if a bigger area is needed to support more individuals.

6. The resource that determines spacing may differ between the sexes. Female distribution determined by food, then male distribution determined by females (Jarman - antelopes).

3: Influence of Renewal Rate: white-tailed mongooses

Waser studied white-tailed mongooses in Serengeti, found very clear spatial groups. Sets of white tails used perfectly overlapping home ranges, but moved independently within the range while foraging. Expected to find that their food was spatiotemporally clumped. It wasn't! They feed almost exclusively on termites and other surface-active insects, which are uniformly distributed and continuously available. Models above predict non-overlapping ranges in this case.

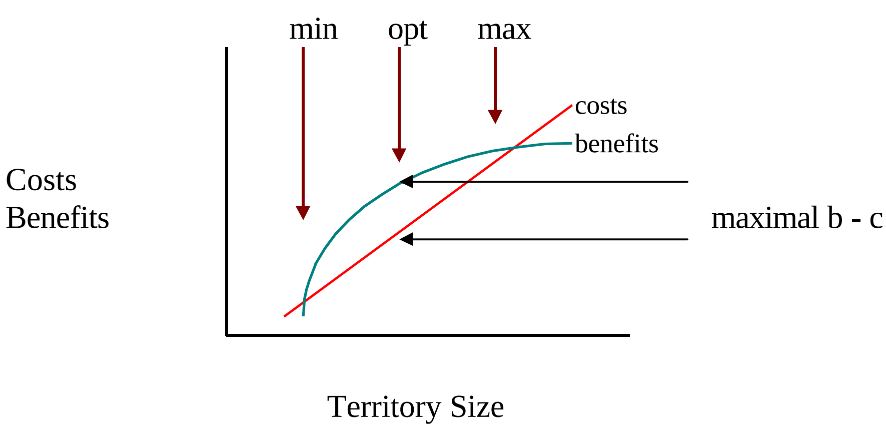
Waser noted that insects renewed very rapidly, with experiments in which he removed all insects from a plot and measured the number available the next night. Found that renewal rate was high enough that there was little cost to sharing a range, even with continuous, evenly distributed food. Two white-tails rarely cross foraging paths in the same night, and by the next night, places visited by the others are back to normal.

Take home message from carnivore studies:
1. Spatiotemporal clumping of resources (patchiness) favors grouping
2. Rapid renewal of resources favors grouping even w/o patchiness.

4. Economic Defensibility: graphical model

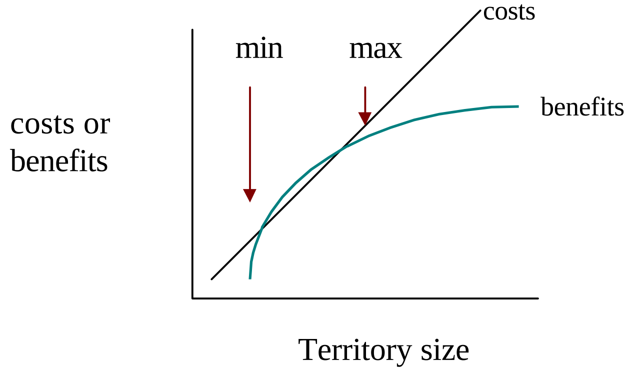
Basic idea is that animals will defend a territory only when it is **economically defensible,** i.e. the benefits of being territorial exceed the costs.

To apply this idea, imagine that individuals defend territories of varying sizes - **how will costs of defense increase as territory size goes up? Probably linear**, more or less, because number of intruders will be linearly related to size of area, all else equal. How will benefits of defense increase as territory size increases? Linear up to a point (more resources in greater area) but eventually animal has all it can use, so benefits asymptote.



Predicts a range of territory sizes, and the best territory size, for given conditions.

What happens if the density of intruders doubled? Cost curve shifts upward, range of territory sizes gets smaller.



If density of intruders gets *really* high, then c>b for all territory sizes.

Gill & Wolf study of golden-winged sunbirds, manipulated intruder pressure, and measured energetic costs (flight time converted to units of energy) and benefits (nectar taken in converted to energy) of foraging. Found that territory size decreased as intruder pressure went up, and the birds eventually ceased defending territories at all once pressure got to c=b threshold

(**Box 5.1 Krebs & Davies; GW sunbird B & C calculations**)

(**Graphical models**: take care about assumptions, b/c conclusions depend on shapes of B & C curves)

(Fig 5.7 Krebs & Davies) Adjustment of territory to match optimum size: Rufous hummingbirds during migratory stopovers establish short-term feeding territories. Adjust size of territory through time, until it is at optimum. Study by Hixson using pesola perches to monitor changes in body mass

5. Economic Defensibility: algebraic model

Carpenter & MacMillen honeycreepers. Nectar feeding birds in Hawaii.

For territoriality to be favored:

E	$+ \ T$	$<$	aP	$+ \ e(1-a)P$
basic cost of living	added cost of territoriality		yield if not territorial	extra yield due to territoriality

If not territorial, get a proportion, *a*, of total production in area used, *P*

e is efficiency of defense (0 to 1) of the resources (1-*a*)*P*, that can be gained by territoriality, i.e. which are in excess of what you get if not territorial.

One extreme: food is so abundant that *aP* meets animal's needs, no benefit to territoriality. Defense begins when needs exceed energy available for 'free', without territorial defense:

$aP < E$, so upper threshold is $P = E/a$.

Other extreme, production is so low that even with extra food provided by territorial defense, needs cannot be met. This threshold occurs when P drops to:

$P \leq E + T$

Combining the thresholds, predicts territoriality when

$E+T < P < E/a$

Carpenter and Macmillen measured these variables, in terms of energy obtained (from nectar) and energy spent (in flight). Tested whether birds were/were not territorial at the predicted thresholds: found remarkably good match.

(Fig 11.4 Davies)