Definitions of Territoriality
There are many.
One end of the spectrum---Odum:
• "An actively defended home range"
• "At the risk of offending semantic purists we are including under the heading of territoriality any active mechanism that spaces individuals or groups apart from one another, which means that we can talk about territoriality in plants and microorganisms as well as in animals."

• Huntingford and Turner---A Behaviorally defined notion. Territorial behavior has 4 components:
  1. Site attachment
  2. Exclusive use of the area
  3. Agonistic behavior
  4. Attack changes to retreat at the territory boundary

Typically refers to an area in space rather than a mobile resource (for example red deer stag and his harem of does)

Not a Home Range!
Huntingford and Turner’s defns are specifically geared toward distinguishing territory from h.r.

Home range is basically just the area in which an individual tends to restrict itself

Example of coatis:
Exclusive home ranges but not territories.

Varieties of Territory
A bit ad hoc:
1. Based on Resource that the owner gets access to:
   - food
   - mates
   - shelter
   - also nest sites

2. Length of Time defended.
   Ranges from hours to year-round

3. Defended by whom and how many?
   Single individuals versus mating pairs, etc.

Phyletic Perspective on Territories
Phyletic a. Biol. Of or pertaining to the development of a species or other taxonomic group.

Winn 1954. Territoriality in Darters (fish)

A continuum of territorial behavior across closely related species from “more primitive” to more recent/more specialized:
• Percina caprodes---lake dweller, non-territorial
• Hadropterus maculatus---drive other males away from females
• Etheostoma (2 spp.) defend females and remain near landmarks
• E. blennoides---high aggression and fixed territories.

Population-level consequences
A fatal blow for the Ideal Free Distribution concept.

Thus, Natl Seln may act to increase proportion of territorial animals in a population.

Costs and Benefits of Territoriality
Benefits:
• Food: lasts longer, lower depletion rates, less variability in supply
• Mates
• Offspring rearing (female salmon)
• Lowered predation (due to nest dispersion)

Costs:
• Acquisition
• Displays and patrolling
• Possibility of injury (though not very common!)
• “Single-Use” Territory
• TTP (Displays and Patrolling really are costly!)

Yarrow’s Spiny Lizards on Mt. Graham
Studying the effects of testosterone implants in male lizards.
(Marler and Moore)
How Large a Territory?

Another simple graphical framework:

```
<table>
<thead>
<tr>
<th>Fitness Currency</th>
</tr>
</thead>
<tbody>
<tr>
<td>XY</td>
</tr>
<tr>
<td>X Territory Size</td>
</tr>
</tbody>
</table>
```

The optimum occurs where the slopes of the cost and the benefit curves are equal (That is where the marginal benefits of a larger territory start to decrease faster than the costs are increasing.)

Curve shapes will depend on environmental quality and population size relative to limiting factors.

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Conditional Territoriality

Some animals are territorial at times and downright gregarious at other times.

Bellbirds in New Zealand.

Extra 25 kJ/day from switching to terr. behav. under low food density

Rypstra (1989) studying a social spider:
- Low Food Density---solitary and highly territorial
- Hi FD---social. aggregations spin webs and individuals are free to go where they will. Fewer insects escape from the group webs.

The bee-eater mystery
- One would expect that individuals that voluntarily choose to be non-territorial will do so because there is not an energetic advantage to holding the territory.

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Explanations for Territory Maintenance

Two interesting observations:
1. Most territory owners don’t forfeit their territories in conflicts with intruders
2. Things don’t often escalate to full-blown fighting

Why could this be? We’ll look at three explanations.

1. The “Arbitrary Rule” ESS hypothesis:

Speckled wood butterfly and sunspot territories. (Davies 1978)

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The Resource-holding Power Asymmetry Hypothesis

Territory owners are bigger and stronger by nature.

This generates predictions:

- Beewolf wasps (O’Neill 1983)
- Pseudoscorpions (Zeh et al. 1997)
- Damselflies, endurance flying, and fat reserves (Marden and Waage 1990)

But note red-winged blackbirds (Shutler and Wetherhead 1991)

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The Payoff Asymmetry Hypothesis

There are certain costs to establishing a new territory, initially

but then the payoffs increase over time because you have an “agreement” with your familiar neighbors

Two testable predictions:
1. If you remove an individual, and let somebody take over his territory, he is less likely to regain his territory if you keep him captive longer
2. The duration of contest to regain the territory should increase with increasing time of being away from its original territory

Krebs 1982: found these trends BUT---not a properly controlled experiment

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African Bee-eaters:

Live in mud-bank colonies, but forage in separate foraging territories that they defend against intruders.

Communal feeding area close to home:
- 100 mg insect/hour average
- Defended, distant territories
- 250 mg insect/hour average!

Yet, some birds abandoned their territory to feed close to home. Why???

Once again (as in the starling, central place foraging example---bringing food back to chicks

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