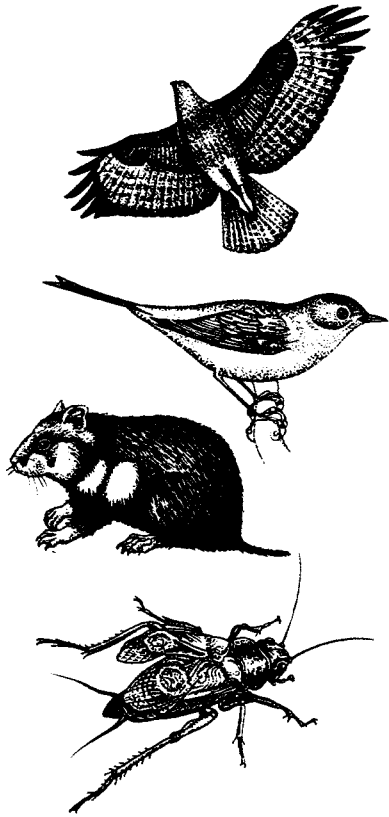
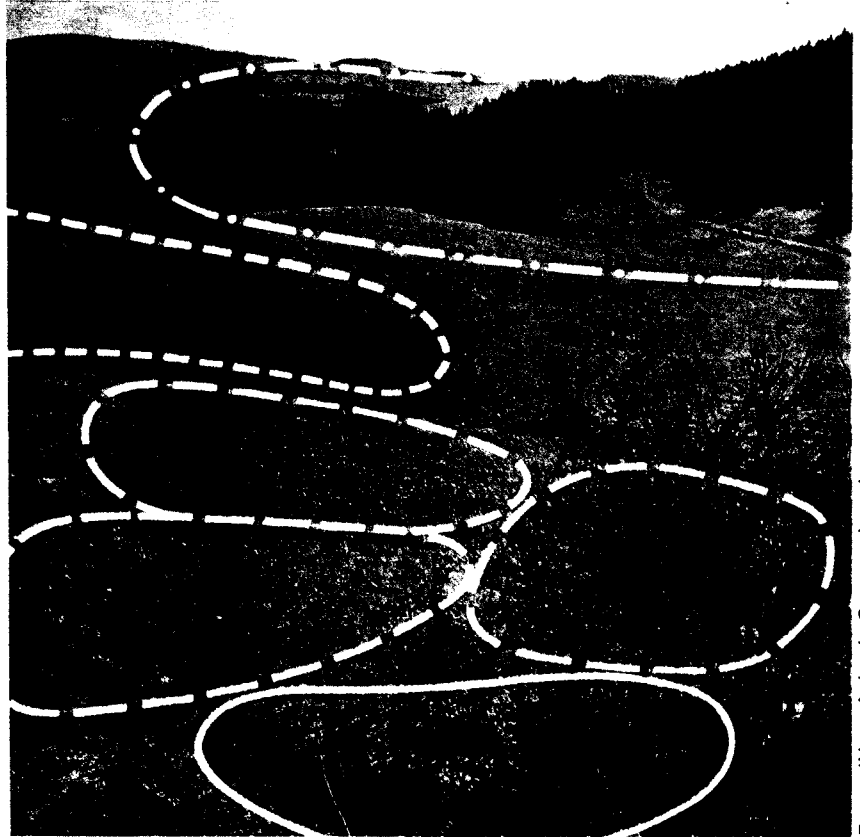


# TERRITORIALITY



Size of the territory of a buzzard, warbler, hamster and a cricket.



From: 'How Animals Communicate'

## AN ECONOMIC APPROACH

Daniel T. Blumstein

A pied wagtail saw another wagtail approach the mountain stream's opposite shore. It dropped the insect it was tearing apart and flew over and chased away the intruder. This accomplished, it returned to its interrupted meal, wiping its bill contently on the ground when completed. Why did the wagtail chase away the other bird? Why do some animals defend certain areas while others share their areas with other con-or hetero-species?

We're going to return to the common assumption in behavioral ecology: behaviours will be performed and/or will evolve when benefits associated with them outweigh costs. In this case, it should be pretty easy to visualize both the benefits and costs.

Many animals forage on renewable resources--those which are replaced over time. For instance sunbirds (or hummingbirds in the Western Hemisphere) drink the nectar of certain flowers. Given reasonable weather, and the appropriate season, the plants will produce nectar on a daily basis. Other animals eat grasses or other plants which will re-grow following partial defoliation. Still other species, such as the wagtail, eat insects which are washed ashore. In each 24 hour period, new insects are washed ashore. The common theme in these different sources of food is that they are renewable — they are replenished over time.

Individuals who forage on renewable resources can potentially spend less time looking for their food. How? Imagine if an individual could monopolize a patch of land (or water, or air) that produced enough food to

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sustain it each day, and that when depleted, it would renew itself. Such a lucky individual could spend its time doing other activities (or nothing if it so desired) given a reliable food supply.

What we've just described is a potential benefit to those individuals who kick out competitors from their patch of renewable food. Defence of space against competitors is called territorial defense. The patch that is defended is called a territory. Territory size and shape is a function of the behaviour of competitors, and the benefits associated with possessing the territory.

Imagine if the patch was so good that many others wanted a piece of it. Other individuals would "intrude" on the territory. There could be at least three possible outcomes from an increase in the number of intruders.

First, the resident could be evicted from its territory. While tragic, this is a rather uninteresting result for the purpose of this essay.



Barrie Britton

Face values, Langur males fighting repeatedly with rivals. This particular male has managed to wrest control of a female troop, and is therefore acting aggressively towards anyone who comes near, photographers included.

From: 'How animals communicate



The voice alone is not enough to discourage an intruder. Gibbon must give the message 'Look at me when I'm talking to you', and display themselves in an obvious spot.

Second, an individual could let others take some of its defended area. Thus, where there was once one territory, suddenly there are several. If the territory produced more food than a single individual could consume, and the readjustment of residents was such that nobody would starve, then the original resident didn't really lose anything and probably gained in that it will have fewer intruders in the future.

A third outcome of an increase in intruder pressure is that a territorial individual could stop defending its territory. Why? Recall the cost/benefit argument. Chasing away potential competitors has a variety of costs: it takes time away from other activities; it is energetically expensive; and there is always a risk of injury or death in an encounter.

Thus, there should be a point at which it is no longer economically efficient to continue to defend a territory.

This lack of defence could come about two ways. One way is that the territory is really good, while another is that it is really bad. When resources are super-abundant, then any costs associated with territory defence may be wasted. Thus, if there is no way you're going to starve, even without a territory, then it's foolish to defend one. Alternatively, if the territory was

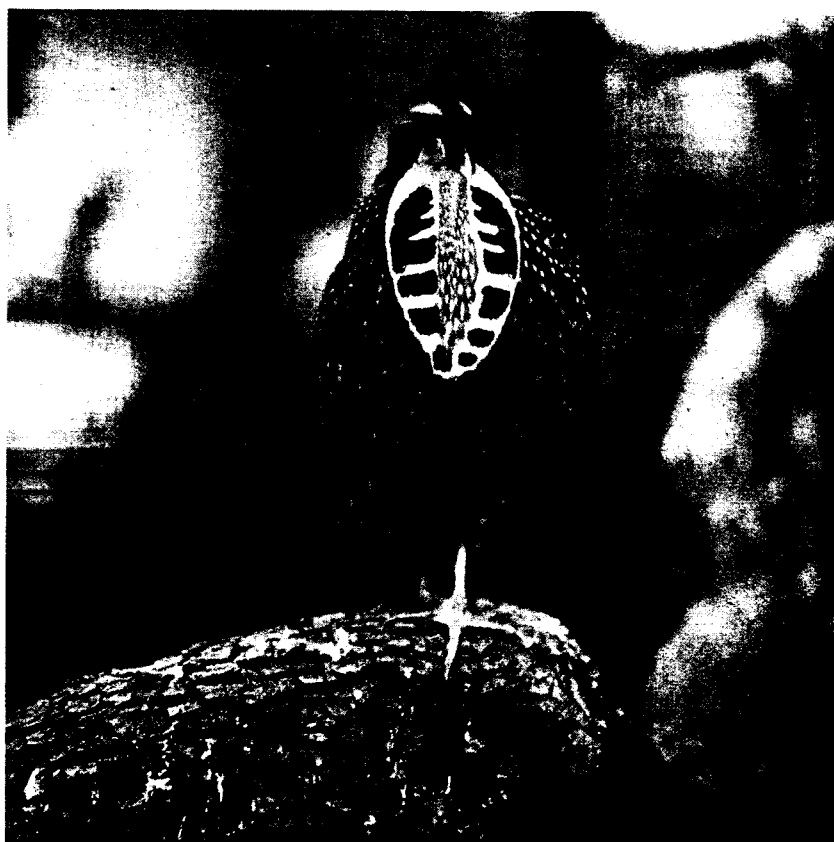
# TERRITORIALITY

where they have been well studied, territorial wagtails will accept a second individual on days when there are many insects, but not on days when there are fewer insects. What does this new wagtail do? It helps patrol the territory and kick out other potential intruders. Thus, by accepting a second individual, the primary territorial resident is reducing the defence costs associated with maintaining its territory.

Sunbirds offer another interesting case where resources explain territorial behaviour. In Africa, one species of sunbird defends enough nectar producing flowers to support it. If suddenly more flowers bloom--intruder pressure increases and the sunbirds will either reduce their territory size or give up defence altogether.

I hope I've painted a particularly clear picture of resource-based territorial defensive behaviour. Things are not always so easy to understand in all cases. It's often difficult to identify a resource or the time frame over which the benefits of territoriality should be computed. Not all resources can be quantified in calories — marmots need burrows for protection from predators as well as to hibernate in. Other species have non-caloric habitat requirements too. Such species challenge us to discover the currencies of costs and benefits.

Keep your eyes open and look around for examples of animals defending territories — they're all around.



The featherless wattle uses its colours as an optical weapon during its territorial disputes.