

Territoriality and Coloniality

Introduction

A territory is that area actually defended by a bird and functions by providing the requirements for life. Most bird species emphasize quantity over quality by having territories just large enough to provide the resources needed during average conditions. However, if conditions are less than optimal, then reproduction may not be successful, due to a lack of resources. A very few species will emphasize quality over quantity by having a territory size much larger than is usually needed. Reproduction is usually less in those populations than most other species. However, in those years of environmental stress, e.g., a drought, then those bird species are still successful, since their larger territory still has enough resources to raise their young.

There are two main types of dispersion patterns for the spacing of individual birds and bird nests. A clumped pattern usually involves birds forming colonies for reproduction, e.g., Royal Terns, and this is coloniality. A more regular spacing indicates territoriality. In this case there exists an almost equal distance among nests within suitable habitat. There are no known examples of a truly random dispersion pattern. Often there will be a combination of these two types, e.g., the King Penguin shows a highly clumped breeding distribution, with a total of less than 50 known colonies, but pairs within a breeding colony defend territories around their nest, resulting in a remarkably regular spacing pattern within the colony.

A Functional Classification of Avian Territories

The vast majority of bird species are territorial to some extent. Consider a functional classification of avian territories consisting of six types of territories included with this handout on a separate page. The effect of territoriality on the bird's survival and reproductive output is to give an overall advantage in comparison to those that do not defend a (suitable) territory. In particular, individuals defending territories will tend to leave more offspring than those that do not defend territories.

There appears to be a positive relationship between a bird species body weight and territory size, i.e., a bird species that is larger will tend to defend a larger territory, as you might intuitively expect. Within a single species, territory size is also negatively correlated with food abundance, i.e., when food is abundant, then territory size is reduced.

Benefit of Having a territory

Competition for scarce resources seems to be a crucial factor in the evolution of territoriality. If all resources were super abundant, then there would be no need for birds to defend them. The benefit of having a territory is that it results in territory owners having either more of a particular resource or a better quality resource. The main resources that birds defend in territories are food, breeding sites, and mates. In some species the resource could be space itself, since an increased distance between neighbors may reduce interference, cannibalism, or predation.

Costs of Defending a Territory

There are costs of defending a territory. Threatening and fighting intruders is time consuming with a lot of energy expenditure. Defending a territory against intruders also increases the risk of injury or even death. An observation has been made that even a very slight injury often indirectly results in the death of that individual. Birds use

communication to avoid actual fights that may cause injury. Even if an individual is the “winner” of a particular conflict, which still results in an actual injury, that same individual, as well as the other combatant, will often die, due to not being at its peak. Birds that are less than at their optimum are preyed upon first. How often do you see an old bird? For example, sparrows will live about two years in the wild, but may live eight to ten years in captivity away from the threat of predators. So there must be a balance between the benefits and costs of maintaining a territory. Defending a territory must be worthwhile in terms of survival or reproduction.

Estimating the Costs and Benefits of Territory Defense from an Energy Point of View

a) Territory and Food

Energy expended each day by territorial birds must be compared with the energy intake each day. If territories are economically defensible then the energy available to the bird in its territory should not be less than the energy it expends in defense of that territory. For example, Golden-winged Sunbirds are the African equivalent of hummingbirds. They defend individual territories outside the breeding season and feed on the nectar of mainly flowers from one species (*Leonotis*). Sunbirds defend territories that allow the nectar levels in the flowers in that territory to increase, since no other Sunbirds are depleting the supply. This reduces the work effort needed for the owner to get his nectar. Specific flower nectar levels, time spent feeding, and time spent defending the territory were determined and results showed a net energy profit each day - for feeding on flowers with more nectar - available because of territory defense. Both field studies and lab experiments verified the result. Basically, birds defend only enough area to “break even,” with benefits only slightly higher than costs. Defending a larger territory than needed is very costly. (However, there are exceptions to this usual arrangement as noted in the introduction. Population sizes remain lower than theoretically possible, because of the resources that are available, however the population size remains more stable over the long term, even when other species have varying population sizes, due to fluctuating conditions of the resources.) Also in these studies it was shown that the size of the resource itself (number of flowers) was the crucial element – not simply the physical size of the territory. A larger size area was defended if the resource was less concentrated. In particular, for Sunbirds a certain number of flowers were defended, regardless of actual territory size. These studies showed that by defending the flowers these birds minimized their daily energy expenditure – rather than other possible options of maximizing the daily net energy gain, maximizing the time spent resting, or maximizing the ratio of gain to expenditure.

b) Territories and Mates

Some bird species only defend territories in the breeding season to acquire mates.

c) Territory and Breeding Sites (Type C)

Some species have territories that are the same as their breeding site. Colonial seabirds defend small territories around the breeding site (basically nest sites) in a way that is similar to other birds defending larger areas. The position of the breeding site is important. Birds in the center of the colony produced more offspring and lived longer than those at the edge of the colony – basically due to decreased predation within the center of the colony.

d) Interspecific Territoriality

Because requirements are so similar most competition occurs among members of the same species. However, some birds defend their territories against other species. This is especially true when other species are competing for the same, important resources. This is true not only for other bird species, but other types of animals as well. For example,

hummingbirds will evict intruding bees and butterflies (and vice versa!) Recall the concept of niche partitioning.

e) Non-breeding Territories

Only a few species defend individual winter feeding territories. Usually only a single bird occupies such a territory. Some species of gulls defend territories for just a few days while on migration.

How Spacing is Maintained

Most of the social signals that birds use are visual and/or auditory, and their function is either the attraction of mates or the defense of resources. Most birds use long-range and intermediate signals. Among passerines the most frequent long-range signals are auditory, i.e., songs and calls. In non-passerines and birds that live in open areas, long-range signals are often visual. Intermediate-range signals may be either auditory or visual. Short-range communication may include chasing and attack. For example, Red-winged Blackbirds use both song and a visual display using red shoulder patches to deter territory intruders. Experiments modifying song and the red shoulder patches (researchers painted the shoulders black and noted the results) have shown the importance of these signals in maintaining territories.

In colonial species, spacing results from two opposing factors, mutual attraction and mutual repulsion. The spacing observed is a compromise between these two factors.

In general, owners of a territory are usually dominant over and able to evict all conspecific intruders, i.e., the owner wins. This probably occurs because owners have already invested a considerable amount of time and effort in territory maintenance, and therefore have more to lose than an intruder, and may, therefore, be prepared to fight harder to hold onto the territory. The owner has a higher motivation.

Consequences of Territoriality for Populations

In general, as the density of a bird population increases, territory size gets smaller, but there is a minimum size, beyond which a territory would be too small to support a bird and its family. Territoriality is thought to limit population density in an area. This seems to be a consequence, not a function. Evidence for this is the fact that if a bird is removed from a territory, then another one which did not previously have a territory moves in. This bird had been living in a substandard habitat and was not breeding.

Coloniality

Most colonial species are territorial and most defend type C territories, which contain no resource other than the breeding site, i.e., the nest. Overall, about 13% of all bird species breed in colonies. This type of breeding dispersion is more frequent among birds whose food supplies are distributed in patches and also unpredictable in space and time, e.g., fish. Virtually all seabirds that use such prey are colonial breeders. Birds that feed in flocks also usually breed in colonies.

Costs and benefits of breeding in colonies can be measured in terms of reproductive output and survival, which are more complex to quantify than energy expenditures considered in territoriality. Two main advantages of colonial breeding are anti-predator advantages and feeding advantages.

a) Anti-predator advantages

Vigilance and mobbing:

In general, the more individuals on the lookout for predators the more likely a predator will be detected – for the benefit of all. An early-warning allows preparation for a

predator, e.g., covering the eggs and young (e.g., penguins) or by mobbing the predator (e.g., gulls and terns). Least Terns and Bridled Terns attacked me in the Bahamas when I went into their nesting areas. In North Carolina Common Terns attacked while I helped repair a fence around the breeding area. (I put Styrofoam under my hat after the first day when the birds pecked my head. The Styrofoam ended up with beak holes in it!)

Position in the Colony:

Individuals at the center of a breeding group are less vulnerable to predators than those at the edge. Reduced reproductive success is well documented at the edge of a colony.

Predator Swamping:

Birds whose colonies are very large simply supply more food than local predators can use. If all the birds in the colony breed at the same time, predation is kept to a minimum. This effect is well documented for seabirds and others, such as the Red-winged Blackbird.

b) Feeding Advantages

The colony may act as an information center. Birds that feed in different areas have different success rates. Birds that were not successful the previous day wait and follow the birds that fly directly to successful feeding areas.

c) Costs of Coloniality

There is evidence that competition is more severe in colonial species compared with those birds that breed spaced out. There is competition for resources such as breeding sites, nest material, mates, and food around the colony.

Risk of misdirected parental care.

Risk of cannibalism, e.g., Herring Gull.

Risk of increased transmission of ectoparasites and disease.

Conclusions

Two main factors determine whether birds live socially or solitarily. These are the special distribution of resources, such as food and nest sites, and vulnerability to predation.

In general, if resources are spatially clumped, then the bird species exploiting these resources will tend to feed in flocks and breed together in colonies. If, on the other hand, resources are more evenly spaced, then the birds will tend to defend large territories and be regularly spaced.

Defense against predation can favor either clumping together or spacing. If prey are camouflaged (e.g., an incubating Woodcock) then predation is probably minimized by spacing out. Alternatively, if joint defense against nest predators is effective, then defense against predation may strongly favor colonial breeding (e.g., in gulls and terns).

Of course, in the real world both the distribution of resources and predation will operate together to control spacing, the end result being a compromise between these conflicting selection pressures. Different degrees of clumping in different species are observed because of the interaction of these two factors.

A Functional Classification of Avian Territories

Type A A large defended area within which all activities, such as roosting, courtship, mating, nesting and feeding occur.

This is the classic "all purpose" territory which is especially frequent among song birds like the American Robin and many corvids (crows, jays). This type of territory may be occupied by a pair or a group of birds (e.g. Florida Scrub Jay). The importance of food in such territories is illustrated by the marked relationship between territory size and bird size. This is exactly what we would expect if food was an important determinant of territory size, since larger birds need more food in absolute terms.

Type B A large defended area within which all breeding activities occur but which is not the primary source of food.

This is a relatively rare type of territory, found in the European Nightjar and Reed Warbler.

Type C A small defended area around the nest.

Some hole nesting and many colonial species utilize this restricted form of territory. Examples include the Starling, Tree Swallow, most seabirds, herons, ibises, flamingos and some weaver finches.

Type D A small defended pairing or mating territory.

Examples include those on leks, of species like Ruffed Grouse and Ruff.

Type E Defended roosting positions and shelters.

Many socially roosting birds defend sleeping positions, e.g. starlings and feral pigeons.

Type F Non-breeding territories.

Some species defend feeding areas either in winter or during the breeding season away from the breeding area. Gulls may defend areas of shore-line for just a few hours while they forage there, both outside and during the breeding season. Permanent winter feeding territories occur in some shrikes.

from Hinde