

# Flocking:

# TO EAT OR BE EATEN

WHEREAS STABLE food resources and defensible spaces promote territoriality, unstable food resources and indefensible areas promote flocking. In certain ways, though, flocks resemble colonies, and flocking behavior has features in common with territoriality. For example, even though a flock member benefits from the group effort, it is subject to a dominance system. White Wagtails in Britain join flocks when food on their territories becomes

inadequate. They also stop defending territories at experimental piles of food and join feeding flocks when the same amount of food is evenly dispersed over a large area. Similarly, crows, jays, and magpies abandon territories and form flocks when feeding conditions deteriorate, mainly when food supplies become less stable and more patchy in distribution.

Flocks range in composition from loose temporary aggregations to organized foraging associations of diverse species. At one extreme are the millions of blackbirds in the United States or the Bramblings in Europe that converge each evening at traditional roost sites. Temporary feeding aggregations of herons and seabirds are also open gatherings of individuals responding opportunistically to special situations.

Multispecies flocks of tropical birds, which feed together daily as a group throughout the year and actively exclude new individuals from membership, are closed social systems, similar in many ways to much smaller family units.

The stable composition of flock membership facilitates recognition of individuals and the development of a dominance hierarchy. Most dominance hierarchies in stable flocks are linear, or "peck right" hierarchies, in which each individual clearly ranks above or below a set of others. If an individual must win merely the majority of encounters rather than virtually all of them to be dominant, the hierarchy is called a "peck dominance" hierarchy. In closed, stable social units, for exam-

ple those of Common Jackdaws, social rank increases gradually in relation to time, individual tenure, and occasional changes in group composition. The advantage of stable dominance relationships is that they lower the frequency and intensity of overt hostility. Aggressive peck rates in stable groups of caged hens, for example, averaged 14 per 15 minutes when a bowl of food was placed in the cage. When group composition changed weekly, peck rates increased to 72 per 15 minutes. Social dominance relationships in flocks are based on mutual recognition among individuals. Hens easily recognize up to 10 other individuals, and one hen could reliably recognize 27 individuals in four different flocks. Physical details serve for individual recognition and, if altered, disrupt the social organization. Hens whose combs are dyed or covered with bonnets are regarded as strangers when returned to their flock.

The marked variations in plumage color of Harris' Sparrows serve as badges of their social status. Dominant individuals have conspicuous, contrasting black markings on the plumage of the head and neck; subordinate individuals have no such markings. Many individuals are intermediate in appearance. Such variations facilitate individual recognition among the members of the large flocks that this sparrow typically forms during winter. The evolution of the variability seems directly tied to the advantages of being dominant versus the advantages of being subordinate. Dominant individuals assert the prerogatives of their rank, including access to food. Subordinates of plain appearance, on the other hand, benefit from flock membership, which they can maintain because they do not threaten the dominant individuals with visual badges of high status. In addition, subordinates are tolerated because they help

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**Medium-sized flock of Brant (*Branta bernicla*), illustrating the difficulty of selecting one target from the group. Photograph by Johann Schumacher/VIREO.**

find food, which dominants can usurp. When dyed with black to look like a dominant individual, subordinates suffer more frequent attacks but do not rise in status because they are not inherently aggressive.

Dominance hierarchies are a conspicuous feature of the associations of birds that follow raiding parties of tropical army ants, which flush large numbers of insects and small reptiles that are usually camouflaged and hard to find. Tropical antbirds and woodcreepers habitually associate with ant swarms and over 50 species of neotropical birds are “professional” ant followers, that is, they obtain over 50 percent of their food from the vicinity of ant swarms. Large dominant species, such as the large Ocellated Antbird, control the central zone of the ant swarm where prey are most likely to be flushed by the dense, leading columns of ants. Smaller, subordinate species, which are chased from this zone, take up stations in peripheral, less produc-

tive foraging zones but move towards the center when opportunity arises. In the presence of Ocellated Antbirds, Bicolored Antbirds occupy the intermediate zone, and the small Spotted Antbirds are shunted to the edge.

#### **FEEDING IN FLOCKS**

Casual aggregations of individuals at rich feeding grounds are obviously fortuitous, but why do unrelated individuals form stable foraging partnerships? Social tensions and the frequency of fights increase with group size. Subordinate individuals could avoid dominant “bullies” by feeding alone. Competition for conspicuous or rich food items also increases in groups. What then are the advantages of feeding together in organized flocks? The answers lie in the inescapable daily concerns of foraging efficiency and predation risk. Some of the advantages are straightforward, practical ones. Flocks of pelicans encircle and trap schools of fish in shallow water;

groups of cormorants and mergansers drive fish toward the shore where they are more vulnerable. Common Ravens steal Black-legged Kittiwake eggs more easily when hunting in groups than when alone, and subordinate birds profit by moving together onto defended food sources where they can overwhelm the territorial individual. Autumn migrants crossing the Mediterranean may escape the attack of one Eleonora’s Falcon, but they have less chance of evading several falcons hunting cooperatively near their colonial breeding areas.

Flock members also benefit from the “beater effect”: Prey that is flushed (and missed) by one bird can be grabbed by another. Ground Hornbills in Africa, for example, walk in a line across fields to catch insects flushed by each other. Drongos and flycatchers participate in mixed foraging flocks and specialize in prey flushed by other birds. Flock memberships also improves foraging in more subtle ways. Group

foraging by pigeons and titmice helps them locate food because members can join successful individuals at rich clumps or concentrate their search efforts nearby. Groups of four titmice in captivity, for example, found more hidden food together than alone. They watched each other's successes and modified the intensity and direction of their searches accordingly. Dominant individuals tend to benefit most because they can usurp the sites discovered by subordinate members of the flock.

Instead of increasing or maximizing individual foraging efficiency, foraging in flocks may help insure that an individual finds at least some food on a regular basis, before its reserves are exhausted. This would be most important during the stressful winter period. The observation that small birds with limited fasting abilities tend to flock more than large birds supports this idea. The security of a large group also enables an individual to relax its personal vigil for predators and hence to feed more actively and to spend more time feeding.

### SAFETY IN FLOCKS

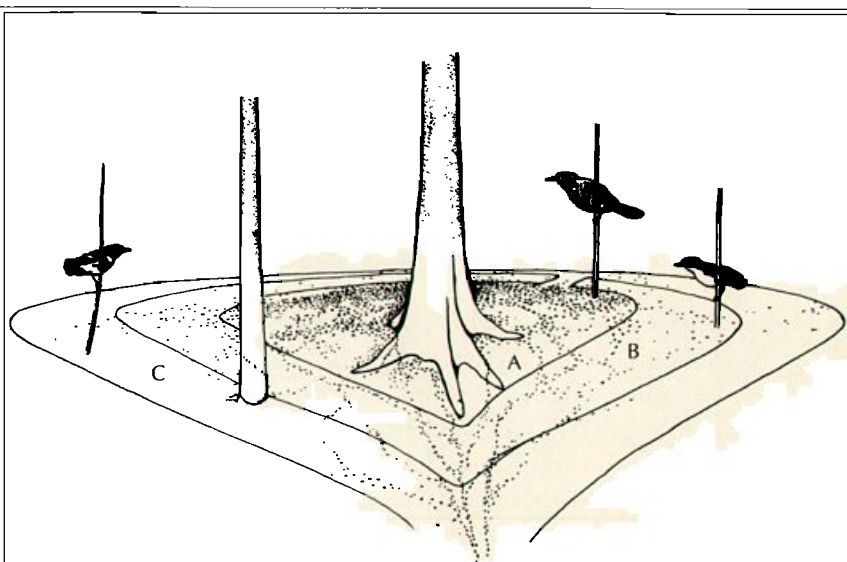
Joining a flock theoretically decreases the risk of being caught and eaten because there is safety in numbers. Predator confusion, the difficulty a predator has in focusing on one bird when many flush, is one advantage. A falcon, for example, risks injury from incorrect contact during a high-speed strike and is reluctant to swoop down on a fast-moving,

## Flock members warn each other of danger so that they can take off at the same time.

swirling flock of birds. It cannot crash full speed into the center of a flock and hope to strike safely. When European Starlings sight a hawk, they flock more tightly together. An individual's chances of being a victim decrease as the number of potential victims in the flock increases and, as in nesting colonies, decrease even further for individuals near the center of the flock. The suc-

cess of a Merlin varied according to the size of the sandpiper flock it attacked. It fared poorly with medium-sized sandpiper flocks, but did well with isolated individuals and with large flocks which were less able to maintain a tight formation.

Predator detection also improves in flocks; greater individual security is the result. Spotted Antbirds are distinctly less nervous and wary when in flocks than when they are alone. Northern Goshawks could not close in on large flocks of Wood Pigeons without being detected. Ostriches stick their heads up randomly to look for approaching lions; at any given time, at least one in the flock functions as a lookout. Flock members warn each other of danger and communicate so that they can take off at the same time. Ducks flush together at the approach of a predator because the individuals synchronize their takeoffs with a series of flight-intention movements that prime every duck's readiness for flight. Flight calls enable longspurs to flush as a group rather than singly. Contact calls enable birds to associate and to maintain a cohesive flock structure even in dense vegetation. Alarm calls serve to alert other members of the social group to possible danger. When one member of a flock spots a predator, it gives an alarm call, and the rest of the flock either freezes or dives for cover. Giving an alarm call would seem advantageous to all but the one that thus revealed its position. Warning calls may seem to be heroic or altruistic acts, but they carry benefits for the caller as well if others in the flock are genetic relatives, such as siblings, parents, or offspring. Each flock member also can count on a certain degree of reciprocity. Most important, by calling loudly the potential victim robs a predator of the element of surprise and thereby reduces the likelihood of attack. The intended victim reduces its own danger as it alerts kin and neighbors.



**The hierarchy of interspecific dominance among birds that follow army ants. Large, dominant species such as the Ocellated Antbird control central sites (zone A) where foraging for flushed insects is best and displace smaller species to outer zones, for example, Bicolored Antbirds to zone B. In turn, the Bicolored Antbirds displace Spotted Antbirds to zone C. Sometimes a subordinate species can infiltrate the central zone, but only such zone-C antbirds as the White-plumed Antbird do this regularly.**

By relying in part on such mutual protection, each individual in a flock can spend less time looking for predators and more time feeding than when alone. However, the time an individual in a flock saves because of decreased surveillance is offset to some degree by the time it loses to involvement in aggressive interactions, which increase in frequency with group size. The amount of time available for feeding should, therefore, be greatest in flocks of intermediate size. Moreover, optimum group size should increase when predators are near and when each bird must spend more time in surveillance. Thomas Caraco and his colleagues confirmed this in studies of Yellow-eyed Juncos in Arizona. In one experiment, average flock size increased from 3.9 to 7.3 juncos when a tame Harris' Hawk flew over the feeding grounds.

#### MIXED-SPECIES FLOCKS AND SOCIAL SIGNALS

Flocks are not limited to members of the same species. Rich assemblages of species forage together. Flocks of chickadees, titmice, nuthatches, woodpeckers, creepers, and other associates are familiar in both the United States and in Europe, and several species of warblers may join them in the warmer months. Noisy gatherings of antbirds, antwrens, woodpeckers, greenlets, flycatchers, and honeycreepers surge through the rainforests of South America. Tropical flocks may include sixty birds of thirty different species whereas temperate-zone flocks average ten to fifteen birds of six or seven species. Curiously, flock size increases primarily as a result of the addition of new species, not more individuals of a few species. Furthermore, flock composition changes regularly as the flock moves along, a result of new individuals joining and others leaving. Individuals join the flock as it moves through their territory, only

to be replaced by neighbors as the flock moves out of it.

Nuclear species provide the main element of a flock structure. In temperate-zone woodlands of North America, for example, titmice and chickadees are nuclear species. Large antbirds and greenlets take this role



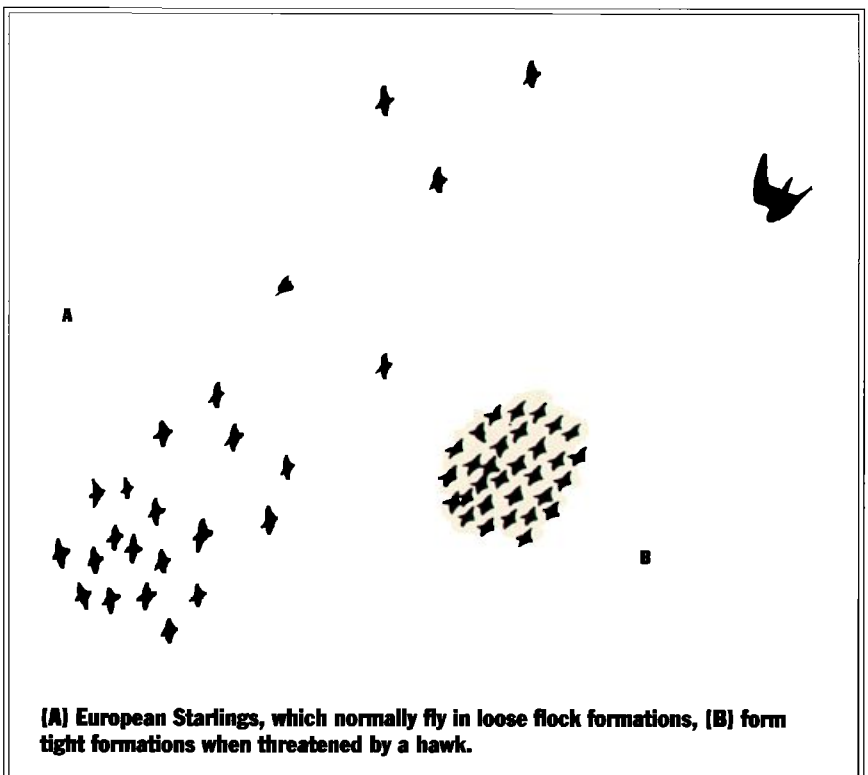
**Massive, dense flock of Ruddy Turnstones (*Arenia interpres*). Photograph by J.P. Myers/VIREO.**

in lowland tropical forests. In eastern Peru, the Bluish-slate Antshrike and the Dusky-throated Antshrike assemble 30 other species with their loud rallying calls early every morning. Plain-colored Tanagers and Blue-gray Tanagers are the usual nuclear species in canopy flocks in lowland Panama but are replaced by bush-tanagers in highland habitats.

Other species, the "followers," join the flocks opportunistically for varying periods and are subordinate to the nuclear species.

Why do birds of various species assemble to feed together and, in particular, why do subordinate species join the nuclear species? In multispecies assemblages, the protection inherent to flocks can be achieved without the costs of increased conspecific competition for food. Furthermore, territorial or rare species that are unable to put together a flock of their own kind can benefit by flocking with other species even though they are subordinate. Foraging success increases in such flocks also. Mixed flocks of several species, each with its own searching skills, increase total scanning efforts for clumped, unpredictable prey. Social learning thus enables each participating individual to profit from the successes and failures of its associates. Individuals of different species can monitor each other's foraging success and modify their search efforts accordingly.

The advantages of interspecific feeding associations are so marked



**(A) European Starlings, which normally fly in loose flock formations, (B) form tight formations when threatened by a hawk.**

### Birds that Flock Together in the Mountains of Tropical America

Western Panama (black and yellow)	Northern Andes (blue, blue and yellow)	South Central Andes (blue, chestnut)
Yellow-thighed Brush-Finch Yellow-throated Brush-Finch Sooty-capped Bush-Tanager	Blue-and-black Tanager Masked Honeycreeper Blue-capped Tanager	White-browed Conebill Blue-backed Conebill Chestnut-bellied Mountain-Tanager Black-eared Hemispingus
Silver-throated Tanager	Black-cheeked Mountain-Tanager	Golden-collared Tanager Plush-capped Finch
Slate-throated Redstart Collared Redstart Black-cheeked Warbler	Hooded Mountain-Tanager Masked Mountain-Tanager Blue-winged Mountain-Tanager Buff-breasted Mountain-Tanager	

that unrelated bird species have evolved similar plumage color patterns that promote flock cohesion. Subordinate species may gain acceptance by resembling dominant flock members. In the South Pacific, for example, certain orioles and friarbirds are confusingly similar in plumage coloration. Orioles are usually bright yellow, but where they inhabit the same region as the dull brown friarbirds, they have the same coloration. Moreover, the appearance of both orioles and friarbirds varies from one island to another. It is possible that by adopting a dull plumage resembling that of the friarbirds, orioles are able to gain access to fruiting trees controlled by friarbirds.

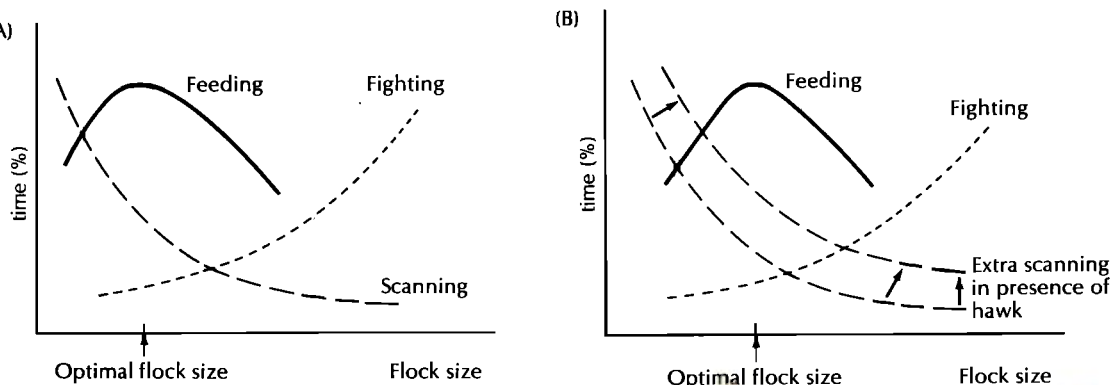
The color patterns of birds that flock together in the mountains of Central and South America offer even more striking examples of

social adaptations. Whereas the neutral, nonthreatening plumage colors of nuclear species such as the Plain-colored Tanager may promote flock cohesion, species that habitually flock together tend to have similar brightly colored plumage patterns. Those species that participate regularly in the montane flocks of western Panama are typically black and yellowish, sometimes variegated with brown and white, whereas bright blue or combinations of blue and yellow prevail in the humid temperate zone of the northern Andes. Farther south in Bolivia, the flock colors switch to blue or blue-gray above and chestnut below. Conceivably, such distinctive color patterns serve as flock "badges," which enhance the social integrity of multispecies flocks. The evolution of plumage colors of flocking birds, however, remains a controversial

topic. Countering the potential value of cohesive "social mimicry" is the need for species distinctiveness. The bold color patterns of many tropical flocking birds may well promote recognition of conspecifics, a phenomenon known to occur in flocks of tropical reef fish.

#### Summary

The defensibility of a given space, the variability of food resources, and the probability of attack are crucial factors in determining avian spatial relationships and social behavior. Territoriality, the most aggressive avian social behavior, is characterized by acts of display intended to discourage the presence of rivals, and by the exclusive continued use of a defined area for an individual and perhaps its mate and progeny. A central feature of territorial behavior is dominance, which also comes into play in the less aggressive social behaviors of coloniality and flocking. The main advantages of coloniality are feeding efficiency and safety from predators. Territoriality and dominance reflect an emphasis on competition, and coloniality reflects an emphasis on tolerance and perhaps cooperation. Flocking shares features with territoriality and coloniality. Individual flock members observe a hierarchical dominance system but benefit from group feeding and defense efforts. ■



**(A) The optimal flock size theoretically results from a balance between time spent fighting other members of the flock, time spent scanning for predators, and time devoted to feeding. An intermediate flock size permits the most feeding time. (B) When a predator hawk is present, more time must be spent scanning and the optimal flock size increases.**