SOCIAL FEEDING BEHAVIOR OF BIRDS

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INTRODUCTION

The associations into which feeding birds enter are many and varied. The simplest are bands of birds brought together by gregariousness; one of the most complex has elements that have earned for it the term "symbiosis." And yet the great diversity is not without order. Surveying the many types of flocking or associations one sees that they can be arranged into series, from simple to complex. Not only that, but the series inter-relate, until rather than a chain or a "tree" we have a whole network or fabric, with analogies in many directions (see fig. 1).

A danger lurks here—that of assuming these relationships to be phylogenetic. They are not necessarily so. Though advanced, complicated behavior probably arose out of simple behavior, usually this seems difficult to prove. Many of the behavior patterns we see probably arose independently, from the basic similarity of birds, the recurrence of similar situations, and the acuity of many birds in profiting by small advantages in their environment.

A phylogenetic approach is only one way of examining a mass of biological data. Besides using the data to sort out blood relationships it is possible to examine them to see how birds have met the problems of their environment, and how their innate tendencies and their physical equipment have resulted in varying behavior patterns under various conditions, or similar patterns under similar conditions, irrespective of relationships.

If these data are arranged according to our present understanding of the phylogeny, all too often what appears a heterogeneous accumulation of facts appears. If they are arranged in an orderly sequence, and phylogenetic conclusions drawn, violence may be done our generally accepted views of relationships.

But an arrangement based on likenesses is of value in showing how behavior could have originated. Though the more complex

behavior cited below did not arise out of the simpler behavior described, it probably did arise from similar simple behavior. A "pseudo-phyletic" series is a term that could be employed for the arrangements used below, and seems more self-explanatory than the "biological series" of Böker (1935) and others. These arrangements give us a framework and a background against which to view examples of behavior.

The many types of associations may be best introduced by a few examples: simple cases such as thrushes (*Turdus*) coming in numbers to a fruiting cherry tree, or sparrows (Fringillidae) feeding in a weed patch; more complex ones such as fish-eating birds spreading out and encircling a school of fish, or herons (*Ardea*) or storks (Ciconiidae) advancing in line across a field for insects, or a hawk (*Falco*) accompanying a train and using it as a "beater"; such specializations as those of eagles (*Haliaeetus*) robbing ospreys (*Pandion*) of their prey, or oxpeckers (*Buphagus*) using the bodies of hoofed animals as their feeding niche, or honeyguides (*Indicator*) leading men to bee trees; and the many species of birds in tropical forests in mixed flocks that are big enough to be spectacular.

The social behavior of birds has been the subject of a host of published notes and papers in which it has been surveyed from different points of view. Notable is Friedmann's paper (1935) giving a review of bird societies in general. Much of his paper is a descriptive, systematic account of aggregation during the nesting season. However, there is brief mention of co-operative hunting, and of numbers of birds flocking about a plentiful food supply. Allee (1931) has given a general review of social behavior in animals in which certain aspects of feeding behavior of birds are considered, especially in regard to the position of the individual in its hierarchy.

The object of the present paper is to illustrate with examples from the literature how certain behavior patterns may have originated out of general tendencies and evolved from simple to complex patterns.

INDIVIDUALS OF ONE SPECIES IN RELATION TO FOOD

Some birds that ordinarily do not hunt in flocks, or at a season when they are not flocking, may gather in numbers about a local food supply. In late summer, before the American robin (*Turdus*

migratorius) begins to flock, it may gather in numbers in a cherry tree to feed, but with no flock behavior outside of the tree. The many turkey buzzards (*Cathartes aura*) that gather at a carcass, or the bald eagles (*Haliaeetus*) that congregate about a rich fishing inlet are in much the same category.

Outside the nesting season many, perhaps most, birds are gregarious. The flocks of weaver birds that visit the rice fields in the Orient; the ducks that crowd into one or another bit of marsh; the sandpipers that keep together on a small bit of the miles of mud flats available; the small parties of chickadees that search for insects through the winter woods; or a line of blackbirds feeding on a stubble field in the early spring—all are examples of this.

There seems to be little or no organization in relation to the food in most of these flocks, but a faint foreshadowing of more orderly, complex behavior can be seen, as in the way the red-winged blackbirds (*Agelaius phoeniceus*) tend to spread out into a long line, so that most of the birds will not be searching over ground already examined by those in the front of the flock. A simple flock structure is also seen in the American merganser (*Mergus merganser*): in a flock diving for fish, as fast as the individuals come up from dives the hind ones swim ahead of those in front and dive again, being in turn succeeded by others. A party of mergansers, fishing together, may drive panic-stricken fish into the shallows, or into some small pool where they may be more easily caught. Even in these cumbersome merganser flocks in which individuals get in each other's way, there are occasional benefits, as when fishes are cornered in a natural corral.

From these associations of birds, large or small in number, one can trace out various modifications of behavior of benefit in different ways to the individuals in securing food. The most obvious of these are given below under the headings:

(1) Spacing of individuals.

(2) Locating food.

(3) Beating for food.

(4) Combining in securing a single item of prey.

Spacing of Individuals

The simple flock composed of birds of one species may be at a disadvantage over individual birds. Grinnell (1920) has suggested this for the ruby-crowned kinglets (*Regulus calendula*)

and the Audubon warblers (*Dendroica auduboni*) of California in winter. The kinglets then rely for food upon small insects, mostly stationary, which are sometimes scarce, as shown by periods when some of the birds starve. To gather food in sufficient quantity they must cover much territory in a limited time. It would be a disadvantage to move in a close flock, competing in a limited area for a limited food supply, and it is advantageous for a bird to avoid duplicating territory that a neighbor kinglet has just scrutinized. Grinnell noted that these birds tended to keep separate in feeding, and were continually uttering calls. These calls, he postulated, were not a means for the birds to keep in touch with each other, as has been suggested, but actually served to keep the birds apart, and he called them sequestration notes.

Locating Food

Some other birds, however, obviously derive benefit from associating in loose flocks while searching for their prey; take, for example, common terns (*Sterna hirundo*) seeking fish in a wide bay. Only here and there, occasionally, do schools of small fish come close enough to the surface for the terns to seize. The loose flock gives a better chance for at least one of the terns to locate a school as it comes to the surface, and as it dives down for its prey the other terns of the flock are close enough to reach the spot and share in the fishing before the school of fish submerges to depths where it can not be reached.

The same principle probably applies to the vultures coming to a kill even when they are not in flocks, but still close enough to observe each other's activities. Of the black vulture (*Coragyps atratus*) in America, Bent (1937, p. 37) writes that "when a black vulture flying and circling at a great height becomes aware of a carcass lying far below it, the bird at first circles down but soon drops with great swiftness, with legs hanging and, at times, wings flapping furiously. Such actions of descent from a height immediately attract the attention of other vultures . . . and they at once follow up the clue. One such action, even a mistaken one, can quickly collect a flock of vultures." More than 237 of these vultures have been recorded at a carcass of a horse.

In Africa, where scavenging birds are much more numerous as to species, one species may also guide another, and this is discussed later. In New Guinea, where the whistling kite (*Haliastur sphenurus*)

gathers to feed on dead wallabies, I found that one bird seemed to lead others to a carcass.

It is probable that this principle of one bird finding food as a result of another's activities in approaching food, or feeding at it, is rather widespread. It can be observed in barnyard fowl (*Gallus*). The chickadees (*Parus*) visiting a feeding station at a suburban window probably attract others—strangers—to visit the place and find food. It was probably this that brought a dozen red-breasted nuthatches (*Sitta canadensis*) to feed on the fat of a deer butchered in the forest (Ball, 1945). The use of decoy ducks in wild fowl gunning might be mentioned here, but their attractiveness may correlate with the ducks' desire for a safe resting place as often as with their wish to find food.

Another example of the activities of some birds which guide other individuals to food is provided by guillemots (*Uria*). Their food may be abundant in a small area at sea, remote from the nesting site. The sea may be shrouded in fog. A group of guillemots on the feeding grounds and a constantly passing stream of birds between it and the nesting colony keep the feeding place located for the colony (Sergeant, 1951).

These examples demonstrate that in many cases the members of a flock, or even widely scattered birds within sight of each other, may benefit if one of their number locates food and unwittingly notifies others. Here we have a type of behavior in which the actions of one bird benefit not only himself, but also others in the group. This is of course not a conscious altruism; it is accidental in the nature of the birds' habits.

Beating for Food

A flock that beats through an area for food has more complex relations between its individuals than do the birds gathering to feed on what one of their number has found. Ideally each bird takes a place in the flock in which it is of help to some other members, and it also profits from the actions of others.

One of the best examples of this co-operative hunting, because it is simple, is Swynnerton's (1915, p. 353) case of his two tame ground hornbills (*Bucorvus cafer*). They would stalk along, side by side, at some little distance apart, and attack such insects as were flushed by either of them in the direction of the other. Swynnerton had also watched parties of as many as four wild birds of the same species doing the same thing.

In England, on October 4, 1931, Mr. William Bruce saw in a recently cut oat field twenty-five common herons (*Ardea cinerea*), lined out in formation, walk systematically across the whole field. On reaching the far side, they returned in similar fashion. Again, on October 25, he saw fourteen herons performing a similar maneuver. They seemed to be beating the ground for a food supply of moles and rats, though such behavior seems exceptional for this species (Ritchie, 1932).

The Abdim storks (*Sphenorynchus abdimii*) in East Africa, recorded by F. J. Jackson (1938, p. 72), leave their roost at daylight, and many hundreds settle on the short-grass plains. There they form into an irregular line, the individuals about three feet apart, and march across the plain, apparently co-operating in a drive for their insect food.

The avocet (*Recurvirostra americana*) and the black-necked stilt (*Himantopus mexicanus*) have been recorded as banding together for co-operative drives on small fry and aquatic insects. Such drives are made in water of wading depth. The birds arrange themselves into compact spearhead and wedge formations and sweep the bottoms with the characteristic back-and-forth side movements of their long bills. As many as 13,000 avocets have been observed taking part in such co-operative feeding projects (Cottam and others, 1942).

The studies of G. A. Bartholomew (1942) on the fishing activities of cormorants on San Francisco Bay show how size of flock influences the arrangement into formation of the birds in fishing. Cormorants (*Phalacrocorax auritus*) may fish singly or in small flocks, but there is no hint of organization in groups of less than four or five birds. Flocks of less than twenty birds are most commonly seen. The organization of these flocks is flexible, but as a rule the birds form a fairly compact group, perhaps one bird to every square yard of water surface, and the flocks tend to assume a roughly circular formation. All the birds in the flock face in the same direction as they swim steadily along, diving for food. There is no flying from back to front of the flock. Apparently these small flocks are searching for individual fishes rather than following schools of fish.

Though the activities of large flocks of up to 1,900 individuals are subject to frequent variations, they always follow the same basic pattern. The formation of these large flocks is gradual and there is no prearranged plan. The first group to alight does not as a rule

begin fishing at once but swims slowly about, with birds diving only occasionally. Apparently additional cormorants flying out to feed locate the swimming flock by sight, decoy to it, and the flock augments rapidly. Active fishing begins before the flock is fully formed, but the birds that arrive later join the fishing flock without disturbing its organization or activity. The actual method of fishing is always the same. The formation is a long, narrow, but closely packed line, which may be curved or indented at various points but is generally at right angles to the direction of movement of the flock as a whole. All the birds swim in the same direction and nine-tenths of them are in the narrow line. In a flock of fifty or sixty birds, this leading rank rarely contains more than a single rank of cormorants, but in a flock of five hundred or more it may be three or four birds deep. The few birds not in this line are scattered loosely behind the main part of the flock. Active fishing is confined almost entirely to the front line.

The movement of the flock as a whole is divisible into several components. All the cormorants swim along the surface in one direction. When they dive they continue to swim straight forward while they are under the water. The birds beneath the water and those on the surface move at about the same speed so that when a cormorant appears at the surface after a dive it is usually in or close to the line of birds swimming there. Perhaps one bird in seven returns to the surface behind the main group, and these rise and fly to the front of the flock. This flying from rear to front produces in the flock a constant rolling motion, which materially increases its speed. Flying is rarely seen in flocks of less than twenty-five birds, and these smaller flocks move much more slowly. Presumably, large flocks are pursuing schools of fish. The break-up of fishing flocks may be gradual, as birds satiated with food drop behind, and rest on the water, or fly away; or it may be sudden, as when the cessation of fishing is the result of the escape of the school of fish. Diving then stops abruptly, the flock loses its formation, and the birds drift about aimlessly and dive haphazardly. If any of these birds find a school of fish, the flock reforms (Bartholomew, 1942).

The wattled starling (*Creatophora carunculata*) in South Africa is known as the "locust bird" and A. C. Stark (1900, p. 24) gives an account of a more elaborate co-operation of many individuals in feeding on locusts. He says that when the starlings are pursuing a flight of mature locusts, they "perform various extraordinary and

beautiful aerial evolutions with the object of intercepting and surrounding a portion of the [locust] swarm, and in doing this their movements closely resemble those of another locust-destroying Starling, the beautiful Rose-Coloured Pastor [*Pastor roseus*] of Eastern Europe and Asia . . . . Starting in a dense 'ball-like' mass, they suddenly open out into a fan-shaped formation, then assume a semicircular arrangement, and finally end by forming a hollow cylinder in which a portion of the locusts are enclosed; as the imprisoned insects are destroyed, the Starlings gradually fill up the hollow of the cylinder until they again assume their 'ball' formation and proceed to follow the remaining locusts . . . . When feeding on the ground, on the young locusts, they advance in long lines, three or four deep, the rearmost birds constantly jumping over those in front of them . . . ."

The white pelicans' (*Pelecanus erythrorhynchos*) co-operative fishing behavior has been well described by Cottam and his associates. The observers, in Oregon, were in a commanding position on a rim rock above twelve white pelicans swimming about. Apparently a school of fish approached the pelicans. Suddenly the birds assumed a circular position surrounding the school and moved cautiously toward the center of the circle, their heads near the surface of the water or partly submerged. The birds moved in unison, making the circle progressively smaller. When the pelicans were close to the school, the birds made rapid jabbing motions and apparently caught and ate many fishes, every bird getting from one to several (Cottam and others, 1942).

In this section we see behavior that is an advance over the earlier types. Instead of individuals of the group spreading out so that each has a better chance at a fresh hunting area, or converging on food once found, their spreading out serves the purpose of helping each other. The proximity of the individuals scares the prey into activity, so that it is more easily caught by some member of the flock, as in beating, and in directing the flight of prey, in driving and in surrounding it. The earlier examples of beating might be of accidental occurrence in the nature of the few ways a flock could feed, but in some of the examples the beating and driving seem to have become a regular part of the birds' behavior.

Individuals Combine in Securing a Single Item of Prey

This category differs from the preceding in that the birds work together to secure a single item of food already in view—food which

without this co-operation might have escaped or been otherwise unobtainable.

The first example is of a mob action, many individuals helping to overcome an animal too powerful, apparently, for one bird. The manner in which birds may assemble has already been given under the section on locating food. The black vulture, *Coragyps atratus*, is ordinarily a carrion eater, and its weak claws and bill seem ill-adapted to taking live prey, though it is known to take young herons from their nests and to be destructive to young pigs and lambs in Florida (Bent, 1937, p. 35). However, there are records of its killing adult wild animals in cases where co-operative action was employed and was perhaps necessary. In Louisiana McIlhenny (1939, p. 472) saw a black vulture alight near a skunk, which stopped and raised its tail, as skunks do when they are preparing to spray their defensive scent on an enemy. Other vultures that were near-by soon joined the one by the skunk. When six or eight had gathered one suddenly attacked it from the side. The skunk discharged its scent without apparent effect on the vultures, which then attacked in a mass. Other vultures circling about overhead joined the group, until there were twenty-five or more about the skunk. They piled on to it and with much flapping pulled it about until it was dead and then devoured it. On another occasion, McIlhenny (op. cit., pp. 473–474) saw a similar attack on two nearly full-grown opossums by 75 or 100 vultures.

There are a considerable number of records of two individuals which co-operated to secure a single item of prey. The bald eagle (*Haliaeetus leucocephalus*), according to Bent (1937, p. 328), occasionally catches ducks on the wing, but oftener pounces on them on the water; ". . . frequently two eagles join in the chase" of a bird on the water, forcing a swimming duck to dive again and again until it is exhausted and easily caught. He also reports two eagles which chased a black duck in the air until it was forced down into the water.

Similar behavior has been recorded for the parasitic jaeger (*Stercorarius parasiticus*), though in this case it was unsuccessful. Anderson (1913, p. 459) says he watched a pair of jaegers chasing a flock of sandpipers. One sandpiper separated from the flock, and the jaegers pursued. They worked together, one darting in while the other turned. However, the sandpiper finally escaped. Presumably if but one jaeger had been chasing the sandpiper it would have escaped sooner; with two their chances of success are greater.

Two ravens (*Corvus corax*) in the Arctic have been recorded by Kumlien (Bent, 1946, p. 194) as co-operating in capturing an arctic hare. "Sometimes the raven would catch the hare by the ears, and hare and raven would roll down the mountain side together thirty or forty feet, till the raven lost his hold, and then its companion would be on hand and renew the attack. They killed the hare in a short time and immediately began devouring it." A somewhat similar bit of co-operation was used by two ravens in capturing a young seal, basking in the sun on the ice, near its hole. "The first manoeuvre of the ravens was to sail leisurely over the seal, gradually lowering with each circle, till at last one of them dropped directly *into* the seal's hole, thus cutting off its retreat from the water. Its mate would then attack the seal, and endeavor to drag or drive it as far away from the hole as possible. The attacking raven seemed to *strike* the seal on the top of the head with its powerful bill, and thus break the tender skull."

A similar attack was recorded by Hiatt (1945, p. 81) in South Africa. Two black crows (*Corvus capensis*) attacked a lizard about twelve inches long. One crow was in front of the lizard, the other behind it. When the lizard was engaged with the crow in front of it, the other seized the lizard by the tail and flung it into the air. As soon as the lizard returned to earth it rushed at the nearest crow, only to have the other run behind it and again seize it by the tail. This fight continued for about ten minutes before the lizard was killed, and one crow flew off with it.

Brown thrashers (*Toxostoma rufum*) defend their nests vigorously against marauders, and quite possibly the parent pair could successfully repel one Florida jay (*Aphelocoma caerulescens*) from their nest, but in April in Florida I saw two Florida jays fight with two thrashers at the latter's nest until the thrashers were so thoroughly vanquished that one of the jays went undisturbed to the nest and carried off an egg. A few minutes later, after another bout of fighting between the two jays and the two thrashers, a jay was again able to go unmolested to the thrashers' nest and get another egg (Rand, 1942b, p. 521).

The following also illustrates another way in which individuals of a species aid each other. The turnstone (*Arenaria interpres*) gets its name from its habit of turning over stones and other objects, as a regular method of uncovering sand hoppers and other food objects. There are at least two accounts by credible witnesses of

several birds joining in overturning dead fish and other objects too large for one bird to turn (Witherby and others, 1940, p. 223).

Bent (1937, p. 329) records three bald eagles (*Haliaeetus leucocephalus*) that co-operated in moving prey already killed. On the Virginia Coast geese and brant form their favorite food. A brant or duck is carried off bodily, but a Canada goose (*Branta canadensis*) is too heavy to be thus easily disposed of, and if one is killed over the water the eagle literally tows the prize along the surface of the water to the shore. In this way an eagle has been known to drag a large goose a half mile. On one occasion Bent quotes from W. W. Worthington, ". . . [an eagle] plunged down and grappled with [a cormorant, *Phalacrocorax auritus*], but was unable to raise it from the water, and after struggling awhile he lay with wings extended and apparently exhausted." After a minute or two the eagle began to fly toward the shore, towing the cormorant, but after progressing a short distance let it go. The first eagle was then joined by two other eagles and by taking turns they soon succeeded in getting it to the shore.

Though the pilfering by individual birds is discussed in a separate section, the following two examples deal with groups of several individuals of one species working together for a common aim. As such they are properly included here.

Three magpies (*Pica pica*) co-operated to rob a golden eagle (*Aquila chrysaetos*), according to Dixon (1933). When the eagle was first seen it was sitting on a ground squirrel it had just captured. Three magpies flying by stopped to investigate. The magpies walked completely around the eagle, and then two of the magpies took turns swooping down at the eagle's head. This attack was repeated five times with increasing intensity until the eagle struck back at its tormentors. In doing this it was forced to relinquish its hold on the squirrel in order to use its talons. While the eagle's attention was occupied by the two attacking magpies, the third sneaked in, on the ground, and carried off the squirrel, which was later shared, without fighting, by the three magpies.

This is very similar to the incident concerning ravens (*Corvus corax*) and a dog in Alaska, quoted by Bent (1946, p. 196) from B. J. Bretherton. The dog had a bone in its mouth. "While so engaged he was espied by a Raven, who flew down and tried to scare the dog by loud cawing, in which he was shortly afterwards assisted by another, both birds sidling up to the dog's head until they were barely out of his reach. Just at this time a third Raven appeared

on the scene and surveyed the situation from an adjacent fence, but soon flew down behind the dog and advanced until within reach of his tail, which he seized so roughly that the dog turned for an instant to snap at him, and at the same moment the bone was snatched away by one of the Ravens at his head."

These are all incidents in which group action was effective.

Discussion

In the beginning, two factors seem to be operative in bringing birds together: the attraction of food and the gregariousness in a species.

The food itself as an attraction has a wider influence when birds by converging on it inform others of its presence. This results in an individual's guiding or leading others to food, and this is important even in non-flocking birds.

In the gregarious species, the disadvantages that may result from close association are especially obvious when many individuals are going over the same area in a short time. A habit of spacing then becomes advantageous. A further benefit if the prey is mobile is that the birds, by spreading out so that each gets a chance at fresh pastures, begin to act as a line of beaters. Some species do this as a regular thing, and some even herd or drive and corral fish. This seems to have passed the point of chance arrangement in some groups and to have become a regular habit. Within a species, the effect of the size of the flock on its organization may be considerable and is well illustrated by the cormorants' mode of fishing.

The presence of food itself affects social species of large or small flocks in two ways: In loose flocks of species seeking a food that may be locally abundant for a short time, the flock acts as a line of beaters, but when one bird locates the food, its actions summon the others to it. In other cases a number of birds may be about the food, either because they were guided to it or because the flock happened on it, and yet the food be unavailable. This may be because the prey is too strong to overcome or too active to catch; because it is in the possession of a strong owner; or because it is too heavy to retrieve. A few birds, or a flock, directing their energies toward securing the prey can be successful where a lone bird would have failed. The simplest cases of this, like the mob action of vultures on a skunk, are unorganized. But the two ravens taking a bone from a dog seem to have known what they were doing.

These are examples of group activity that profits most of the individuals. It would be advantageous to the species to adopt this group activity regularly, for the birds that co-operated more effectively would get along better. We have here behavior on which selection could act, and in certain species this seems to have happened. But where group activity is usual it is in the more generalized beating and herding of prey, rather than in the closer co-operation of a few individuals for the attainment of an end already in view.

BIRDS OF ONE SPECIES ASSOCIATING WITH A NON-PREY ANIMAL (NOT NECESSARILY A BIRD) IN FEEDING

We have seen in the previous section how individuals of a single species may be found together in feeding, and that modification in behavior may accompany this. Presumably, much of this flocking results from gregariousness—a "liking" for being in flock.

The associations of a bird with another species of animal, aside from those due to accident or similar food or habitat preference, are surprisingly common. Most of the conspicuous "one-species-with-another" associations recorded are between one bird and a non-bird species; not a few associations are with man or his activities. Perhaps ease of observation has been a factor in this, for there are affinities between species of birds, as will be apparent in the next section. The various stages of association, from casual ones apparently based on curiosity, to complex, regular ones, and to obligate relationships, are particularly clear in these relationships between two species, and the advantages to one of the species are often very evident. The benefits often, perhaps usually, accrue to only one species.

Though many of these examples concern bird with non-bird associations, the same principles of benefit are applicable to bird with bird relationships, as will be seen in comparing the case of the cattle heron's (*Bubulcus ibis*) association with cattle and that of the bee-eater (*Merops nubicus*) with the bustard (*Choriotis*). The clarity with which the factors emerge in these simple cases will aid in understanding the more complicated relationships discussed in the next section.

In this section the data will be discussed under the following headings:

(1) Casual associations of no benefit to the bird.

(2) Associations profitable through beating or driving activities of one species.

(3) Associations profitable through the providing of scraps of food by one species.

(4) Associations profitable through flesh or parasites provided by one species from its own body.

(5) Pilfering and robbing of one species by another.

Casual Associations of no Benefit to the Bird

Sometimes, apparently, a bird may perch on some other animal for no other reason than that it presents a perching place. This seems to be the case of an African vulture (Aegypiidae) that perched on a standing sheep (Huxley, 1945), though sheep, living or dead, could soon come to have meaning to a vulture.

Sometimes birds approach and examine an animal as though curious about it.

Murphy (1936, **2**: 946) quotes Vallentin in regard to the Falkland kelp goose (*Chloephaga hybrida*) and its pronounced curiosity in areas where it is not disturbed. Frequently when having his lunch near the sea in West Falkland quite a number of these birds would gather round him, some walking up within two or three yards of him.

The goshawk (*Astur gentilis*) also presents a simple case of this. Ordinarily it is a solitary, shy, forest bird. But in the early autumn the full-grown birds of the year may investigate and follow a man who enters their haunts. In Waterton Lake Park, Alberta, in heavy spruce forest, two juveniles screamed at our intrusion, and one of them came flying to perch in a tree overhead and peer down at us. In the Yukon, in late summer, I have seen young goshawks approach a man, scream at him, and even follow him through the forest, flying from tree to tree (Rand, 1948, p. 14).

In the forest at high altitudes in New Guinea a little fantail flycatcher (*Rhipidura albolimbata*) often came up to look at an intruder who was standing quietly in the forest, then went unconcernedly about its feeding. From this habit of coming up to inspect us we gave it the name of "friendly fantail." Its associations were not limited to man, for it was sometimes found in the little mixed flocks composed mostly of warblers (Mayr and Rand, 1937, pp. 161, 162).

Not very different is the case of the tropic birds (*Phaethon*). They are birds of the high seas and appear to have considerable curiosity. They will frequently circle around a ship or travel above it for a time (Alexander, 1928, p. 322). Tropic birds have a strong flapping flight like that of pigeons, and feed on fish. They benefit neither by gliding on the air currents disturbed by the ship, nor by the garbage thrown overboard.

Albatrosses (*Diomedea*) that follow ships will be brought up later, for possible benefits concerned. But aside from benefits, the black-footed albatrosses (*Diomedea nigripes*) were found by Yocom to be sociable and curious birds. When resting or loafing on the water they were attracted to any box, plank, or floating object that came along. A floating box often formed the nucleus of a loitering flock. A pintail (*Dafila acuta*) that had been shot and crippled drifted away and was followed by an albatross for a mile or more, the albatross pecking at it apparently from curiosity. A shark, swimming near the surface with its dorsal fin exposed, usually attracted several seemingly curious albatrosses, but no association with the porpoises and whales present was seen (Yocom, 1947).

Ravens (*Corvus corax*) will be mentioned in a number of other connections, but apparently at times their following seems to be from curiosity, as in the case quoted by Nelson (1887, p. 166). Ravens appear to enjoy sailing about in gales and in midwinter when Nelson and his party were rounding a cape in Alaska on a narrow icy shelf between the sea and the cliffs, with a gale blowing and an ever-present danger of slipping with the sledge into the sea, a raven appeared overhead and sailed along over them, croaking for the length of their passage of the cape.

Perhaps here, too, should be mentioned the habit of barred and great horned owls (*Strix varia* and *Bubo virginianus*) that come into the trees about a noisy group of people gathered at a camp fire in the forest; apparently the owls are curious.

These incidents are quoted as cases where birds sometimes associate with human or other animals or moving things, apparently from curiosity or sociability. Though such associations may be uncommon they are usually not prolonged and seem to be of no benefit to the bird that seeks them out. But if, by chance, some associations should be of benefit on occasion, one could easily see how they would be continued. Such actually appears to have happened, as is shown in the next section.

Two kinds of groupings not considered further here, though with some points of similarity to the above, are those in which one bird may investigate, pursue, and peck at another harmless bird, and those in which birds scold an owl, or join a band of birds scolding an owl or a snake. However, though these may suggest curiosity as an initiating factor, they seem to stand in the same relation to defense or protective behavior as the above examples stand in relation to feeding behavior.

Associations Profitable on Account of the Beating or Driving Activities of One Species

One animal, moving about, may startle into activity or drive from hiding other smaller animals in which it has no interest. If a predator, interested in these smaller animals, happens to be attracted to the larger animal that is unwittingly scaring them out, the predator finds an unconscious helper in its hunting.

The best example of this is shown by hawks that accompany trains and use the trains as "beaters" to flush birds roosting near the railway track so they are more easily seen and caught. In northwestern Mexico, on one day's train trip, February 2, six different pigeon hawks (*Falco columbarius*) were seen doing this. The hawks, a single bird each time, hung back several cars from the front of the train. As the small birds hurried away from the tracks, ". . . without any thought of any aerial attack . . ." they became easy victims (Kenyon, 1942). In East Africa similar observations are on record. F. J. Jackson (1938, p. 149) writes of the lanner falcon (*Falco biarmicus*) that flew for over a mile abreast of, and sometimes within a few yards of, his railway carriage. Now and again it crossed over from one side of the line to the other, by either darting ahead of the engine, or over the train, until they came to a thicket of castor-oil plants. From this a small flock of colies (*Colius*) flew out as the train passed, and one was instantly seized by the falcon and carried off to a tree. Several other times a large falcon, believed to have been referable to this species, hunted in a similar fashion under a steep rocky hill, a few miles beyond Gilgil Station, for quail, doves and other birds disturbed by the passing train. Jackson also records this at other places. He writes that there can not be doubt that on each occasion the bird was deliberately using the passing train to disturb and reveal its quarry.

Though some birds habitually follow cattle in an established behavior pattern, with the raven in British Columbia this is ob-

viously a recently acquired trait, for cattle have been in the range of the raven (*Corvus corax*) in British Columbia but a comparatively short time. Theed Pearse writes that on Vancouver Island he has seen ravens following cattle, picking up the insects disturbed (Bent, 1946, p. 191).

The snowy egret (*Egretta thula*) and the little blue heron (*Florida caerulea*) at least occasionally have the habit of following a drove of pigs on the Florida prairie, apparently picking up small grasshoppers startled by the pigs (Howell, 1932, p. 103). This, too, must be a recent habit, no older than the introduction of pigs into Florida.

I have just given a number of instances of species which occasionally associate with animals or things that serve as beaters scaring out prey. Some associations were apparently casual, some more or less recently acquired habits. Below are given some associations that are regular and apparently of long standing.

The cowbird (*Molothrus ater*) of North America used to associate with the buffalo but with the disappearance of the buffalo and the introduction of cattle has transferred its associations to cattle. "During the summer cowbirds gather about pasturing cattle and search for the insects stirred up by the beasts, or, as the cows lie tranquilly chewing their cud, the birds may be seen walking about upon their backs, engaged in ridding them of flies and other pests, or merely resting quietly there in perfect security." (Forbush, 1927, p. 425.) In South America there are other cowbirds, one very similar to the North American species in habits. Friedmann (1929, p. 55), in comparing four species of cowbird in North and South America, points out that the amount of flying insects eaten by each species is in direct proportion to the extent to which they seek the neighborhood of grazing animals.

The introduced starling (*Sturnus vulgaris*) in the United States also has the habit of walking along with grazing cattle, apparently for the insects stirred up, though Forbush (1927, p. 406) says it also lights on the backs of cattle and sheep in search of ticks or other insects.

In Africa the association of the buff-backed heron (*Bubulcus ibis*) with cattle is especially well known, and there have recently been discussions as to whether or not the birds catch ticks from the cattle. Vincent (1947, p. 489) writes from Natal that the egrets accompany the cattle on foot. "The normal procedure is for each animal in a large scattered herd of cattle to be accompanied by one, two or sometimes three of the egrets, the birds walking wherever

the beast may go, normally moving on each side of the head as it grazes. Their progress is punctuated by short runs at insects, mainly grasshoppers, aroused by the movements of the bovine. . . ." When the beasts move to a new place the egrets will not fly, but run frantically. They may not use their wings for hours at a stretch. The birds' activities are closely bound up with those of the beasts: when the latter lie down, the birds are inclined to cluster about a few particular beasts, leaving others unattended. Sometimes they snap at flies (not ticks) on the beasts but soon they settle to sleep with the cattle.

The piapiac or black magpie (*Ptilostomus afer*) of northern Africa lives in parties often near native villages and sometimes follows grazing herds of cattle, sheep, goats, donkeys and wild game, apparently for the insects disturbed by the animals (Bannerman, 1948, p. 38).

The ani (*Crotophaga sulcirostris*) of tropical America also commonly attends cows for the sake of the insects the latter scare up. In this case a study has been made showing the advantage of this association to the ani. An ani, feeding by itself, takes an average of two minutes to find an insect; when the ani is accompanying a cow, it averages three insects every two minutes; that is, hunting with a cow as a beater is three times as effective as hunting alone (Rand, 1953).

The pied starling (*Spreo bicolor*) of South Africa also has the habit of following cattle, either to catch the disturbed grasshoppers or to pick up engorged ticks that may fall from them (Roberts, 1948, p. 317); it also perches on cattle.

On the northern frontier of Kenya the carmine bee-eater (*Merops nubicus*) and the Kori bustard (*Choriotis struthiunculus*) are common, and the bee-eater often rides on the back of the bustard, which makes no objection as it walks about. The bee-eater flies off periodically, apparently to snap up insects frightened up by the bustard. T. H. E. Jackson (1945), who watched the birds in this country, found bee-eaters following him when he was walking across grassland, keeping level with him, and flying down and seizing grasshoppers he flushed. Later, travelling by lorry across similar grasslands, he found flocks of bee-eaters accompanying the lorry and swooping down in front of it to catch the grasshoppers that scattered at its approach. Both man and his motor lorry were substituted for the bustard. The ordinary feeding method of the carmine bee-eater was to perch on isolated bushes and hawk insects from them.

But when bustards were about, the bee-eaters used them, the moving bustard apparently being a greater attraction than the stationary perch.

A similar example, but furnished by quite different birds and mammals, is the association of forest hornbills (*Tropicranus albocristatus*) and monkeys in Africa. The hornbill, usually travelling singly or in pairs, has the habit of following bands of monkeys through the tree tops. The monkeys feed on fruit, while the greater part of the hornbills' diet is insects. It has been postulated that the monkeys in their movements through the trees drive insects from concealment, and that these are caught by the hornbills, this being the key to the association. This habit of this hornbill is so well known that in places it is known as the "monkey bird." In Borneo a drongo shrike (*Dicrurus*) follows macaques, and in Celebes another drongo accompanies the monkey *Cynopithecus* in a similar manner (Chapin, 1939, p. 352). From the Philippine Islands comes another case. Stott (1947), after comment on the above associations, writes that in the mountain forest of Zamboanga Peninsula the black-mantled fairy bluebird (*Irena cyanogaster*) accompanies troops of the long-tailed or crab-eating macaque with apparently the same end in view. In August, September, and October of 1945 this handsome bird was seen regularly, seldom associated with its own kind but almost invariably encountered singly and in company with a band of macaques. This habit is so well known to the inhabitants that their name for these birds means "sentinel of the monkeys" and they believe that it acts as a guard.[1] More probably the birds benefit, as do the hornbills.

But it is not only on the land that such relationships occur. The man-o'-war bird (*Fregata*) has been said to appear to be in league with the bonito for maintaining perpetual war against the flying fish, the one harrying them in the water, the other in the air, and frigate birds have been seen following foraging schools of large mackerel, apparently for the fish they drive to the surface (Murphy, 1936, **2**: 937).

The co-operative actions of a flock of white pelicans (*Pelecanus erythrorhynchos*) have been mentioned earlier. But several observers say that they have seen in Utah white pelicans herding fish, and Forster's terns (*Sterna forsteri*) and California gulls (*Larus californicus*) flying overhead and darting down to pick up small carp and

[1] Dr. D. S. Rabor, of Negros, tells me that a drongo (*Dicrurus*) rather than the fairy bluebird is usually known as "sentinel of the monkeys."

chubs which the pelicans missed or forced to the surface (Cottam and others, 1942).

Associations Profitable Through the Providing of Scraps of Food by One Species

In these examples the birds are not taking something startled into activity by the other species but are taking scraps left or made available by it.

According to Forbush (1927, p. 382), the blue jay (*Cyanocitta cristata*) in the New England forests is a curious bird and will approach and examine an intruder into its haunts. Further, "Curiosity often induces the jay, while keeping mostly concealed, to follow a man for a considerable distance through the woods. . . ." In the normal course of events, an occasional jay may benefit by the remains of a lunch, or from the by-products of dressing a deer, but ordinarily there are no benefits to the bird.

In the Canada jay, the habit of approaching to look at a man and following him is still more developed than in the blue jay. But all the blue jay's stealth and shyness are gone, and the Canada jay is one of the most tame and familiar of birds. Living in the northern forests, a country where men may be few but where their outdoor activities often make food available, the Canada jays gather about or follow a man from curiosity or interest. The first time they see a man, as with some young birds in the autumn, they may profit by his leavings. As Forbush (1927, p. 385) says: "It follows the hunter, and the sound of a gun attracts rather than repels it, as it has learned to associate that sound with meat. It trails after the trapper, and robs traps of their bait and even eats small animals caught in them. Camp is no more than established when the Moose Birds 'rally round' eager to snatch any bit of meat or other edible substance."

The brown skuas (*Catharacta*) in the Antarctic, out of curiosity or hopefulness, always follow a man who goes a-birding with a gun, and under such circumstances the collector must be quick to save his game. Murphy says they soon learn to expect to be fed by human beings, which may be why one skua followed him regularly as he rowed back and forth in his dory between ship and shore at South Georgia. It would set its wings and glide very slowly along, scarcely more than arm's reach above his head (Murphy, 1936, **2**: 1030).

Inca terns (*Larosterna inca*), according to Murphy, are very inquisitive creatures, circling rapidly about, now and then making startling passes towards a person's head, swerving aside just before they might strike. The Inca terns also seem always to be hovering about the head of a rising sea-lion. When the animal appears, mouthing and tossing its fish, the terns are like a cloud of flies, sometimes dropping almost into the seal's jaws for morsels. Murphy also saw Inca terns fluttering in the same manner above rising humpback whales in the Humboldt Current (Murphy, 1936, **2**: 1146).

Another relative of the jays with mammal associations is the magpie (*Pica pica*). There are several of these, of which one belongs here. Locally, magpies are dependent for food to a certain extent on the scraps left by carnivorous mammals. Attention was once directed to the location of a coyote in a thicket by the commotion of magpies over it, and Skinner, in the Yellowstone Park region, writes that magpies find coyote kills so promptly that he sometimes thinks the magpies follow the coyotes (Bent, 1946, p. 150).

The raven (*Corvus corax*), when hard pressed for food in winter in the north country, will follow the dog teams and fight for the steaming dung as soon as it is dropped by the dogs (Bent, 1946, p. 190). Correlated with this is the magpies' habit of frequently lingering near horses, elk, and buffalo for the sake of the manure (Bent, 1946, p. 150).

From this it is a short step to the gulls and albatrosses that follow ships for the offal that may be thrown overboard. (Their gliding on air currents caused by the ship may be a point here, too.)

Ship-following must have developed since navigation began, and thus within historic times; but Lack (1944) records a more recent, related behavior of the black-headed gull (*Larus ridibundus*), which uses the wash of a ferry boat on the shore to uncover food:

"As the boat started to move down the river, Black-headed Gulls began to collect and to show excitement. They followed along the mud banks of the river, which were exposed as the tide was low, and settled on the edge of the water wherever the bow wave produced by the vessel caused miniature waves. Once the waves ceased at any particular place, the gulls left and followed the ship along to another favourable place. The birds on several occasions anticipated the arrival of the bow wave, flying along rather ahead of the vessel and settling in expectation of its arrival .... It is an interesting extension of the bird's normal habit of feeding on the edge of the waves with an incoming or receding tide."

The same principle that underlies the well-known habits of gulls, robins, etc. in following the plow for the sake of worms turned up, is illustrated by the mechanical digger incident recorded by Smith (1946): During very cold weather, digging was carried on by a mechanical digger that turned up the earth to a depth of several feet, well below frost level. A large number of worms and similar creatures were unearthed, and the wake of the digger became a foraging area for many of the half-starved birds of the district; thrushes (*Turdus*), blackbirds (*Turdus merula*), redwings (*Turdus musicus*), stonechats (*Saxicola torquata*), and kestrels (*Falco tinnunculus*) all followed peacefully.

Not very different is the advantage to the starling of association with turnstones (though here an element of pilfering may come in). In the Faeroe Islands numerous starlings (*Sturnus vulgaris*) habitually associate with the small flocks of turnstones (*Arenaria interpres*) on the low shore. They appear to profit on occasion by the turnstone's habit of rummaging among weeds and other jetsam, which exposes the food organisms beneath (Williamson, 1947, p. 437).

From the point of view of the development of behavior, the examples given next are an advance over following a predator in that the birds are at their feeding grounds and appear to recognize and noisily welcome another intruder, associating him with an increase in food made available.

In the Falkland Islands the favorite resorts of the sheath-bill (*Chionis alba*) were the penguin and shag rookeries, where these birds were constantly on the lookout for both droppings and eggs. "A joyful and almost humanly sentient greeting they give to any man who seems likely to disturb a colony of cormorants and thus to open up a supply of eggs." (Cobb *in* Murphy, 1936, **2:** 1003.)

A similar recognition of certain human activities is recorded for the dusky gull (*Larus fuliginosis*) in the Galapagos Islands, by Beebe. These gulls were the constant companions of Beebe's party at the islands. They trotted up and down the beaches in train of human beings, and whenever the seine was drawn their excitement became keen. They would fairly hop up and down with eagerness when the fish began to leap over the net, and would afterwards gorge themselves until the tails of little fishes protruded from their beaks. Ordinary apparatus they were content to watch in silence, but they apparently learned to recognize at once the long poles of the seine, which they greeted with outcries that were interpreted as rollicking peals of laughter (Murphy, 1936, **2:** 1047–48).

This behavior appears to be an advance over recognizing and following man as a supplier of food. In such behavior the birds recognize and greet man as he approaches an area where the birds are already feeding or waiting to feed.

An extreme specialization in this behavior is one in which one species of bird profits by the activities of a mammal, and influences the behavior of the mammal to make it more advantageous to the bird. This is shown by the common honeyguide of Africa (*Indicator indicator*). This bird locates one or more bee colonies, then waits for the passing of men, whose attention it attracts by a persistent chattering. If a man wishes to learn the location of the hive he follows the bird, whistling occasionally to it. The bird flies noisily ahead, perching, and flying on again when the man catches up. Finally, at the hive, the honeyguide makes short, aimless flights, returning to the location of the hive. The bird may have led the man several hundred yards. When the man opens the hive, the bird feeds on the wax and the larvae that are discarded. Thus the bird influences one predator's actions, leading it to food otherwise inaccessible to the bird, which can profit by the scraps left by the predator. Chapin (1924), who has speculated on the origin of this habit, points out that without the predator, the honeyguide would not be able to get any bee larvae or wax. And yet bees' wax is commonly found not only in the stomachs of the species that guide men, but also in the stomachs of several other species that do not do so! Chapin suggests that the wax-eating species that do not guide men possibly depend on other, smaller predators such as squirrels or monkeys.

Chapin suggests that honey-guiding had its earliest beginning in the honeyguides that happened on hives robbed by some other animal, where the birds profited by the scraps left. Chapin doubts that this would supply them with as much plunder as they now get (hypothetical). The next step, again hypothetical, was that the birds began to accompany bee-hunting lower mammals (hypothetical). Finally, in the present condition, the birds became the leaders. Only one instance of this seems known, the honeyguide leading the honey badger (otherwise hypothetical). Once this habit became well worked out with lower mammals, man would have been worked into the association as a matter of course, as Chapin points out.

This seems logical; and other cases of following a predator are known—jays following coyotes, and skuas following a gunner. But the hypothetical steps in development do not seem as clearly adum-

brated as they are in another series it is possible to construct. It is this: the honeyguides feed on bees about the hives (and there are many references to such behavior). When predators approach and open the hive the honey eaters profit by feeding on wax and larvae (hypothetical), and quickly come to create a commotion when they see a predator approach (hypothetical). The next step, locating a predator (man) at some distance from the hive, and flying, calling, to the hive so the predator follows (known in only one species of bird), is short.

This postulates a simpler chain than does Chapin, and the hypothetical steps are adumbrated by the sheath-bills, which call excitedly when men approach cormorant colonies and drive off the birds, so making eggs more available; and by gulls, which recognize men with nets approaching a fishing place where they will make fish available, and set up an outcry.

Hoesch (1937) has given some other suggestions, but further information on the ordinary, day-by-day life of the honeyguides is necessary before further speculation is justified.

We have in this section seen how the simplest cases, in which birds benefit from occasional scraps, can be connected with a complicated behavior pattern in which the bird helps in making scraps available, which scraps are an important part of its food.

The instances detailed in this section bear some relation to pilfering, discussed below. Perhaps the basic difference is that here the picking up of scraps by the birds does not deprive the provider of an appreciable amount of food. When the pilferer has taken its food, the provider must seek a new supply.

Associations Profitable Through Flesh or Parasites Provided by One Species from Its Own Body

The perching of a bird on another animal may be rare and without significance, as in the case of the vulture perched on a sheep's back. Sometimes such an unusual act may have beneficial feeding effects for the bird, as in the case of the North Carolina phoebe (*Sayornis phoebe*) that perched on a man's head and arms and used these perches as vantage points from which to capture mosquitos that swarmed around the man (Brimley, 1934, p. 237).

Many species that roost on cattle have been said to secure ticks (but this should be verified by stomach examinations). In one case at least, that of the cattle heron (*Bubulcus ibis*), apparently the species does not eat ticks (North, 1945).

A number of other bird species such as the cowbird (*Molothrus*) of America, the piapiac (*Ptilostomus*) of northern Africa, and the pied starling (*Spreo bicolor*) of South Africa commonly perch on the backs of other animals, but do little if any of their feeding there.

With the magpie (*Pica pica*), locally and at times at least, the perching on large mammals may be correlated with feeding. In Montana, Berry (1922) recorded as a new local habit that magpies perched on livestock, especially sheep, pecked open sores or cuts and caused the death of sheep; but the habit is older than that. Magpies not only perch on domestic livestock, but also on mule deer, wapiti, and bighorn sheep, pecking insects off the heads and backs (Bent, 1946, p. 149); and Farley writes of central Alberta that in the buffalo days (buffalo were plentiful until 1875) magpies were very numerous, and flocks followed the hunting parties and lived on the refuse of the hunt. The birds were considered a great pest on account of their habit of alighting on horses with saddle or harness galls and persistently pecking at the sores until the death of the animals resulted. With the extinction of the buffalo the magpies disappeared, and they had only returned to the country much later (Bent, loc. cit.). Though an old habit, the carrying of it to the extreme that produced dead ungulates seems to be a local and sporadic thing. Berry (1922) writes that ordinarily the wool of a sheep is ample armor for it, but when freshly shorn the sheep has no protection against the magpie, and if a cut of the shears here and there has opened up raw flesh, it is here the magpie starts to peck. The sheep seems utterly helpless. The kidneys are particularly favored, and the magpies soon learn the location of these and how easy it is to drill a hole to them, eating fat and then the kidney itself. Death soon results.

This, of course, brings to mind the kea, a parrot (*Nestor notabilis*) of New Zealand, which under natural conditions feeds on vegetable matter and small animals such as insects. With the introduction of sheep into New Zealand (there were no large mammals previously) some keas acquired a taste for sheep flesh by finding it lying about where sheep had been killed. After that they learned to light on the backs of sheep and tear open the hide to expose the flesh. Some sheep are thus killed, but apparently only a small part of the population of keas has developed this habit. It is said to be possible to eliminate losses by not leaving any of the sheeps' flesh or fat about and thus eliminating the possibility of the birds' acquiring a taste for flesh (Oliver, 1930, pp. 409, 410). Perhaps it is pertinent in

this connection to point out that the kea is a very curious, inquiring bird, and there are records of its using its strong beak in tearing up man's unguarded possessions in examining them. A shepherd, returning to his hut, found a kea had entered through the chimney and with its powerful mandibles had created havoc. "Blankets, bedding, and clothes were grievously rent and torn . . . and everything that could be broken was apparently broken very carefully. . . ." (Buller, 1888, p. 169.)

The most highly developed bird–parasite-provider relationship is that of the oxpecker (*Buphagus*) with hoofed animals of Africa. The oxpecker is structurally modified for living on hoofed animals, and apparently confined to this habitat for feeding. The birds are called oxpeckers, or rhinoceros birds, because of this close association with domestic stock (from camels and cattle to pigs and goats) and game (except elephants and hippos). They are also called tick birds because of their habit of eating ticks from the animals. The oxpecker lights on any part of the animal and climbs all over it with rapid, jerky movements, feeding on ticks and other blood-sucking parasites. The sharp, curved claws are modifications that enable the bird to cling to and move up and down the vertical sides of an animal as easily as a woodpecker does on a tree trunk. The rather long, pointed tail with stiffened shafts to the feathers may also serve as a prop, as with woodpeckers. The bill of the oxpecker has exceptionally sharp cutting edges, and the bird uses it to "scissor" over the hide of the animal, obviously an effective method of getting parasites that are fast on the skin. That these birds actually feed on parasites has been questioned, but Moreau, by stomach analysis, has shown conclusively that they do. They also eat living flesh and drink blood from sores or wounds on the beasts. Though oxpeckers sleep elsewhere at night, and nest in holes, much of their day seems to be spent on their hosts, feeding and resting. Moreau has even seen one riding on the flanks of a greater kudu that was going at full speed. The animals pay them little attention. If driven from one beast the birds go to another, their movements resembling those of blowflies on meat in their pertinacity and appearance of brainless tropism (Moreau, quoted from Bannerman, 1948, pp. 108–111).

The close relationship between beast and bird is indicated by their distribution in West Africa, where game is scarce and the oxpecker depends on domestic cattle. The birds occur only in the areas where cattle are kept, at altitudes high enough, or far enough north, to escape the tsetse fly (Bannerman, 1948, pp. 104 ff.).

The oxpeckers (there are two species, *Buphagus africanus* and *B. erythrorynchus*) are aberrant starlings—dull-colored birds about as large as American robins. In structure and habits they differ greatly from any of their near relatives. They benefit by the association in that their host supplies them food. The host benefits by having ticks removed, and when the host is a game animal it benefits also in that the birds may be the more wary, and, by spotting a hunter and crying out noisily, give the alarm and enable the host to escape the hunter. Moreau has suggested that the relationship be called symbiosis. It apparently is an obligate relationship on the part of the bird. But that, too, is foreshadowed by simpler behavior in other species.

Pilfering or Robbing of One Species by Another

Another way in which we have one species associating to its benefit with another, is to have one species sharing in the food gathered by the other. Upon occasion the second species may make little or no protest, perhaps because of its temperament or the abundance of food, or the second species may make strenuous efforts to avoid giving up its food. Sometimes the food may appear to be shared almost as a matter of course (see coot and ducks below), or it may be given up or lost only after much effort to retain it (see kingfisher and dipper, or ibis and grackle, below).

An unusual occurrence, perhaps successful because of the surprise element, concerns a sparrow hawk (*Falco sparverius*) perched on a telegraph wire with a small rodent in its mouth. A loggerhead shrike (*Lanius ludovicianus*) was sitting near-by. Suddenly leaving its perch, the shrike flew directly and swiftly toward the hawk, snatched the prey and made off with it, leaving the hawk apparently dumbfounded (Hill, 1945).

A similar unusual meeting involved a kingfisher (*Alcedo atthis*) and a dipper (*Cinclus cinclus*). A kingfisher that had been successfully fishing alighted in a tree, three feet over a pool. Below it, a dipper was obtaining food and bringing it on shore. "It appeared about to eat its catch when the Kingfisher dropped on to the 'shore' and there was a momentary scuffle. The Dipper departed and the Kingfisher ate the Dipper's food. The performance was repeated once and possibly twice again, but on the last occasion the scuffle took place a little further away from us . . . ." The dipper finally left, and the kingfisher returned to its fishing (Grist, 1934, p. 304).

Another example, in which the victims made efforts to escape, is the following: At Lake Okeechobee, Florida, "The ibis [*Plegadis falcinellus*] . . . feed very largely on crayfish, which they secure by probing the holes made by these creatures." Grackles (*Cassidix mexicanus*) swarm near. "These latter would swarm about the ibis, and no sooner would one of the latter seize a crayfish, than it would immediately tower into the air with it, only to be instantly beset by from one to three or four grackles. A series of aerial gyrations would follow, with the almost inevitable result of the ibis losing the crayfish to one of its sable tormentors." (Sprunt, 1941, p. 587.)

Robins are the victims of a number of species that take from them the worms they find on the lawn. Apparently it is not uncommon. I've seen starlings take worms from robins on the lawns in Chicago, and the following instances are from published descriptions: Van Tyne (1946) writes that he noticed a starling stealing food from a robin (*Turdus migratarius*): ". . . I noticed a Starling (*Sturnus vulgaris*) run at a Robin and drive it away from the worm it had begun to dig up. Apparently the Starling failed to get the food that time, but in the next five minutes the Starling made four more raids, all of them successful. The Robin did not attempt to fight or to defend the food; it simply moved off a foot or two and continued to forage." Each time, after the starling had eaten the worm, it waited for the robin to pull up another, then repeated its action. The next week Van Tyne saw a female brown thrasher (*Toxostoma rufum*) do the same thing to a robin.

Similar behavior on the part of the English sparrow (*Passer domesticus*) in robbing robins is recorded by Pershing (1930) as follows:

"Observing Robins when feeding on the ground, you will sometimes see one or more English Sparrows hopping around near them, and when the Robin finds a worm they will walk up to him quietly and boldly, take it out of his mouth, with scarcely a protest from the Robin. A few days ago I saw a sparrow take a worm out of a Robin's mouth and fly off with it, and the Robin simply went on hunting for another one . . . . A neighbor of mine saw a Robin robbed six times of six worms, one right after the other, by a small flock of sparrows which had gathered around him, while the Robin kept on hunting for more worms."

Apparently it is not uncommon for gulls to take food from fish-catching ducks. In New England Mr. J. A. Farley saw a red-breasted merganser (*Mergus serrator*) emerge from a dive with an

eel, when a herring gull (*Larus argentatus*), which had been standing on the ice, flew, and in a trice got the eel away from the merganser. The process was not always as simple, as was indicated on another occasion. A merganser came up with an eel, and a herring gull, which was on the watch, flew at it; but the duck immediately dived. Twice more, when the merganser came up with an eel it eluded the gull, but the fourth time, a shorter interval lapsing during each dive, the merganser dropped the eel and the gull seized it in the water (Forbush, 1925, p. 186).

Lovell (1945) has recorded similar behavior of American mergansers (*Mergus merganser*), which adapted their behavior to help them avoid the depredations. Lovell saw twelve or fifteen herring gulls and eight American mergansers fishing in a creek: "Soon a male merganser after a deep dive came up with a large fish in its bill. Instantly five or six of the gulls took wing and converged on the duck. The nearest gull easily snatched the fish, but being unable to swallow so large a mouthful soon lost it to another gull. The other gulls fought for possession until the fish was torn to bits." This recurred several times. "After a while, we noticed a gradual change in the fishing tactics of the mergansers. One came up with a fish. As usual, several gulls went for it, but before they could snatch it, the merganser dived with the fish still in its mouth. He came up 20 feet away in an open space and while swimming as rapidly as possible swallowed the food before the gulls could reach him . . . . Other mergansers also developed a watchfulness which enabled them to retain more and more of their fish. They seemed to pick spots in which to surface as remote as possible from the gulls, and they swallowed their catch while avoiding the attacks of the gulls by swimming or diving."

Pearse (1921) records a somewhat similar instance in which the glaucous-winged gulls (*Larus glaucescens*) were parasites on American golden-eyes (*Glaucionetta clangula*). Golden-eyes swim on rivers where salmon die after spawning, then dive down and tear off a piece of the rotten flesh of the fish, coming up to the surface to eat it. "I have on several occasions seen a Glaucous-winged Gull swimming by a feeding Golden-eye, watching its every move and as it returned to the surface make a dart at the duck, and so causing it to drop the piece of fish, which was at once picked up by the Gull."

Gulls (*Larus*) have also been reported victimizing lapwings (*Vanellus vanellus*) (Johnston, 1945), and Baldwin (1946, p. 97)

tells of laughing gulls (*Larus atricilla*) stealing fish from the eastern brown pelican (*Pelecanus occidentalis*):

"In the early summer it is not unusual to see Laughing Gulls (*Larus atricilla*), in both breeding and non-breeding plumage, following the pelicans, with as many as five gulls often harassing a single pelican. Just after the pelican has completed the plunge and before it can swallow the fish protruding from its bill, a gull may flutter in, alight on the water or even on the pelican's head and seize the fish. A pelican has never been observed to show anything but stoic calm during this procedure."

Communal pilfering develops when several species of birds are feeding together and one of them can more easily secure the food than can the others. This is well illustrated by the coot, the widgeon, and various diving ducks. Forbush (1925, p. 208) writes that in southern United States waters "where Canvas-backs [*Aythya valisineria*], Scaups [*A. marila* and *A. affinis*), and Redheads [*A. americana*], all excellent divers, are numerous and are diving continually on the feeding grounds, bringing up succulent roots, bulbs and other parts of submerged water-plants, the active Baldpate [*Mareca americana*, which is an indifferent diver] waxes fat by stealing tidbits from the hard-working diving ducks." It has even been suggested that the baldpate is primarily a parasite on diving ducks. It has also been recorded as attending on coots (*Fulica americana*) that were diving and bringing up weeds from the bottom, and pilfering from them. Coots are recorded as pilfering from diving ducks, as well as from each other. Though sometimes quarrelsome, apparently the coots often take this intraspecific pilfering as a matter of course.

The above cases illustrate more or less peaceful appropriations of food, some apparently of casual occurrence, others regular.

As one examines cases of pilfering by hawks, there comes in an element of the threat and the use of force that adumbrate the more evolved relationships detailed later.

Bent (1938, p. 29), quoting Ridgway, said that it was interesting to watch prairie falcons (*Falco mexicanus*) follow marsh hawks (*Circus hudsonius*) and compel them to give up their game, which was caught by the falcons before it reached the ground, this piracy being not an occasional, but a systematic habit. However, it evidently is not a widespread habit, as it is not often reported.

The following is interesting, as pilfering occurred twice in quick succession, and two species of hawks and a crow were involved.

Bent (1937, p. 89) quoted W. B. Savary, who "... saw a marsh hawk [*Circus hudsonius*] with a mouse in its claws trying to escape from three crows [*Corvus brachyrhynchos*] that were pursuing it in an endeavor to get the mouse. So close at last were the crows that the hawk let its prey drop; without checking its flight, the leading crow snatched up the mouse and continued on, to be at once followed by a caracara [*Polyborus cheriway*], which, in turn, forced the crow to drop its prize."

The victimizing of the osprey (*Pandion*) by the bald eagle (*Haliaeetus leucocephalus*) in America has attracted much attention and most writers on either bird have mentioned the habit. The following account by Vennor, quoted from Bent (1937, pp. 371 372), tells how two bald eagles co-operated in robbing an osprey, though frequently one eagle acts alone:

"On first hearing the shrill screams of its pursuers, the poor bird made desperate efforts by straight flight to reach the drowned woodlands in which its nest and young were located; but long before it reached these its course was intercepted by one of the Eagles, while the other made repeated and fierce stoops at it from above. The Fish Hawk, however, still held firmly to its prize, and made repeated attempts to baffle the onsets of the Eagle, in many of which it was successful. Before long both birds had risen to a great height—the one alternatingly surmounting the other; but we could still detect every now and then the gleam of the fish in the sunlight. Suddenly, the Fish Hawk was seen to descend with great velocity towards the water, and we thought the poor bird had been struck, and perhaps mortally wounded. It, however, as suddenly checked its downward course, and the Eagle which had as quickly followed it, shot past and far below it; and now once more the pursued bird made straight for its nesting site, but again was intercepted by the other Eagle, which, made desperate by the protractedness of the chase, struck fiercely at it with piercing screams. Baffled on every side, wearied and blinded with the repeated buffetings of the Eagles, the Fish Hawk, with a scream of rage, let go its prize, which fell headlong towards the water." An eagle then swooped down and seized the fish.

Though the osprey-eagle relation has received much attention in America, the eagle has also been recorded as forcing vultures (*Coragyps*) to disgorge (Bent, 1937, p. 330), and has been recorded as forcing the marsh hawk (*Circus hudsonius*) to relinquish its prey (Baldwin, 1940).

In South Africa, the related sea eagle (*Haliaeetus vocifer*) is reported to rob ospreys as well as pelicans (*Pelecanus*) and kites (*Milvus*) of their booty (Stark and Sclater, 1903, p. 312). In West Africa, this eagle is recorded as robbing its less powerful neighbors, but only pelicans (*Pelecanus*) and cormorants (*Phalacrocorax*) are mentioned (Bannerman, 1930, p. 270). F. J. Jackson (1938, p. 227) does not mention this eagle as robbing other birds in the lake country of Africa, and comments on the amicable relations there, as contrasted with the reported robbing of ospreys by eagles in South Africa.

In Malaya, the related white-bellied sea eagle (*Haliaeetus leucogaster*) makes a practice of robbing other birds of fish (Robinson, 1927, p. 76), and the same species, in New Guinea, has been recorded as following and striking at the whistling kite (*Haliastur sphenurus*), causing it to drop its food, which the eagle recovered (Rand, 1942a, p. 295).

I found the related fish eagle (*Haliaeetus vociferoides*) very common in northwest Madagascar, but I never saw it attempt to rob any other species of its food.

Here we have a small group of eagles in some of which robbing is commonly practiced over a wide geographical area, but there appears to be geographical variation in this habit.

Skuas and jaegers (*Catharacta* and *Stercorarius*) are gulls that have become birds of prey. As well as capturing many fishes and other animals, they eat carrion and attack shearwaters, gulls and terns and force them to give up the food they have secured. When the victim, on the wing, drops the fish or other food, the skua may plunge down and seize it before it reaches the water (Alexander, 1928, p. 204). Apparently these habits are common to the jaegers that nest in the Arctic, and also to the species of the Antarctic.

Frigate-birds (*Fregata*) feed on fishes and other creatures picked up from the surface of the ocean, but they also pursue boobies, pelicans, cormorants, gulls or terns, and other birds and force them to disgorge fishes they have caught. Other sea birds are easily overtaken, and if they are slow in disgorging, the frigate bird may deliver a blow with its beak that can dislocate a wing or cripple a leg (Alexander, 1928, p. 260). Apparently all the five species in the family have similar habits.

The behavior of a band of frigate birds in relation to an osprey (*Pandion haliaetus*) they had robbed in southern Florida is interesting, as affording a glimpse into the innate blindness of this

robbing behavior. Dr. Gill wrote that a number of man-o'-war birds had robbed an osprey and that then the poor bird was chased about in the air and all its frantic attempts to escape were headed off, until it dropped into the water. Even there its tormentors continued the attack, forcing it under water until it was finally killed. In this case the harrying of the osprey was carried beyond the point where it yielded useful returns (Bent, 1937, p. 372).

Discussion

In the previous section (pp. 17–37) we had birds coming together because of the attraction of food or from intraspecific gregariousness, with resulting organization, mutual aid, and benefits.

In this section we have a bird (or birds) associating with some other bird or other animal. Sometimes it is a casual, accidental association. In many cases curiosity or an expression of the tendency common in the animal world to follow another animal seems to be an important factor in the start of the habit.

This is illustrated by examples given first. But as the more regular associations are reviewed, it seems evident that benefits derived from the associations have caused their development until the associations are definitely part of the behavior patterns of the species. More than one series is plainly discernible, one leading to the customary use of a mammal as a beater, another to the body of an ungulate as the sole feeding niche of a bird, another to a guiding of a predator to food for the sake of the scraps the predator will leave.

Yet another series, which involves robbing, may have somewhat different early stages. Casual association and curiosity may have been important in its early stages. But another factor, the appeal of the food held by one bird, may have been the initiative factor that started a bold and strong or agile bird to pilfering or robbing. There is also the possibility that pugnacity, or a tendency for a vicious sort of play, may have had its part in the piracy of the frigate birds, as, for example, where the pestering of a fish-less osprey was carried on without profit until the death of the victim.

The many examples presented here seem to indicate that food benefit has been the important factor in causing these associations to develop and to become regular habits. These regular habits have in turn resulted in structural evolution in one case, as shown by the oxpeckers' adaption for feeding on ungulates, and both are surely fixed genetically.

The great age of some of these associations is also indicated, the oxpeckers having become physically adapted to this habit, while the youth of some others, such as gulls following ships, and robins plows, is obvious.

The fact that such a specialization as robbing may prevail throughout a group is brought out by the frigate birds, where all the species seem to have the same habit. But its lack of importance as a single character in classification is indicated by a group of sea eagles, almost all of which have the habit. In the eagles, however, there is geographical variation in it, as the habit seems inexplicably absent from certain areas.

MANY SPECIES OF BIRDS FEEDING TOGETHER

We have already seen how certain factors such as abundance of food can bring individuals of a non-gregarious species together; how individuals can be led to food by others; and how individuals in a flock can arrange themselves so that they feed more effectively than do solitary individuals. Between individuals of two species we have seen how examples of chance association can be connected by intermediate steps to profitable and regular associations.

All the factors involved may be effective, singly or in combination, in bringing feeding groups of many species together and in holding them together. They are discussed under the following headings:

(1) Food Availability and Habitat Preference.
(2) Guiding to Food.
(3) Gregariousness and Attraction Between Species.
(4) Large Scale Beating by One Species or Other Factor.
(5) Mixed Foraging Parties of Insect-Eaters.
(6) Mixed Flocks of Sea Birds.

Food Availability and Habitat Preference

The availability of food in quantities may bring individuals of many species into close proximity. They may feed at one place. The feeding of many scavenging species at a carcass in eastern Africa illustrates this well. F. J. Jackson (1938, p. 133) records ravens (*Corvus*), kites (*Milvus*), brown vultures (*Necrosyrtes monachus*), both griffons (*Gyps ruppellii* and *Pseudogyps africanus*), and

eared and white-headed vultures (*Torgos tracheliotus* and *Trigonoceps occipitalis*) gathered at the carcasses of two mules.

When termites or white ants swarm they provide an abundant supply of food attractive to many diverse species of birds, which gather to feed on them. Sometimes in the literature there seems to be confusion between the birds gathering to feed on termites, and the birds gathering to feed on the insects driven out by army or driver ants. The latter are treated later, while some examples of termite feeding are given below.

In Abyssinia, Cheeseman (Cheeseman and Sclater, 1935, pp. 156–157) wrote:

"Another bird-feast happens on the high plateau when the white-ant queens emerge from the ground in nuptial flight . . . . When a rise commences the nearest bird sentinels fly into the air, take a queen, and return to their perch to break off the wings. This action is a signal for waiting birds of many species to hasten to the spot and join in. The air is soon full of steadily rising ants that look like small helicopters, and each tree-top or vantage point is being used as a perch by ascending and descending birds until darkness ends the orgie. Many unexpected species take part. The little Hobby, *Falco cuvieri*, dashes to and fro, doing great execution. The Canary, *Spinus citrinelloides*, was a surprise to me, as I had considered it was purely a seed-eater; they are, however, moderately skillful. The most clumsy performer was a Cuckoo, *Clamator cafer*, which, seeing the other birds feeding, tried his luck, and gave a very clown-like performance. The Sunbird, *Chalcomitra cruentata*, took up his post near the exit and caught his victims on the ground before they took flight. The following were experts, seldom missing their ant in the air, and were regular attendants: The Chat (*Thamnolaea albiscapulata*), the Grey House-Sparrow (*Passer griseus swainsoni*), and the Glossy Starling (*Lamprocolius chalybeus*); the two latter came in large flocks. Most birds remove the wings before swallowing the juicy body."

Another example comes from western Canada (Cowan, 1942): "One of the most interesting phenomena associated with the mass dispersal flights of [the termites there] is the large number of gulls, swifts, and nighthawks that rapidly congregate over the area. The gulls are, for the most part, Bonaparte's Gull (*Larus philadelphia*) and Short-billed Gull (*Larus canus brachyrhynchus*) with a few California Gulls (*Larus californicus*) and these birds will frequently penetrate two miles or more from salt water while 'termiting.' All

feeding is carried out on the wing, the gulls circling and hovering . . . . Usually along with the gulls are members of Black Swifts [*Nephoecetes niger*] and nighthawks [*Chordeiles*]."

The importance of a fruiting tree in bringing numbers of birds together was well illustrated by Beebe (1916, pp. 58–61), in writing of the birds visiting a single tree in the Brazilian jungle. It was a tall tree bearing small fruit. The first day he secured 16 species of birds from this tree, and the second day, 14 species, only one of which was represented in the previous day's collecting. He had spent five hours at the tree and had secured 29 species of birds.

In New Guinea some fruiting fig trees attracted most of the fruit-eating birds of the forest, and it was common to find thirty or forty birds feeding in such a tree, including a starling (*Mino*), a shrike (*Pitohui kirhocephalus*), several species of pigeons (*Megaloprepia*, species of *Ducula*, and *Ptilinopus*) and cuckoo shrikes (*Edolisoma*) (Archbold, Rand and Brass, 1942, p. 238).

Flowering trees may have similar congregations in New Guinea. "About some large-crowned, flowering trees there were sometimes 100 to 200 birds at a time, feeding, hopping about and darting back and forth. At some trees they included the lories: *Charmosyna josefinae* (rarely), *C. pulchella* (the most common), *C. rubronotata* (rarely) and *C. wilhelminae* (rarely), and the honeyeaters (*Myzomela cruentata*, *M. eques*, *M. nigrita*) and occasionally *Meliphaga analoga*, *Toxorhamphus iliolophus*, *T. novae-guineae*, *Melilestes* and *Oedistoma*. In some trees there were mostly lories and *M. eques;* in other trees, mostly honeyeaters." (Archbold, Rand and Brass, 1942, p. 242.)

Sea birds similarly gather about food. Murphy (1936, **1**: 487) believes that despite the vast territory of the southern oceans the whaling industry has possibly caused changes in distribution and populations of some birds by making carcasses of whales available (more than 10,000 in a single year). He quotes from Lester: ". . . Immediately after whaling had commenced and the carcasses were brought into Whalers Bay, there appeared to arrive from nowhere a vast multitude of birds. Never have I seen such numbers as there were in this harbour. There were Giant [*Macronectes giganteus*], Silver, and Antarctic [*Thalassoica antarctica*] petrels, Black-backed gulls [*Larus dominicanus*] and Wilson's petrels [*Oceanites oceanicus*], but these counted for little when compared with the thousands upon thousands of Cape pigeons [*Daption capensis*]; the water and air were filled with their bodies, and all had but one object in view, that of feeding upon whale."

The limited suitability of habitat that may bring many birds into a small area is well illustrated by the ponds and marshes on the short-grass prairie of western Canada. Travelling over the plains, where few birds other than occasional horned larks (*Otocoris alpestris*), long-spurs (*Calcarius*) or savanna sparrows (*Passerculus sandwichensis*) are to be seen, the change in bird life as one comes to a prairie slough is nothing short of spectacular: ducks of several species swarm; there are grebes in abundance, and perhaps a nesting colony of Franklin's gulls (*Larus pipixcan*) or a few black terns (*Chlidonias nigra*); along the margins are avocets (*Recurvirostra americana*), godwits (*Limosa fedoa*), killdeer (*Charadrius* (*Oxyechus*) *vociferus*) and spotted sandpipers (*Actitis macularia*).

While none of these associations seem to lead directly to social behavior in feeding, it is easy to imagine that birds of species that may feed in groups on an abundant food supply or in favorable habitat would quickly come to associate the sight of a group of birds with food or good habitat, and if alone and hungry would fly to join them.

Guiding to Food

Arising directly out of feeding in numbers about a plentiful food supply, comes the case of one bird following another to food.

I have already mentioned the many scavengers about a carcass in East Africa, and F. J. Jackson (1938, pp. 127 143, especially 134) writes that some of the birds approach a kill directly, flying at so low an altitude that they could not possibly see the carcass, and that the first kites, crows, and vultures flying to a carcass are evidently the clue that other species follow.

Nichols (1912, p. 46) has suggested that amongst petrels and albatrosses also the sight of some birds going to food attracts others. He writes: "I fancy that if any delectable food becomes available, birds at a distance see others go to it and fly towards them and we presently have streams of birds flying towards it from all the surrounding sea."

Earlier I have shown how individuals of one species may guide others to food, and this is an extension of the same principle to include diverse species.

Gregariousness and Attraction Between Species

Some species shun others and are shunned in turn, even though habitat and food preferences are similar. In regard to flocking

tendencies, the double-crested cormorant (*Phalacrocorax auritus*) gathers in large fishing flocks with definite formation, and flying flocks "decoy" to flocks already on the water. But when swimming, they stay in pure flocks. Bartholomew saw Pacific loons (*Gavia arctica*), red-throated loons (*Gavia stellata*), American mergansers (*Mergus merganser*) and other fish-eating water birds within less than a yard of cormorants, and none of these species paid any attention to the other. He also saw flocks containing from fifteen to twenty cormorants frequently come in contact with rafts of swimming ruddy ducks (*Erismatura jamaicensis*) or mixed white-winged surf scoters (*Melanitta deglandi* and *M. perspicillata*). The cormorants swam through the flock of ducks, moving along as though there were not a duck within miles, while the ducks swam leisurely aside, leaving a lane of open water for the cormorants (Bartholomew, 1942, p. 20).

On the other hand, though gregariousness is a term usually applied to individuals within one species, apparently it can transcend specific limits.

That mixed flocks sometimes seem to be simply the result of gregariousness seems indicated by the following account: Murphy (1936, **1:** 489) writes that "an interesting feature of the feeding of Tubinares is the intimate association of birds of various sizes and various sub-groups. In the [oceans of the] southern hemisphere one rarely sees bands comprising only one species, or even half a dozen species . . . ." Within a few minutes Murphy has seen fourteen species and almost as many genera. "Even in the northern oceans the bands of wandering and migrating shearwaters usually include 2 or 3 species, not counting the smaller petrels, such as *Oceanites* and *Oceanodroma*, which often mingle with them."

Flocking in shore birds well illustrates the beginning of mixed flocks, and the attractions between certain species.

Some species, normally gregarious, frequently mix with other gregarious species and the two species move as units in one flock. This is well shown by sandpipers and other shore birds (Nichols and Harper, 1916; Nichols, 1931).

Frequently when an individual becomes separated from others of its kind it will join with a flock of some other species. Sometimes there seems to be considerable attraction of one species for another; a solitary feeding or resting lesser yellow-leg (*Tringa* (*Totanus*) *flavipes*), for example, will spring up and follow a passing greater

yellow-leg (*T. melanoleucus*), and there seem to be certain regular interspecific associations.

Nichols (1931, pp. 184–185) summarizes this aspect of flocking in shore birds: even gregarious species may fly singly, but lone shore birds usually are more noisy and fly more hurriedly than flocks of the same species. Such behavior is usually correlated with finding the companionship they seem to be seeking. Two individuals and even three, usually but not always of the same species, frequently travel in company so often that it can hardly be mere coincidence. Gregarious as they are, a lone shore bird would be unlikely to leave (or not follow) two birds. Gregariousness varies with the species, from slight in the Wilson's snipe (*Gallinago delicata*) to great in the dunlin (*Pelidna alpina*), and the birds tend to enter into mixed flocks in proportion to their own flocking tendency. Also, some species have an active tendency to seek the company of other species, while some merely tolerate others, the smaller species tending to show the former, the larger the latter behavior. Furthermore, there are special cases of affinity. It may be well to mention some of these preferences (from Nichols, 1931, p. 182) as seen on Long Island near New York City:

The species that occur singly or in flocks (usually small) of their own kind are the woodcock (*Philohela minor*), Wilson's snipe (*Gallinago delicata*), the solitary sandpiper (*Tringa solitaria*), the spotted sandpiper (*Actitis macularia*), the upland plover (*Bartramia longicauda*), and the killdeer (*Charadrius vociferus*).

The stilt sandpiper (*Micropalama himantopus*) and the lesser yellow-legs (*Tringa flavipes*) fly with the dowitcher (*Limnodromus*).

The semipalmated sandpipers (*Ereunetes pusillus*) mix indiscriminately with the least sandpipers (*Pisobia minutilla*), and single dowitchers (*Limnodromus*) or pectoral sandpipers (*Pisobia melanotos*) as well as an occasional white-rumped sandpiper (*Pisobia fuscicollis*) fly with considerable flocks of these smaller species.

Single white-rumped and red-backed sandpipers (*Pisobia fuscicollis* and *Pelidna alpina*) flock with the sanderling (*Crocethia alba*) on open shores.

The black-bellied and golden plover (*Squatarola squatarola* and *Pluvialis dominica*) (occasionally) and the lesser yellow-legs (*Tringa flavipes*) fly with the greater yellow-legs (*T. melanoleucus*).

The Wilson's phalarope (*Steganopus tricolor*), the dowitcher, the stilt sandpiper, the pectoral sandpiper (occasionally), the greater

yellow-legs and the turnstone (*Arenaria interpres*) fly with the lesser yellow-legs.

The marbled godwit (*Limosa fedoa*) and the willet (*Catoptrophorus semipalmatus*) are said to have flocked together in the days of their abundance.

The golden plover used to fly with the Eskimo curlew (*Phaeopus borealis*) and vice versa.

The knot (*Calidris canutus*), the willet (*Catoptrophorus semipalmatus*), the greater yellow-legs (*Tringa melanoleucus*), the golden plover (*Pluvialus dominica*) (occasionally), the ringneck plover (*Charadrius semipalmatus*), and the turnstone (*Arenaria interpres*) fly with the black-bellied plover (*Squatarola squatarola*).

The ringneck, when single, flies with almost any species, large or small, from the greater yellow-legs (or even an aloof Hudsonian curlew, *Phaeopus hudsonicus*) to the least sandpiper.

Probably similar data could be built up for other groups—for ducks, for instance—but this shore-bird account is adequate to make it clear that there is not only intraspecific gregariousness, but also a tendency toward interspecific gregariousness, stronger between some species than others.

That the gregariousness in shore birds is based on food benefits seems unlikely, in view of their usual method of feeding—they run along the water's edge, getting organisms that are more or less stationary or even are buried in the mud. Co-operation in "beating" or "herding" prey seems to be of little importance to them. A further strong argument against food benefits between the species in the associations cited above is that they are based on observations of flying birds.

That these are not simply aggregations resulting from similar habitat preference is indicated by the great stretches of beach without birds at certain times, over which the shore birds feed in flocks, utilizing but a small part of the habitat at one time.

I have shown that certain species associate with other species, apparently because they "like" to do so. We have here another way to the beginning of the mixed flock—interspecific gregariousness!

In land birds there are cases in which individuals shun others of their own species but seem to attach themselves to flocks of other species. This is best shown by the downy woodpeckers (*Dendrocopos pubescens*). I have raised the related cactus woodpecker (*D. scalaris*) and the red-cockaded woodpecker (*D. borealis*) and found

that they quarrel fiercely with their own kind. This seems not to be correlated with an attempt to secure food, or position; the proximity of one bird seems to call forth an innate pugnacity in the other. The two young red-cockaded woodpeckers were very tame toward me; both stayed in one cage but one finally killed the other by a blow on the head in a quarrel (Rand, 1942b, p. 522). The downy woodpecker in winter seems similarly intolerant of others of its species; it shuns its own kind and there is a record of one, in March, killing another. However, despite this antagonism to their own kind, single downy woodpeckers habitually join roving winter bands of chickadees (*Parus*) and nuthatches (*Sitta*).

Large Scale Beating by One Species or Other Factor

We have already seen how one species can beat out prey that another species profits by. Before going on to discuss multiple beating it is advisable to show how certain single factors, acting on a large scale, can attract a considerable variety of birds.

Swynnerton (1915, p. 353) has pointed out how fires scare out insects and thus serve as "beaters" in making insect prey available. The effect is indicated by the following account:

Cheeseman (Cheeseman and Sclater, 1935, pp. 155, 156) writes of northern Abyssinia: "Big grass stretches are dry enough to burn about January, and grass-fires extend uncontrolled for hundreds of miles . . . . The smoke of the fires attracts insect-eating birds, such as Bee-eaters and Rollers, from long distances, and they fly over the flames, catching grasshoppers and moths. A fire is seldom unattended by the beautiful Carmine Bee-eater, *Merops nubicus*. They fly in and out of the ascending smoke, and the sun catches their burnished red plumage, giving them the appearance of blazing embers. Lizards and mice that do not get under ground are roasted wholesale, and the blackened ground behind the fire forms the scene of a bird-banquet. Hawks, Eagles, Kites, Marabouts and other Storks sit gorged to repletion."

Chapin (1932, p. 224) has also already pointed out how flocks of birds, fires, and swarms of driver ants passing through an area have a comparable effect in serving as beaters to force out insects and make them available.

Chapin (1932, p. 216) writes that in Africa driver ants move in long, winding columns through the forest. They carry prey, and these ants also drive insects and other small animals from their

retreats. Certain ground birds, particularly among the thrushes and the bulbuls, are most in evidence where these driver ants are on the move. This has been recorded in West Africa, in Cameroon, and in Fernando Po as well as in the Belgian Congo. Chapin writes that in a typical case, where driver ants were crossing a road, there were a half-dozen small brown thrushes (mostly *Alethe castanea woosnami* and one or two *Alethe poliocephala carruthersi*), two rufous thrushes (*Neocossyphus rufus gabunensis*), one *N. poensis praepectoralis*, and one bulbul (*Bleda syndactyla woosnami*). Apparently the birds were attracted by the ants. The thrushes darted down amongst the ants and apparently ate either the prey the ants were carrying or the animals that the ants startled from their retreat. Judging by examinations of the stomachs of the birds collected, the ants themselves are rarely eaten.

Chapin also summarized information from South America where birds of very different families, notably formacariid birds, attend the American representatives of the driver ants, and suggested in regard to certain other birds that some of the observers may have confused ordinary flocking and groups attracted to driver ants.

Somewhat similar (though an effect of pilfering may come in) is the manner in which certain gulls gather about fishing cormorants. Bartholomew (1942, p. 19) writes that the feeding flocks of double-crested cormorants (*Phalacrocorax auritus*) on San Francisco Bay often have other species associating with them, including the western gull (*Larus occidentalis*), the glaucous-winged gull (*L. glaucescens*), Bonaparte's gull (*L. philadelphia*), the California gull (*L. californicus*) and the ring-billed gull (*L. delawarensis*). The gulls fly above the fishing cormorants, occasionally dropping into the water and picking up a fish. As soon as the fishing stops the gulls scatter.

On one occasion cormorants were catching viviparous perch, some of which were pregnant. As the cormorants shifted the perch preparatory to swallowing them some of the perch gave birth to young, which were spewed forth into the water. The Bonaparte gulls that were flying about the cormorants dropped down and picked up these new-born fishes, which the cormorants made no attempt to eat.

Mixed Foraging Parties of Insect-Eaters

In the tropical forests the flocking of insect-eating birds in big, mixed parties is so conspicuous as to be spectacular. As Chapin has written (1932, p. 220) many naturalists have discovered this

habit independently. In Madagascar, where this flocking apparently is as pronounced as it is anywhere, it impressed me greatly and I wrote of it as follows:

"As we hunted through the forest, hours would pass sometimes without the sight of more than a very occasional paradise flycatcher or blue coua. Then, suddenly, the trees about us would be alive with birds, as we encountered one of these flocks. The flock was often traveling rapidly and its different members gleaned their food from the tree tops to the ground cover. For a time the birds would be all about us, then, as the flock passed on, the forest would be as quiet and desolate as before." (Rand, 1936, p. 250.)

Bates (1863, p. 334), writing of the Amazon, indicated that this type of flocking is equally pronounced there. He says: ". . . one may pass several days without seeing many birds; but now and then the surrounding bushes and trees appear suddenly to swarm with them. There are scores, probably hundreds of birds, all moving about with the greatest activity—woodpeckers and Dendrocolaptidae (from species no larger than a sparrow to others the size of a crow) running up the tree trunks; tanagers, ant-thrushes, hummingbirds, fly-catchers, and barbets flitting about the leaves and lower branches. The bustling crowd loses no time . . . . In a few minutes the host is gone, and the forest path remains deserted and silent as before."

In the more temperate Australian area it is also conspicuous. Gannon (1934, p. 122) writes that when he is looking for birds the bush may seem deserted for a considerable time: "Then suddenly a bird note is heard and perhaps a Grey Fantail [*Rhipidura flabellifera*] is seen, then almost immediately other species are noted—a Rose Robin [*Petroica rosea*], a Tree-Creeper [*Climacteris*], a pair of Jacky-Winters [*Microeca fascinans*], a small flock of Thornbills [*Acanthiza*], a Yellow Robin [*Eopsaltria*] and perhaps a Golden Whistler [*Pachycephala pectoralis*] . . . . Then, with a goodly number of birds noted, one passes on."

Stresemann (1917) has given us a summary of this phenomenon, showing it to be world-wide and discussing its implications, but Swynnerton's (1915) paper on the same subject has critical observations that have not been surpassed, and Chapin's (1932, pp. 220–224) summary is also important.

A great many other observations have been made on this mixed flocking, and the following are some of the more important accounts, arranged geographically:

North America	Odum (1942)
Eurasia	Stresemann (1917)
Central America	Belt (1874)
South America	
Venezuela	Beebe (1947)
Brazil	Davis (1946)
British Guiana	Nicholson (1932)
Peru	Taczanowski (1884)
Amazonia	Bates (1863)
Africa	Swynnerton (1915) Chapin (1932) Moreau (1948) Winterbottom (1943, 1949)
Madagascar	Rand (1936)
Southern Asia	Stanford (1947) Stresemann (1917)
Malay Archipelago	Stresemann (1917)
Philippines	McGregor (1920)
Australia	Gannon (1934) Hindwood (1937) Chandler (1937) Sedgwick (1949)
New Zealand	Stresemann (1917)

Sometimes in the literature there is a tendency to consider birds gathered about a favorable food supply—a flowering or fruiting tree, a swarm of insects, a swarm of driver or army ants—or birds in an especially rich habitat, or even a chance gathering of birds, as forming a mixed foraging flock. But these foraging flocks differ in that they move about more or less together, the bird staying in the association and feeding in it, the many species being intent both on their feeding and on keeping together as they move.

Composition of Flocks by Species: In the Holarctic region the winter flocks tend to consist of one or more species of titmice (Paridae), nuthatches (Sittidae), a creeper (Certhiidae) and a woodpecker (Picidae). In the migrating season, especially, many other species may feed and travel together. In North America the bands of migrating wood warblers (Parulidae) and vireos (Vireonidae) are good examples.

Davis (1946), who studied flocking in Brazil, discusses the various species comprising the flocks there. At one locality thirty-four species were regular members of the groups in second-growth forests. A warbler and an ant bird were the most common members; most species belonged to the woodhewer and the ovenbird families; twenty-one species were accidentals. At another locality in virgin forest, thirty-two species were regular members of mixed groups and eighteen were accidentals; though there were more species in the

virgin forest, there were fewer individuals of each species. Summarizing these, we have cuckoos (Cuculidae), one species, accidental, in flocks; hummingbirds (Trochilidae), one species, accidental; trogons (Trogonidae), one species, accidental; woodpeckers (Picidae), three species, regular, but scarce birds and usually only one to a flock; woodhewers (Dendrocolaptidae), several species, one or more species usually present, pre-eminently flocking birds; ovenbirds (Furnariidae), some species true flocking birds and the core of most mixed flocks; antbirds (Formicariidae), another family of which the members are pre-eminently flocking birds (some species also following army ants); gnat-eaters (Conopophagidae), accidental; cotingas (Cotingidae), several species, regular; mannikins (Pipridae), casual; tyrant flycatchers (Tyrannidae), a few species true flocking birds; leaf cutters (Oxyruncidae), one species, a true member of flocks; thrushes (Turdidae), three species, accidental; vireos (Vireonidae), one species at least usually present; honey-creepers (Coerebidae), one species, scarce, but probably a true flocking species; warblers (Parulidae), one species a member of most flocks; tanagers (Thraupidae), some species regular; finches (Fringillidae), three species, accidental.

For the tropical rain forests of the Congo we have Chapin's account (1932, pp. 220 ff.). He says that a full list of the birds of these flocks would not be easy to draw up. Some species that join the flocks do not persistently follow them. Some species are only occasionally seen in the flocks and could not be included without hesitation. The flocks may contain as many as forty or fifty individuals, following a common course.

As more characteristic members of the flocks he gives three species of bulbuls (Pycnonotidae), two babblers (Timaliidae), two sunbirds (Nectariniidae), three flycatchers (Muscicapidae), two woodpeckers (Picidae), a drongo (Dicruridae), and several weaver birds (Ploceidae), and he lists as also occurring regularly enough to mention, two thrushes (Turdidae), two more bulbuls, two more flycatchers, a piculet (Picidae), three shrikes, another thrush, and two more babblers—about thirty species of more or less regular occurrence. A squirrel or two is often associated with these flocks. Extremely pertinent are his comments on the birds of the savannas (op. cit., p. 237). Speaking of the Guinean savanna he says that mixed bird parties are anything but typical, contrasting with the condition in the rain forests. However, some small mixed flocks occur, comprised of a creeper (Certhiidae), one or more warblers

(Sylviidae) and a titmouse (Paridae). This association of titmouse and creeper recalls similar associations in the Holarctic.

Winterbottom (1943), writing of the woodland bird parties of northern Rhodesia, states that a drongo (Dicruridae) occurs most frequently in parties with the following, in decreasing order of frequency of occurrence: a flycatcher (Muscicapidae); a woodpecker (Picidae) or a shrike (Laniidae), depending on the area; a warbler (Sylviidae); an oriole (Oriolidae); a helmet shrike (Prionopidae); a weaver bird (Ploceidae); and another warbler (Sylviidae). Other commonly occurring species are a white-eye (Zosteropidae), a barbet (Capitonidae), a cuckoo shrike (Campephagidae), and a wood hoopoe (Phoeniculidae), with the addition of two Palaearctic migrants, a warbler (Sylviidae) and a flycatcher (Muscicapidae). He gives sample counts of other flocks with many other species in them.

In the rain forests of Madagascar I found (Rand, 1936, pp. 250–252) that almost all the more common insectivorous birds except those of the forest floor were seen at least occasionally in these flocks, and sometimes even the rare ones also. From ten to fifteen species and even more were frequently found in one flock. The most commonly occurring were two species of warblers (Sylviidae), two flycatchers (Muscicapidae), one sunbird (Nectariniidae), a white-eye (Zosteropidae), several vangas (Vangidae), a cuckoo shrike (Campephagidae), a coral-billed nuthatch (Hypositttidae), several babblers (Timaliidae), a weaver bird (Ploceidae), a coua (Cuculidae), and a thrush (Turdidae).

The composition of the bird parties in the great forests of northeastern Burma is discussed by Stanford (1947). He lists, with no classification as to regularity of occurrence, some forty-seven species observed in mixed flocks, including six species of titmice (Paridae), two parrot bills (Paradoxornithidae), three nuthatches (Sittidae), nineteen babblers (Timaliidae), two woodpeckers (Picidae), one creeper (Certhiidae), two flycatchers (Muscicapidae), one warbler (Sylviidae), and a white-eye (Zosteropidae).

In the Malay Archipelago, on Seran, Stresemann (1917, p. 137) found up to fifteen species represented in the flocks, including the following: one species of cuckoo shrike (Campephagidae), one bulbul (Pycnonotidae), five flycatchers (Muscicapidae), two pachycephalas (Laniidae), one warbler (Sylviidae), two white-eyes (Zosteropidae), one flower pecker (Dicaeidae), one drongo (Dicruridae), and one weaver bird (Ploceidae).

For Australia we may quote Sedgwick's (1949) listings, in which he tabulates up to sixteen species found in mixed flocks in one area, including three species of flycatchers (Muscicapidae), six warblers (Sylviidae), one pachycephala (Laniidae), one flower pecker (Dicaeidae), four honeyeaters (Meliphagidae), and one babbler (Timaliidae). Other reports often stress the importance of nuthatches (Sittidae) as well as other species in these flocks.

The lists of species could be greatly extended from the literature, and additional field studies would add many more. From my observations in Madagascar it seemed that any of the common forest birds would be found at some time or other in the flocks.

Enough has been said to show that in each area there are groups of birds that flock. From area to area they may be composed of quite different species, not closely related. Similar influences are presumably at work.

HABITAT UTILIZED: Chapin (1932, p. 221) has perhaps best pointed out how the big mixed flocks of the forests of the Congo utilize various available habitats, "each bird occupying itself according to its proper propensities, some skulking along on or near the ground, others hopping and flitting through the undergrowth, while some of their comrades scour the foliage of the lower branches of the taller trees, dense tangles of hanging vines, or climb up the trunks and limbs, getting ants and other insects from the bark."

In Madagascar the coverage of the forest was more complete, even into the tree tops. The flocks' ranks contained birds that frequented all the forest associations except that of the forest floor. Some were in the tree tops, gleaning through twigs and leaves; others specialized in branches of the tree tops; another group was largely confined to the trunk and larger limbs; a group occupied the middle spaces in the forest, often ranging up into the tree tops and down into the ground cover; and another group occupied the ground cover. Sometimes the species would all be moving as a single loose flock without organization; sometimes the larger species were in the forepart of the flock and the smaller species would follow. A flycatcher frequently was found in the wake of such a flock, and a large solitary vanga (Vangidae) usually preferred the outskirts of the flock.

Moreau (1948, p. 119) mentions mixed foraging parties in eastern Africa (Usambara) and brings up the question as to the amount of habitat overlap in closely related species in these flocks. His pre-

liminary conclusions are that where closely related species occur in a flock, their respective foraging habits are complementary.

SIZE OF FLOCK: In the rain forests of the tropics these flocks appear to reach their greatest size, though, as Chapin (1932, p. 221) has pointed out, in these forests it is difficult to count and evaluate the flocks. Belt (1874, p. 123), writing of Nicaragua, speaks of flocks of hundreds of individuals and more than a score of species. Chapin (1932, p. 221) says that such a flock in the Congo forests may contain forty or fifty individuals, but Swynnerton (1915, p. 348) records as many as forty or fifty individuals of one species of bulbul in one mixed African flock. Some of the flocks I saw in Madagascar certainly contained at least a score of species and more than a hundred individuals. Chapin (1932, pp. 237, 262) has pointed out that the flocks in the woodlands and savannas in Africa are much smaller and less characteristic than are those in the rain forests.

In Brazil, Davis (1946, p. 180) found that the flocks usually had from four to six species (varying from one to sixteen). Winterbottom, in Rhodesia (1943, p. 440), recorded an average of seven to nine species in the flocks he tabulated. Sedgwick's (1949) results in Australia varied from three to six, three to ten, two to four, and two to eight species per flock, varying with the locality. Gannon (1934, p. 126), for Australia, gives up to many scores of individuals of a dozen or more species.

Wing (1941) has worked on the average total weight in grams of winter flocks of one species in North America, correlating this with food and feeding range, a technique that may be kept in mind, even though its application is not immediately apparent.

Comparisons of the gross size of flocks, resulting from counting the number of individuals and species, seems a sterile approach. The question of what constitutes a flock becomes important, and one can get the average size of a flock of white-breasted nuthatches as 2.29 individuals (Wing, 1941).

Nevertheless, the association of only two species is as worthy of attention as is the more complex groupings. As Sedgwick (1949) has pointed out, we may see more clearly the factors that may be operative and the structure and activity of the small flocks, and constancy of association of certain species within the flocks seems more important (see p. 56).

WANDERING OF THE FLOCK: There is some evidence that the mixed flocks of birds do not wander, homeless and haphazardly, through the forest, but have their own ranges. Chapin (1932, p. 221)

writes that these flocks in the Congo forests very often take some definite direction. Nicholson (1932, p. 74) followed mixed bird parties in British Guiana and found that they were confined to well-defined localities in their wanderings. Stanford writes (1947, p. 508) that in Burma "it will be found that these traveling flocks tend to take the same route day after day, and often several times a day, passing one particular bush, or tree, or patch of bamboo, and ignoring the jungle on either side of the route."

Davis (1946, p. 179), writing of Brazil, says that the flock spends the day wandering about a small area.

Bates (1863, p. 335), writing of Amazonia, says that there appeared to be only one of these flocks in each small district, and as it traversed chiefly a limited tract of woods he could generally find it any time he wanted to do so.

Daily Formation of the Flock: The best information we have on this is Davis' account (1946, p. 179): "The mixed flocks are formed shortly after dawn. On numerous occasions individual birds were seen in the dim light coming together, beginning to call, and soon forming a group. Once formed, the flock spends the day wandering about a small area. There is somewhat less movement during the middle part of the day, and possibly each flock has fewer individuals and species [then]." Odum (1942, p. 511) also gives data on daily flock formation in the eastern United States.

Seasonal Changing in Flocks: In the north temperate zone mixed flocking is largely a winter and a migratory period phenomenon (Odum, 1942, p. 526). Stresemann (1917, p. 142) believes that in the tropics breeding birds retire from the flocks to nest.

Though bird flocks occur throughout the year in the tropics, the number of flocks Davis (1946, pp. 178, 179) found in Brazil decreased in the breeding season, though the number of species and individuals in the flocks did not decrease correspondingly. Davis (op. cit., p. 179) believes that many tropical birds do have territories, and that it seems likely that the individuals leave the flock to take up territory during the breeding season.

However, Winterbottom (1949, p. 262) writes that while he has implied that nesting tends to prevent mixed flocking, it does not do so entirely; he has seen a mixed party pass the nest hole of a woodpecker, when opportunity was taken by the parents to effect a change-over on the nest.

Chapin (1932, p. 223) writes that in the rain forest of the Congo there is no season when the "hunting parties are not in vogue.

They are by no means associations of young or non-breeding birds." In the area Chapin was writing of, many species of birds breed at all times of the year and he found many birds with enlarged gonads in these mixed flocks. He questions Stresemann's statement that birds actually nesting retire from the flocks. In Madagascar I also found birds with enlarged gonads in mixed flocks (Rand, 1936, p. 252).

Sedgwick (1949, p. 10) writes that flocking occurs in Australia any month of the year but is infrequent in the breeding season.

In the tropical rain forest, mixed flocks evidently do exist throughout the year and do contain breeding birds, though flocks are not so frequent during the breeding season. Away from the equator and from rain forest, flocking probably becomes increasingly seasonal.

Davis (1946, p. 179) brings out an interesting matter: The number of individuals per species tends to remain constant throughout the year, despite the breeding season, which one might think would increase the number of young birds and add them to the flocks.

STABILITY OF FLOCKS: Beebe (1947, p. 161) is inclined to believe that the mixed bird flocks of Venezuela are units that stay together. Sedgwick (1949) also thinks the flocks in Australia are semi-permanent. The evidence that these flocks may be restricted to one limited area, drawing all the birds from that area, suggests that in general this may be true. However, Odum's (1942) studies of chickadee flocks in the eastern United States, where he says the composition as to individuals may change from day to day, and even from hour to hour, indicate that this evidence needs to be checked.

STRUCTURE OF THE FLOCK, AND ITS ACTIVITY: Certain classifications of the components of flocks have been proposed. Gannon (1934, pp. 124, 125) proposes to distinguish:

(a) Primary association formers; flocking species.

(b) Secondary association formers; more or less solitary species that are attracted by the first category, and by their activity attract others.

(c) Others.

This classification was supported by Sedgwick (1949, p. 10). Winterbottom (1949) at first followed the same functional type of analysis in his earlier classification, as follows:

(a) Nucleus species.

(b) Circumference species.

Davis (1946) on the basis of frequency of occurrence only, divides the components of the flocks into:

(a) Regulars.

(b) Accidentals.

Winterbottom (1949) finally combined his own earlier, and Davis' classification as follows:

(a) Nucleus species.

(b) Other regular species.

(c) Regular accidentals.

(d) Accidentals.

He also suggested a fifth category, "accidental nucleus" species.

As will appear later, I think a functional approach in classification is preferable, with the adjectives "regular," "uncommon," or "rare" to indicate the degree of frequency of occurrence. I would suggest the following:

(a) Nucleus species, which seem to be essential in the flock formation.

(b) Attendant species, which accompany the nucleus species.

(c) Accidentals; as their name implies, these species appear in the flock by accident, and do not properly belong to it. The list of accidentals could be indefinitely prolonged, probably, in the forest habitat, to include most of the forest avifauna.

It must be kept in mind that more than one nucleus species may be present in a flock, and that mutual aid may reinforce an interspecies gregariousness between two nuclear species; but it does seem that certain species, the nuclear flocking species, take the lead, and others follow them, and that within the flock there may be certain associating tendencies.

The idea that there are "nucleus" species and "attendant" species seems adumbrated by Bates (1863, p. 335), who records the Indian belief in Amazonia that a little gray bird leads the flock. Gannon (1934, pp. 124–125) also points this out and goes on to show that at times at least in his section of Australia certain warblers known as thornbills (*Acanthiza*) seem to lead the way. He suggests that other more noisy species attracted to the thornbills are also

important in forming mixed flocks, as their activities are more noticeable. These are his secondary association-formers.

In the United States, Odum (1942, p. 511) found that the black-capped chickadee (*Parus atricapillus*), as a species, was definitely the leader in mixed autumn flocks that included arboreal warblers (Parulidae) and vireos (Vireonidae). The chickadees were much the noisiest and by their vocal signals seemed to control the flock. He also quotes work to show that Carolina chickadees (*Parus carolinensis*) and tufted titmice (*Baeolophus bicolor*), both Paridae, share in the leadership of mixed autumnal flocks in Tennessee.

Such associations within the flock were plainly evident in the Madagascar work (Rand, 1936, pp. 251–252). After listing the more characteristic species to be found in the flocks, I noted that while sometimes most of them might be found in one flock, at times the larger species were in the forepart of the flock and as they passed on the smaller species would appear; a paradise flycatcher (*Tchitrea mutata*) was frequently found in the wake of a flock, and a curve-billed vanga (*Vanga curvirostris*) seemed to prefer the outskirts. Sometimes a flock would consist of smaller species entirely, sometimes of the larger ones. The rare black vanga (*Oriolia bernieri*), when found, was usually associated with the commoner helmet bird (*Aerocharis prevostii*) and the latter usually with flocks of the much more common white-headed vanga (*Artamella viridis*). The rare *Tylas eduardi* also favored the company of the common white-headed vanga.

Swynnerton (1915) had already had the idea of nucleus species and has given the best observations to show the relationships within what he called "hunting parties." In one instance about a dozen bulbuls were feeding in guava trees, and about the bushes, hawking backward and forward, over and around, were several swallows and bee eaters snapping up the insects dislodged by the bulbuls. Swynnerton was even able to distinguish one insect that flew from a bulbul only to be snapped up by a bee eater. That a "nucleus" species may also become an attendant species is shown by another observation when a flock of waxbills (Ploceidae) was seen hunting, while above them was a party of the same bulbuls mentioned above, keeping pace with them for the sake of insects put up by the waxbills. The complexities of a mixed flock arose with several bishop birds (Ploceidae) that were sometimes with the bulbuls, sometimes with the waxbills.

Swynnerton's observations, which are summarized below, on the inter-relations of big mixed "drongo hunting parties" are also especially good. In one flock in the forest a large party of bristle-necked bulbuls (*Phyllostrephus terrestris*) worked the lower part of the forest; above them came a large party of forty to fifty Barratt's bulbuls (*P. flavostriatus*) exploring the vegetation. With these latter, but usually just above and to one side of some small working party were a pair of forest drongos (*Dicrurus*) and of white-spotted flycatchers (*Trochocercus albonotatus*). The flycatchers, besides watching the "beaters" and snapping up small insects put up by them, did some searching among the leaves and so took a small share in the "beating." The drongos, however, confined themselves to taking insects on the wing, several times dashing to within a foot or two of a beater in pursuit of some object flushed by it. Swynnerton even identified as a beetle an insect that was dislodged by a bulbul and snapped up by a drongo. Another bird, when in pursuit of an insect it had flushed, was joined by its neighbors, one of which snapped up the insect in the air. Once a bulbul flew to a flycatcher, drove it off, and took some object from a leaf in front of it.

Swynnerton gives other examples indicating that beater-attendant relationship, mutual aid, and competition actually exist in these mixed flocks, and that some species more than others act as beaters (and presumably leaders, and nucleus species) in these flocks.

Chapin (1932, p. 223) has summarized various opinions as to the function of these flocks. Newton and Pycraft thought that these sociable habits were founded on mutual aid in seeking food. Swynnerton, though he thought mutual protection might be a factor, also inclined toward this view, and Chapin himself inclines toward the function of co-operative hunting, though he thinks a combination of factors may be at work.

Many other papers have contributed to this topic, usually only indicating that the type of flocking occurred in certain areas and noting the species involved, though certain new ideas and aspects have emerged.

However, much of the attention has centered on the rich aggregations of birds in these flocks in the tropics. It seems to me that a clearer understanding of how these flocks came into being, and their significance, is indicated by a comparative study of flocking birds. Stresemann (1917) has already classified flocking into three categories: flocks of one species; simple mixed flocks whose origin is bound up with mutual aid in seeking food; and compound flocks,

such as we have discussed in this section, originating in gregariousness. Davis (1946) has suggested that the primary motivation in flocking behavior may be the urge to associate in groups, but that possibly it first developed in relation to army ants, and then continued in the absence of ants.

From the present study it seems that gregariousness, curiosity, similar food habits, and co-operative hunting (with one species profiting by another's beating and pilfering) acting together, or in varying combinations, are sufficient to account for the formation of these mixed flocks, even though there may be other incidental benefits.

Mixed Flocks of Sea Birds

Large mixed flocks of the oceanic birds known as Tubinares (Procellariiformes) are characteristic of southern oceans, and though further observations may indicate that the factors involved are different from those that produce the mixed foraging parties of land birds, the mixed flocks of pelagic birds appear to be comparable. As has been mentioned, Murphy (1936, **1**: p. 489) writes that "an interesting feature of the feeding of Tubinares is the intimate association of birds of various sizes and various sub-groups."

In this connection Nichols (1914) has pointed out that large, medium-sized, and small species of Tubinares may gather at one time to partake of the scraps from a ship, and that the smaller birds are satisfied with crumbs left by the larger. Perhaps a similar relationship exists when they are feeding on natural food, but it would seem that interspecific gregariousness had brought them together in the first place. Nichols believes that the great variation in size in the order Tubinares (Procellariiformes) may be the result of intraordinal competition, in the absence of interordinal competition. It is possible that this pronounced flocking has had an effect in intensifying intraordinal competition.

Discussion

As one would expect, one finds the factors prominent in intraspecific feeding groups and in simple, two species relationships operating in these mixed groups: the attraction of food itself, gregariousness, and curiosity. Some modifications of associations that were reviewed earlier again appear here, transcending specific limits. Gathering about food, guiding to food, and mutual aid in beating are particularly evident. A further point that emerges in this section,

beyond the simple interspecific associating, is the marked tendency for some species to associate with certain others. It is even usual for certain species that regularly shun their own kind to attach themselves to flocks of certain other species; that is, they are solitary intraspecifically but gregarious interspecifically. This complex of factors may all be at work in one large mixed feeding flock.

The mutual-aid aspect is especially evident in the mixed foraging parties, but there are other aspects, notably in the case of those species that do not take part in beating, but use others for beaters, and the species that pilfer. There are both advantages and disadvantages of this flocking. Undoubtedly gregariousness plays a part in the formation of these flocks, but probably the food benefits are the most important. That this is so is indicated by the fact that birds congregate about grass fires and droves of army ants when these make food available in quantity.

Specialization of association in these mixed bird parties has not gone as far as in the cases of one species accompanying another, discussed in the previous section. But they are very common, even characteristic of the forest avifauna of all continents, and represent the customary method of hunting of many species. The components of the flock vary from continent to continent, even representatives of different bird families composing the bulk of the flocks, but the advantages seem to be the same.

DISCUSSION

We have shown that it is possible to construct a number of series that connect simple social behavior such as gregariousness in feeding with such complex and specialized behavior as the obligate relationship of the oxpecker to hoofed animals; the honey guiding of *Indicator;* the robbing of the osprey by the eagle; and the mixed foraging flocks of the tropical forests.

We will examine these series, which with their inter-relationships could be said to form a fabric, from a number of points of view, examining advantages and disadvantages involved; intelligence and purposefulness; recent origin of some habits; their indication of the adaptability of birds; their phylogenetic significance; and their bearing on speciation.

As many authors have pointed out, a complex of factors, notably those connected with threatened danger and self-preservation, may be effective in group behavior.

There are also certain factors that affect a flock to its disadvantage more than they do solitary individuals. In the flock there are disadvantages of competition for a common food supply. These necessitate additional movement of the birds, perhaps of little moment in such mobile creatures. Further, the organization of the

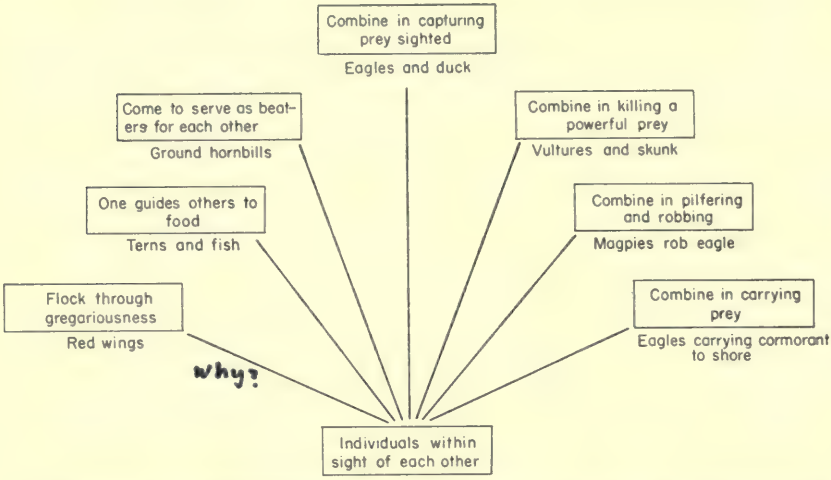

FIG. 1. Some possible feeding developments, within a species, when several hungry birds are within sight of each other; with examples.

feeding flock is sometimes modified to lessen this very disadvantage. Pilfering by one individual from another of the same species would seem to be a disadvantage, but some interspecific associations are built on this very factor. Flocking has sometimes been considered to be an advantage to the flock in making predation more difficult, through many pairs of eyes that watch for danger; through the cries of one bird that warns many; through individuals that act as sentinels; and even through the rather improbable dazzle pattern effect of the flock, making it more difficult for a predator to pick out an individual bird. There are however possible disadvantages; for example, a flock of birds is noisier than an individual and advertises its presence more thoroughly than would solitary individuals. In my two years in Madagascar many of the birds I collected were from flocks, and I was always alert to follow up the calls of certain species that I had learned were usually in mixed flocks. These flocks were a help to me in collecting. Possibly the danger-escape and predator-invitation effects cancel each other.

Though factors other than food-getting advantages may be operative, it would appear that in the examples discussed in this paper the food advantages are sufficient to account for the development of many specialized social behavior patterns.

FIG. 2. Some possible results of a bird associating with another animal, from curiosity or chance; with examples.

The acquisition of new habits as outlined here necessitates no highly developed intelligence and no awareness of the result, nor is any purposefulness postulated beyond satisfaction correlated with certain associations. If we assume that chance, curiosity or something very like it, and or gregariousness are operative in bringing together birds of one species, or a bird and one or more other species of animal; if we assume that birds come to associate certain conditions with certain food benefits and modify their behavior to secure more satisfaction accordingly; and if we assume that a species' behavior, or at least its tendency to behave in a certain way is variable, and that the variation is heritable, we have postulated psychological processes of low order, but sufficient to fit the present thesis.

In the theoretical course of events, a bird comes in contact with another bird or other animal, and through this contact food benefits accrue. The bird comes to associate certain benefits with these contacts and then has an added incentive to seek them out. Certain individual birds are more prone to do this or are quicker at it than others. These are the birds most likely to survive. Through selection, the seeking of the association and the profiting by it become a part of the usual behavior of the species. Thus "new" habits arise.

Some of the associations discussed are old. That of the oxpecker feeding on ticks on hoofed game is old enough for this aberrant starling to have become structurally adapted for it. The fact that the habit of robbing other birds of their food, practiced by frigate birds, skuas, and certain fish eagles, is so widespread can also be taken to indicate age of the habit. But to illustrate that habits are ever changing and new ones constantly appearing, we have only to remember that the following of ships by albatrosses and gulls can be no older than navigation; the feeding of Antarctic water birds on whale carcasses (and their consequent extension of range in the far southern oceans) is not older than whaling; and the following of a plow by robins for worms turned up by it is not older than the plow. The sheep-eating of the kea goes back only to the introduction of sheep into New Zealand. Still more recent is the falcon's habit of using trains as "beaters," and the association of black-headed gulls with ferry boats, for the food washed up on the beach.

SOME ASSOCIATIONS OF VARYING DEGREES OF ANTIQUITY

A. Recent; probably less than 100 years old:
   - Falcons using trains as beater (p. 20); since trains were used.
   - Gulls profiting by wash of ferry boat on shore (p. 25); since ferry boats were used in England.
   - Kea parrot eating sheep (p. 29); since sheep were introduced into New Zealand.

B. Moderately recent; probably several hundreds of years old:
   - Robin following plow for worms (p. 26); began with cultivation of land.
   - Gulls following ship for scraps (p. 25); began with navigation.

C. Moderately old, as firmly established in species:
   - Buff-backed heron using hoofed animals as beaters (p. 21).
   - Hornbill using monkeys as beaters (p. 23).

D. Still older, as well established in a group of widely distributed species:
   - Frigate birds robbing terns, etc. (p. 36).
   - Sea eagles robbing osprey, etc. (p. 35).

E. Still older, as structural modifications have evolved correlated with the relationship:
   - Oxpecker's obligate relationship to bodies of hoofed animals for feeding habitat (p. 30).

Some of the associations are obvious adaptations affecting many birds, like the flocking of sea birds about whale carcasses, or the gathering of robins to follow a plow. But others are obscure and unexpected and they involve few individuals, like the behavior of the falcons and gulls just cited.

The quickness with which apparently minor favorable aspects of an association are seized on and used indicates the remarkable acuity of the birds, their readiness to seize every advantage, and possibly the pressure of the environment that makes this necessary. Not only is every part of the habitat used, but every aspect of the environment that offers an advantage is exploited. When, through man's activities, new opportunities are made available, these are likewise made use of.

Habits are often used in working out phylogenetic relationships. Certainly they can be indicative. But no habit should be given any more importance than a single morphological feature; the webbed feet of loons, ducks, gulls and cormorants do not indicate close relationship, nor does the swimming habit of loons, cormorants, coots, and phalaropes; the hooked bill of the skua, the frigate bird, and the eagle is no better or worse evidence for a close relationship than is their habit of robbing other birds of their prey. Apparently many species have independently evolved similar habits to meet similar conditions. This is particularly evident in the big mixed foraging bird parties, which, with different species, sometimes of quite different families, replace each other in various parts of the world. The quickness with which pronounced habits can come into being, notably the falcon-train and the kea-sheep relationships just mentioned, is also a warning against attaching too much phylogenetic importance to any one set of habits.

And yet habits, like structure, presumably evolved from simple to complex, and are still evolving. The speed with which new social habits can arise emphasizes the improbability of finding actual phylogenetic series in existing groups of birds. From the basic similarity of birds, and their tendency to respond in similar ways to similar situations, we may expect the examples that seem to illustrate the expected stages in the development of a habit to be actually unrelated. They have arisen anew a number of times, and have reached varying levels. Nevertheless, these series, pseudophyletic though they are, are of value in showing the steps through which the complicated behavior probably arose or could have arisen. They help us in evaluating the various examples.

Recently, the importance of ecological differences between species inhabiting the same areas has been given much attention. It has been said that if two closely related species occupy the same area, their requirements must be different. Species that have the same ecological requirements can not live together. The trend of evolution has been to reduce competition. And yet, in the social feeding behavior reviewed above, many cases seem to be increasing competition. In the mixed foraging parties, many individuals of several species may be competing for the same food; indeed interspecific competition for the same individual insect is recorded! Presumably, in some cases, especially in birds with closely similar feeding habits, the mutual aid in feeding more than outweighs the disadvantages. But in some cases, as in that of an eagle robbing an osprey, or of a drongo in a foraging party snapping up an insect that another bird was pursuing, or of the bulbul that drove off a flycatcher and took its prey, there was benefit to only one of the birds concerned.

It is quite true that in many mixed foraging parties of the forests many species search for their food in different ways, from flycatching to gleaning from trunk, twig and leaf, and at different levels, from ground to tree top. But closely related species do occur in these parties, and active competition does occur (for a discussion of this see especially Moreau, 1948, pp. 119–121).

This seeming paradox of social behavior that increases competition, which evolution has been working to reduce, is also apparent in flocks of pelagic birds, and Nichols (1914) has suggested that it has had an effect on speciation in the Procellariiformes. This group, including the albatrosses, shearwaters, and petrels, shows a tremendous range in size between species, all of which have more or less similar habits and commonly gather into mixed flocks. It is possible that intraordinal competition has been a factor in evolution, producing the great range in size in the group, thus reducing the competition that had been intensified by gregariousness.

SUMMARY

Social feeding habits of birds, outside the breeding season, are considered from the viewpoint of possible stages through which the more complex patterns have evolved. Behavior patterns are examined and compared, and arranged according to their similarity in organization and usefulness. This discloses a number of series, each starting with the simple and becoming more and more complex.

Intraspecific social behavior is examined first, as it is simpler, and the factors involved tend to be more easily seen. Gregariousness is very pronounced in birds and seems to be the main starting point for these associations. This flocking could be a disadvantage when food was limited. But various modifications or organizations of

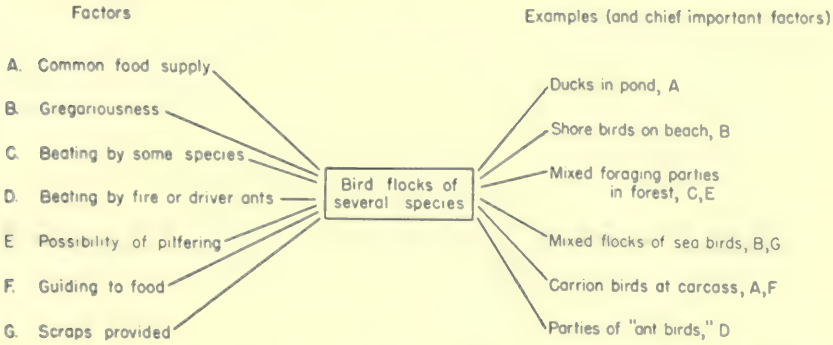

FIG. 3. Some factors possibly influencing the formation of flocks of severa bird species; with examples.

the flocks exist that not only cancel out such disadvantages, but make a position in the organized flock more advantageous than solitary feeding. The most obvious of these are: spacing out of the flock to reduce competition; the leading of some individuals to food by others going to it; the beating or driving of coverts, which flushes prey into accessibility; and combining of individuals to capture, kill or otherwise secure food already sighted.

The feeding associations of birds transcend species limits, and there are many concerned with non-bird animals, including man and his extensions (ships, etc.). Here curiosity or chance seems to be the main starting point. The bird seeking the association is often the chief beneficiary, through the beating activities, the providing of scraps, and the providing of parasites and even flesh of its own body by the animal accompanied. Another series in this category is the pilfering or robbing of one species by another.

In flocks in which many species of birds keep together, many of the factors involved in the simpler cases mentioned above are discernible, and it is probable that several may work together, reinforcing each other.

Protection from predation by flocking is probably of no great importance.

The data given illustrate the extreme acuity of birds in seizing on small elements in their environment that provide food benefits. They show that such occasional benefits may lead to new habits; that new habits are still arising; and that simple or occasional associations in some species are more complex or regular in other species.

We can see how the complex behavior patterns evolved if we postulate psychological processes of a low order, satisfaction or benefits being associated with the presence of certain conditions; variability in the birds in the ability to recognize such associations; and the selection of certain favorable variations until they become a part of the normal behavior pattern.

However, the rapidity with which new patterns develop, and similar patterns that evolve in unrelated birds, indicate that these behavior patterns are not necessarily phylogenetic. But even so, they give a background showing examples of the stages through which complex behavior probably passed and how it originated.

Some mixed bird parties increase competition between species, offsetting some at least of the mutual aid of the associations.

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