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Author(s): Douglass H. Morse

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ECOLOGICAL ASPECTS OF SOME MIXED-SPECIES FORAGING FLOCKS OF BIRDS

DOUGLASS H. MORSE

Department of Zoology, University of Maryland, College Park 20742

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Abstract. Mixed-species flocks of birds composed of chickadees, titmice, woodpeckers, nut-hatches, creepers, kinglets, and wood warblers were studied in several habitats in Louisiana, Maryland, and Maine. Chickadees and titmice usually led these groups. Both the size of the flock and density of birds varied with the habitat. An inverse relation existed between the density of birds in a habitat and the percentage of them that were species participating in flocks. Individuals of species regularly participating in flocks sometimes were found away from them. The tendency for such an individual to be in a flock was inversely related to the density of birds in the habitat. Hostile interactions were infrequent in flocks, being mostly of an intraspecific nature. A dominance hierarchy existed between the different species in flocks. A definite distance was maintained between individuals. As flock size increased the area occupied per individual decreased. The larger flocks were, the faster they usually moved. Each species favored certain parts of the habitat when foraging, though overlap existed between almost all pairs of species. The commonest species (chickadees, titmice, kinglets) overlapped heavily. Subordinate species foraging in the presence of dominant species changed their areas of foraging, but little or no tendency was seen for subordinates to affect the foraging of dominants. Subordinates might either spread out over alternative foraging areas or concentrate their activities more strongly in a few areas. Most flock members responded markedly to predators; however, few predators were observed during the study. Many of the responses seen were delivered to inappropriate stimuli.

Several factors suggest a direct relationship between population density and food supply. Flocking appears to be an effective adaptation to difficult conditions. If a species adjusts its foraging in the presence of another species, possibilities of hostilities should be minimized. Subordinate species usually moved to parts of the habitat to which they were well-adapted. If dominant species are absent, however, opportunism by the subordinate may allow it to take advantage of otherwise unused resources. Dominants may obtain a more predictable portion of the food supply by participating in flocks than if solitary. Constant movement may insure that birds obtain the most readily available food. Large flocks may move rapidly because their individuals are more crowded than those in small flocks. With this restriction either increased speed or more concentrated foraging would be predicted. The low frequency of predators suggests that evasive responses of flock members formerly may have been more advantageous than at present.

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INTRODUCTION

The grouping of small insectivorous birds into flocks of two or more species is a familiar occurrence in many parts of the world. While considerable effort has been expended in studying these groups, no comprehensive comparative study treating both their foraging and social behavior has appeared. Furthermore, in spite of the work expended, the function(s) of such groupings generally remains a matter of speculation.

I commenced studies upon mixed flocks in July, 1962, and continued through December, 1968. The specific aims of this undertaking were to gather a variety of quantitative and qualitative data that would describe the ecology and behavior of certain flocks and that would be of value in determining what advantages participating individuals might obtain. Flocks I studied are formed about one or more members of the titmouse family (Paridae). Other frequent members include woodpeckers, nuthatches, creepers, kinglets, and wood warblers. Work reported in this paper was conducted in three areas: Louisiana, Maine, and Maryland.

Before continuing, it is necessary to define a flock as treated in this paper. Any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species is considered a flock. This represents a slight modification of Hinde's (1952) definition. A group of individuals that is drawn together only by some extrinsic factor such as a localized food or water source may be termed an aggregation. Hence, ant-following groups, such as those described by Willis (1966a) would be considered aggregations, rather than flocks.

Mixed insectivorous flocks are loosely organized groups. Their composition may change, though many members remain together for considerable periods of time, through most or part of a day, reforming flocks on subsequent days (Odum,

1942). The change in composition is particularly noticeable during periods when flocks contain many migrants, though these transients usually appear to be of little importance in determining the actions of a flock. A change of members is also frequent where some individuals in a flock occupy territories and drop out when the remainder of the group leaves its area (see Moynihan, 1962). These groups almost always are on the move, rather than remaining for considerable periods within a limited space. Participants may be left behind a flock as a result of differences in horizontal foraging speeds (see Fitch, 1958), though in this study separated individuals usually regained contact with a flock within a few minutes.

Several possible explanations for the existence of mixed foraging flocks have appeared over approximately the last 100 years. Three have appeared repeatedly.

One has been that presence in groups conveys protective advantages upon the individuals involved. Bates (1864) in his journal of travels on the Amazon and Belt (1874) in his journal from Nicaragua supported this explanation, while Moynihan (1962) is a recent adherent. Stresemann (1917), Chapin (1932), Hindwood (1937), Wallace (1941), and Winterbottom (1949) have also recognized the possible importance of a protective function. In this regard it is important to note that most (or all) flocks contain species that have strongly developed predator alarm systems, and that their sheer numbers alone will increase watchfulness. On the other hand, some workers (Beebe, 1947; Morley, 1953) have commented that increased conspicuousness when in flocks makes the individuals more vulnerable to attack by predators than they would be out of a flock.

Several workers have suggested that participation in flocks results in an improvement in food gathering. This argument generally has taken two forms, the first being that participants will bene-

fit from the large number of insects flushed during their constant movement. Adherents to this explanation include Neave (1910), Swynnerton (1915), McGregor (1920), and Rand (1936). All of these workers were concerned with flocks of the tropics; this explanation in itself could not account for the existence of flocks during a cold winter season. Furthermore, it appears that many or all of the tropical flocks commented upon include species that seldom, if ever, capture insects on the wing.

Newton (1896), Moreau (1948), and Slud (1960) have all suggested that foraging in a flock results in a more efficient method of finding food, though they present little quantitative information to support such an interpretation. Both Miller (1922) and Short (1961) point out that the spacing maintained in these assemblages lessens the probability that an individual will forage in the same station that another one has just utilized.

Sharpe (1905), Gannon (1934), Wing (1941), and Sedgwick (1949) have hypothesized that a gregarious "urge" forms the basis for these groups. Short (1961) and Moynihan (1962) have clearly pointed out, however, that the presence of such a condition must be explained on the basis of extrinsic factors that would carry a selective advantage.

Lastly, Wynne-Edwards (1962) has proposed that these flocks are epideictic phenomena, regulating the density of insectivorous birds in the woodlands where they are found. While some workers have hypothesized advantages of more than one type for members of mixed flocks, only Moynihan (1962) has stressed the point that the advantages are probably very different for different species and for individuals of the same species at different times. One major purpose of this paper will be to evaluate the conclusions mentioned above in light of the data obtained, keeping Moynihan's cautions in hand.

DESCRIPTION OF THE STUDY AREAS

During the fall and winter from 1963 to 1965 I studied flocks in three forests in Louisiana, with supplementary observations being made in other locations. The principal study areas included:

1. Mature deciduous forest four miles south of the Louisiana State University campus, East Baton Rouge Parish ($30^{\circ}23'N$, $91^{\circ}11'W$). This low flat woodland was covered partially by a few inches of water for at least half of the fall and winter. The most frequent species of trees include Nuttall oak (*Quercus nuttallii*), sweet gum

(*Liquidambar styracifolia*), and hackberry (*Celtis occidentalis*). The tallest trees reach a height of 30 m. American hornbeam (*Carpinus caroliniana*) is a common member of the understory, and blackberry (*Rubus* sp.) and dwarf palmetto (*Sabal minor*) are sporadically prominent in the usually sparse ground cover. Further description of this forest may be found in Morse (1967a).

2. Mixed pine-deciduous forest three miles northeast of Satsuma, Livingston Parish ($30^{\circ}34'N$, $90^{\circ}51'W$). Large parts of this area also were flooded during much of the fall and winter. A deciduous forest covers its lower parts, and Water-oak (*Quercus nigra*) is the principal species. Scattered southern magnolia (*Magnolia grandiflora*), beech (*Fagus grandifolia*), and chestnut-oak (*Quercus prinus*) occur through slightly higher parts. American hornbeam is a common member of the understory while dwarf palmetto is the most prominent species in the ground cover. On ground not subject to regular flooding, loblolly and spruce pines (*Pinus taeda* and *P. glabra*) predominate. Tree cover in this area is approximately 50% coniferous and 50% deciduous, and since the pines grow on many small elevated hummocks in the tract, clumping of tree species is not marked. The tallest trees reach a height of 30 m.

3. Longleaf pine forest three miles west of Fluker, Tangipahoa Parish ($30^{\circ}51'N$, $91^{\circ}28'W$). This is a pure stand of longleaf pine (*Pinus australis*) 15–18 m in height, with blackjack oak (*Quercus marilandica*) forming a scattered understory. Further description of this forest and the one at Satsuma may be found in Morse (1967b).

In addition to these three plots, observations were taken less frequently in two other localities. One was a pine-deciduous forest approximately three km north of study area 2, which was similar to the main area, except that the ratio of trees was approximately 75% coniferous to 25% deciduous. Greenbriar (*Smilax* sp.) was prominent in the understory here. The other was a riparian woodland along the east bank of the Mississippi River on the west edge of the campus of Louisiana State University, Baton Rouge ($30^{\circ}24'N$, $91^{\circ}11'W$). The principal species in this forest were cottonwood (*Populus deltoides*) and willows (*Salix* sp.).

During the fall and winter of 1965 to 1968 I studied flocks at Cedarville State Forest, Brandywine, Prince George's Co., Maryland ($38^{\circ}38'N$, $76^{\circ}49'W$). Three different habitats were investigated there.

1. Deciduous forest. This is principally a stream bottom association dominated by tall sweet gums and tulip-poplars (*Liriodendron tulipifera*), which in some instances reach a height of over 30 m, and somewhat shorter red maples (*Acer rubrum*). American holly (*Ilex opaca*) is abundant in the understory.

2. Mixed pine-deciduous forest. Most of this forest is approximately 50% scrub pine (*Pinus virginiana*) and 50% mixed deciduous species. Principal deciduous species include white, willow, and scarlet oak (*Quercus alba*, *Q. phellos*, and *Q. coccinea*) and pignut (*Carya glabra*). This forest averages 20 m in height.

3. Scrub pine forest. Most of the trees in this forest are 15–20 m in height, and the growth is quite dense. Except where minor man-made disturbances appear, few other species of trees are to be found.

In addition, a plantation of loblolly pines was also studied at Cedarville, but not enough observations were made there to permit quantitative description.

In the summers of 1962 to 1968 I studied flocks on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln Co., Maine (43°56'N, 69°24'W). Hog Island is 132 ha in size, and lies immediately adjacent to the mainland. It is largely covered with spruce (*Picea rubens* and *P. glauca*) 18–25 m in height, except for one section of several hectares consisting principally of white birches (*Betula papyrifera*) 15–18 m in height, which in addition to the spruce forest was the subject of intensive study. A further description of Hog Island may be found in Morse (1967a, c, 1968). Supplementary observations were made in mixed coniferous-deciduous forests on the adjacent mainland.

Further observations were made at and around Webster, Androscoggin Co., Maine, (44°04'N, 70°05'W) in December and January, 1963–68, in coniferous, mixed, and deciduous woodlands. In each instance the principal coniferous species were white pine (*Pinus strobus*) and balsam fir (*Abies balsamea*), and the principal deciduous species were red maple, red oak (*Quercus rubra*), white birch, gray birch (*Betula populifolia*), and quaking aspen (*Populus tremuloides*).

METHODS

Several types of data were obtained. First, information on the location and manner of foraging of the participants was taken following that of Gibb (1954, 1960), with the habitat being divided into a number of stations on the basis

of height and part of foliage (trunks, tips of foliage, etc.), 5 min or more after approaching a group each bird was recorded where first observed while foraging. Efforts were taken to avoid making more than one period of observation on a bird during a day or more than two during a period of a week. Since most birds were unmarked, it is possible that individuals were counted twice in a day upon rare occasions. If a flock was observed for 15 min or longer, a count was made of all species observed and the numbers of each in the group. Species that showed a tendency to participate in these groups were counted each time that they were seen either in or away from a flock. Censuses were taken to determine the density and composition of bird life in the different areas studied during the winter. The technique follows that recommended by *Audubon Field Notes* for their yearly winter bird censuses. Briefly, 6 to 8 counts were made of the birds observed on plots of 25 acres (10 ha) or more. The totals were then averaged and calculated in density per 100 acres (40 ha). All hostile interactions and unambiguous joining or following actions were tallied. Data were gathered concerning individual distance and the area occupied by a flock at a given instant. The rate of horizontal movement of flocks that were observed for 30 min or more was determined by pacing the distances traveled during such times. Lastly, any responses to potential predators or responses similar to those given to predators were recorded. In all cases data were collected in the field either with the use of pencil and clipboard or by dictating into a portable tape recorder.

By remaining 25 m or more from individuals during observations, disturbances may be kept to a minimum. If one ventures too close, the result of disturbance is conspicuous, and usually consists of the individuals mobbing the investigator in a manner comparable to the way in which they advertise the presence of a predator not in flight (see Hinde, 1952).

DESCRIPTION OF THE FLOCKS—COMPOSITION

Though in each geographical area the leaders of the flocks were members of the family Paridae and the other species participating belonged to nearly the same families, variations in composition occurred at the species level, and hence I will consider the species compositions and density from each area separately.

Louisiana. In Louisiana flocks usually were formed about Tufted Titmice and/or Carolina Chickadees, with varying numbers of other spe-

TABLE 1. Frequency of presence and abundance of birds in mixed-species flocks in Louisiana.

Species	Habitat					
	Coniferous		Mixed		Deciduous	
	% of Flocks in Which Found	Mean No. When Pres., with S.D.*	% of Flocks in Which Found	Mean No. When Pres., with S.D.	% of Flocks in Which Found	Mean No. When Pres., with S.D.
Red-bellied Woodpecker	45.6	1.2±0.4	42.3	1.4±0.6	43.5	1.5±0.5
Yellow-bellied Sapsucker	8.8	1.2±0.4	19.2	1.0±0.0	17.4	1.3±0.6
Hairy Woodpecker	14.0	1.1±0.3	5.8	1.3±0.6	8.7	1.0±0.0
Downy Woodpecker	35.1	1.3±0.4	48.1	1.2±0.5	78.3	1.3±0.4
Red-cockaded Woodpecker	43.9	1.6±0.6	0.0	—	0.0	—
Carolina Chickadee	86.0	3.6±1.4	98.1	3.3±1.2	82.6	3.6±1.2
Tufted Titmouse	98.2	3.1±1.1	88.5	2.9±1.2	87.0	2.9±1.2
White-breasted Nuthatch	24.6	1.5±0.5	0.0	—	0.0	—
Brown-headed Nuthatch	98.2	5.0±2.3	3.8	3.5±2.1	0.0	—
Brown Creeper	43.9	1.7±1.0	44.2	1.8±1.0	47.8	2.3±1.2
Golden-crowned Kinglet	33.3	2.2±1.8	44.2	2.2±1.3	39.1	2.2±1.6
Ruby-crowned Kinglet	71.9	2.0±1.3	63.5	2.6±2.5	69.6	2.4±2.6
White-eyed Vireo	0.0	—	5.8	1.0±0.0	0.0	—
Orange-crowned Warbler	1.8	3.0±0.0	5.8	1.3±0.6	13.0	1.3±0.6
Myrtle Warbler	38.6	7.8±14.0	23.1	3.8±4.3	65.2	3.3±2.4
Pine Warbler	91.2	5.3±4.1	32.7	1.8±0.9	13.0	2.0±1.0
Number of flocks	57		52		20	
Mean number of individuals/flock	22.8±14.0		12.1± 7.6		13.2± 7.2	

*Mean numbers of individual species in Tables 1-4 refer to mean number when represented in flock. The mean for the total number of flocks observed may be determined by multiplying this figure by the fractional form of the percentages found in each preceding column.

cies associated. The species participating in these flocks are listed in Table 1, along with their frequency in flocks and their mean abundance (including standard deviations) when present. With few exceptions, though the standard deviation is substantial, it is considerably smaller than the mean, serving as an indication of the moderate constancy of numbers of individuals of a species when present in flocks. One major exception is that of the Myrtle Warbler, which often (particularly in the pine forests) displayed a strong tendency to form temporary large groups that often participated only for limited periods of time in the movements of mixed flocks. Attachment of Myrtle Warblers to mixed flocks was not strong, particularly when these birds were present in high densities. The only other exception was the Ruby-crowned Kinglet. When this species arrived in the fall it was gregarious; however, it appeared later in the season to become territorial. Hence, there is a bimodal distribution in the abundance of this species in the flocks, roughly divisible into fall (October-November) and winter (December-January) groups. The densities for these subunits of time are: coniferous forest, 2.1 (26 flocks) in fall and 1.6 (23 flocks) in winter; mixed forest, 3.4 (27 flocks) and 2.0 (14 flocks); and deciduous forest, 3.6 (9 flocks) and 1.2 (6 flocks).

Maryland. The flocks in Maryland showed many similarities to those studied in Louisiana. Tufted Titmice and/or Carolina Chickadees again formed at the core of flocks. Participants and their frequency and abundance in flocks appear in Table 2.

Maine. Data on flocks were gathered in both late summer, at the time that flocks were beginning to form, and in late December and January. In both situations a single species, the Black-capped Chickadee, played a role comparable to that already described for Tufted Titmice and Carolina Chickadees. However, in some other respects the species compositions varied markedly. Hence, these data will be discussed separately.

1. Late summer. In addition to permanent or winter residents a large number of migrants and summer residents joined flocks in late summer (Table 3), and they accounted largely for the differences in size of flocks at the two seasons. The flocks were in the process of formation and fluctuation from late July until early September, when observations were terminated.

2. Winter. In the winter both the number of species and number of individuals in a flock was considerably lower than during the late summer (Table 4). However, all the regular winter members were also represented in the late summer.

Tables 1-4 indicate that there are definite differences in flock composition from habitat to

TABLE 2. Frequency of presence and abundance of birds in mixed species flocks in Maryland.

Species	Coniferous		Mixed		Deciduous	
	% of Flocks in Which Found	Ave. No. When Pres., with S.D.	% of Flocks in Which Found	Ave. No. When Pres., with S.D.	% of Flocks in Which Found	Ave. No. When Pres., with S.D.
Red-bellied Woodpecker	20.8	1.2±0.5	61.7	1.3±0.5	42.1	1.2±0.4
Yellow-bellied Sapsucker	4.7	1.6±0.9	15.0	1.1±0.2	10.5	1.0±0.0
Hairy Woodpecker	0.9	1.0±0.0	23.4	1.2±0.5	8.8	1.0±0.0
Downy Woodpecker	39.5	1.1±0.4	58.3	1.4±0.5	56.2	1.2±0.4
Carolina Chickadee	95.3	5.4±0.9	100.0	5.8±1.2	91.2	5.3±0.9
Tufted Titmouse	56.6	2.6±0.9	88.4	3.2±1.1	77.3	3.1±0.9
White-breasted Nuthatch	7.5	1.5±0.5	38.4	1.8±0.7	19.3	1.5±0.5
Red-breasted Nuthatch	21.7	3.6±1.8	26.7	1.7±0.6	5.2	1.1±0.2
Brown Creeper	43.4	1.2±0.5	75.0	1.2±0.4	31.6	1.3±0.4
Winter Wren	2.8	1.0±0.0	1.6	1.0±0.0	7.0	1.0±0.0
Golden-crowned Kinglet	76.4	3.4±0.9	90.0	3.7±1.1	66.6	3.0±1.1
Ruby-crowned Kinglet	25.5	1.4±0.7	21.6	1.3±0.5	26.9	1.2±0.4
Myrtle Warbler	55.7	1.3±0.6	14.9	1.2±0.3	10.6	1.2±0.3
Pine Warbler	9.5	1.1±0.2	0.0	—	0.0	—
Number of flocks	106		60		57	
Mean number of individuals/flocks	12.8±5.4		17.9±6.8		12.6±5.8	

TABLE 3. Frequency of presence and abundance of birds in mixed species flocks in Maine-summer.

Species	Coniferous		Mixed	
	% of Flocks in Which Found	Ave. No. When Pres., with S.D.	% of Flocks in Which Found	Ave. No. When Pres., with S.D.
Hairy Woodpecker	17.9	1.2±0.4	31.4	1.1±0.3
Downy Woodpecker	14.3	1.3±0.4	45.7	1.2±0.4
Black-capped Chickadee	82.1	5.7±2.3	74.3	4.2±1.6
Red-breasted Nuthatch	78.6	3.5±2.2	80.0	2.8±1.6
Brown Creeper	35.7	1.4±0.9	31.4	1.6±0.9
Winter Wren	10.7	1.0±0.0	22.9	1.3±0.4
Golden-crowned Kinglet	57.1	4.1±2.0	57.1	3.6±1.9
Red-eyed Vireo	0.0	—	8.6	2.0±0.8
Black and White Warbler	46.4	1.6±0.7	60.0	2.0±1.0
Parula Warbler	17.9	1.0±0.0	34.3	2.0±1.1
Yellow Warbler	14.3	1.5±0.5	11.4	2.0±1.2
Magnolia Warbler	35.7	1.1±0.3	54.3	1.9±1.6
Myrtle Warbler	28.6	1.8±0.8	28.6	1.8±1.4
Black-throated Green Warbler	46.4	2.2±1.0	62.9	2.3±1.6
Blackburnian Warbler	35.7	1.5±0.7	28.6	2.9±1.3
Chestnut-sided Warbler	3.6	1.0±0.0	8.6	1.3±0.5
Bay-breasted Warbler	0.0	—	5.7	2.0±1.0
Ovenbird	0.0	—	8.6	1.0±0.0
Yellowthroat	3.6	1.0±0.0	20.0	1.9±1.0
Canada Warbler	7.1	1.0±0.0	25.7	2.4±0.8
American Redstart	7.1	1.0±0.0	8.6	2.0±0.8
Baltimore Oriole	0.0	—	5.7	1.0±0.0
Brown-headed Cowbird	0.0	—	8.6	1.0±0.0
Number of flocks	28		35	
Mean number of individuals/flock	14.8±5.4		16.4±8.7	

habitat and geographic area to geographic area. The number of species participating in flocks in Louisiana was slightly larger than in Maryland, though the two areas shared most species (12 of 16). The major difference is the result of a few species found largely or completely in the longleaf pine forest, plus two species occurring uncommonly toward the northern end of their win-

tering range in Louisiana (White-eyed Vireo and Orange-crowned Warbler). Average sizes of flocks in Louisiana and Maryland were quite comparable in four of the six habitats, the exceptions being found in the single habitats supporting the lowest density in both areas, the longleaf pine forest in Louisiana and mixed forest in Maryland.

TABLE 4. Frequency of presence and abundance of birds in mixed-species flocks in Maine-winter.

Species	Habitat					
	Coniferous		Mixed		Deciduous	
	% of Flocks in Which Found	Ave. No. When Pres., with S.D.	% of Flocks in Which Found	Ave. No. When Pres., with S.D.	% of Flocks in Which Found	Ave. No. When Pres., with S.D.
Hairy Woodpecker	—	—	4.2	1.0±0.0	—	—
Downy Woodpecker	—	—	16.7	1.3±0.4	27.3	1.7±0.5
Black-capped Chickadee	92.9	6.8±2.2	95.8	7.7±2.6	90.9	7.6±2.0
Boreal Chickadee	7.1	1.0±0.0	4.2	1.0±0.0	—	—
White-breasted Nuthatch	7.1	1.0±0.0	29.2	1.6±0.5	27.3	1.3±0.5
Red-breasted Nuthatch	78.6	1.1±0.3	33.3	1.5±0.5	—	—
Brown Creeper	21.4	1.0±0.0	29.2	1.1±0.4	27.3	1.3±0.5
Golden-crowned Kinglet	50.0	3.4±1.5	75.0	2.8±0.8	72.7	2.8±1.6
Number of flocks	14		24		11	
Mean number of individuals/flock	9.2±4.1		10.8±3.6		10.1±3.9	

In the flocks studied in late summer in Maine there were many species involved that migrated from that area and were not represented in winter flocks; they made up 17 of the 23 species recorded in the flocks, with 13 of the 17 being wood warblers. The 6 species that remained, plus a few others not recorded in the summer, made up the wintering flocks, which were lower in both numbers of species and in individuals than other flocks studied. Also, winter flocks in Maine were dominated in numbers by one species, the only case studied where this situation occurred. This species, the Black-capped Chickadee, made up roughly three-fourths of the individuals in flocks. Five of the 8 species recorded in flocks from Maine in the winter were represented in the winter flocks of all three geographic areas. A sixth, the Red-breasted Nuthatch, was recorded from Maryland, and seen upon occasion in flocks in Louisiana, though not in any of the ones reported upon in this study. The Black-capped Chickadee is closely related to the Carolina Chickadee, while the last species recorded in Maine, the uncommon Boreal Chickadee, is a totally new entity. Thus, these data point out the great similarity in the taxonomic composition of flocks over a wide geographic area.

A comparison of the coefficients of variation (S. D. \times 100/mean) of the flocks in the different geographical areas indicates that the absolute variation increased in an approximately linear fashion with the mean (Fig. 1). However, these values are greater in Louisiana than in Maryland or in Maine in winter (Fig. 1). The high variability in Louisiana of numbers of Myrtle Warblers and, to a lesser extent, Ruby-crowned Kinglets is responsible for much of this difference where it occurs. In Maine in late summer vari-

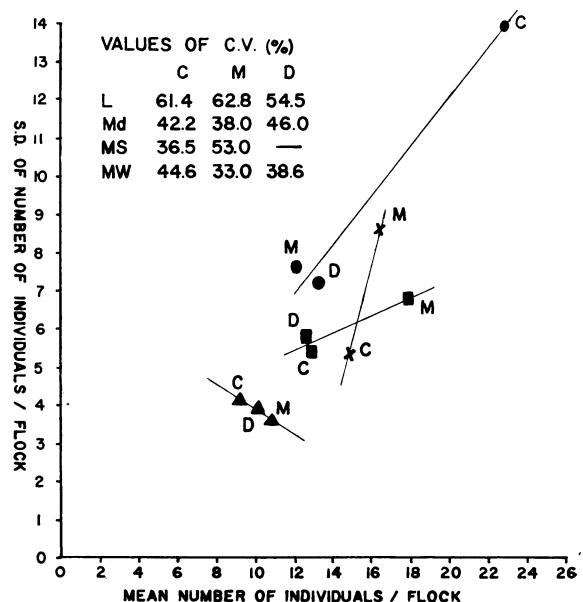


FIG. 1. Relation between mean numbers of individuals per flock and standard deviation of number of individuals per flock. Inset lists coefficients of variation (C.V.) of flock size. Circles = Louisiana (L), squares = Maryland (Md.), X's = Maine in summer (MS), and triangles = Maine in winter (MW).

ability was considerably higher in the mixed forest than in the spruce forest. Migrants were much commoner in flocks of the mixed forest than in those of the spruce forest, and variability in numbers was high in these species. The negative slope of the winter data from Maine runs counter to those from the other areas. However, the range of means in this case is considerably lower than that from the other areas. The sample size is small also, and it probably would be unwise to

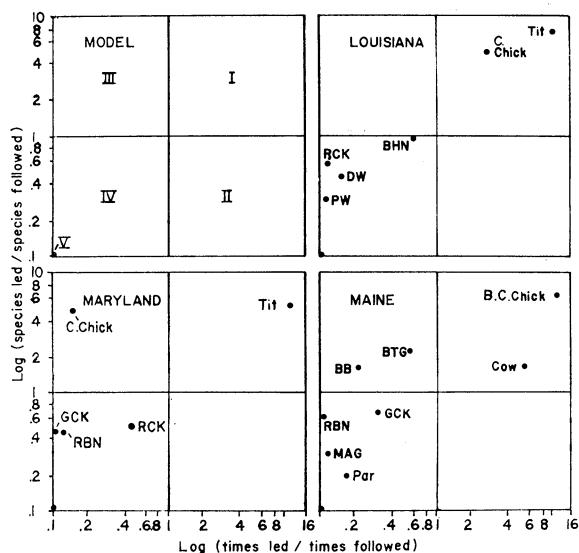


FIG. 2. Categories of flock members depending upon their tendency to lead and to follow other species. Model in upper left, determinations from three geographic areas in upper right and bottom. DW = Downy Woodpecker, B. C. Chick = Black-capped Chickadee, C. Chick = Carolina Chickadee, Tit = Tufted Titmouse, RBN = Red-breasted Nuthatch, BHN = Brown-headed Nuthatch, GCK = Golden-crowned Kinglet, RCK = Ruby-crowned Kinglet, Par = Parula Warbler, Mag = Magnolia Warbler, BTG = Black-throated Green Warbler, BB = Blackburnian Warbler, PW = Pine Warbler, Cow = Brown-headed Cowbird. In addition, the following species were placed in Category V: Louisiana—Red-cockaded Woodpecker, Brown Creeper, Golden-crowned Kinglet, White-eyed Vireo, Orange-crowned Warbler, Myrtle Warbler. Maryland—Red-bellied Woodpecker, Yellow-bellied Sapsucker, Downy Woodpecker, White-breasted Nuthatch, Brown Creeper, Myrtle Warbler. Maine in summer—Hairy Woodpecker, Downy Woodpecker, Brown Creeper, Winter Wren, Ruby-crowned Kinglet, Red-eyed Vireo, Black-and-White Warbler, Yellow Warbler, Myrtle Warbler, Chestnut-sided Warbler, Ovenbird, Yellowthroat, Canada Warbler, American Redstart.

speculate upon this matter until additional data are gathered.

ROLES OF MEMBERS

It is of convenience to categorize members according to the roles that they play in flocks. While several attempts have been devised to classify the status of birds in flocks (Winterbottom, 1943, 1949; Davis, 1946; Moynihan, 1962), none is truly operational under the conditions that I experienced. Hence, I have organized a classification (Fig. 2) in which species are categorized for two parameters, the ratio of species led to species followed and the ratio of times that a species led to the times that followed. These data were collected only in unambiguous situations. At these

times the action of an individual (the follower) immediately followed that of another (the leader) and was oriented in its direction. Species are placed in categories I to V, with I representing the true leaders, II and III the secondary leaders, IV the usual followers, and V of the absolute followers. No species fit into category II in this study. In only one case where a large sample exists is there a difference in status of a species in different geographic areas. Where small sample sizes exist, it would be possible for species placed initially in Category V to move to another category, most likely Category IV. However, some species appeared in Category V in all the areas studied, suggesting that Category V represents more than an artifact of Category IV. Categories I and II are roughly similar to Moynihan's "passive nuclear species," III and IV to his "active nuclear species," and V to his "attendant" species.

Since only unambiguous observations of leading and following were gathered, they represent ratios rather than an absolute frequency of the behavioral patterns. Data from the various habitats are combined in each geographic region.

Louisiana. Only the chickadee and titmouse fit into Category I (true leaders) (Fig. 2). In inter-specific actions, with one exception chickadees followed only titmice; titmice only followed chickadees. Chickadees displayed a stronger tendency to follow titmice than titmice did to follow chickadees. The vast majority of these actions involved titmice and/or chickadees (Table 5).

Maryland. Similarly to Louisiana, Tufted Titmice and Carolina Chickadees are the only two species that lead other species regularly (Table 6). However, due to its particularly strong tendency to follow titmice, the Carolina Chickadee qualifies for Category III (secondary leader) (Fig. 2). Nevertheless, the titmice did not occur in all flocks (Table 2), and flocks lacking them contained a considerable number of species other than chickadees. The chickadees displayed a nearly complete lack of following responses toward other flock members.

Maine. The vast majority of following responses in flocks during late summer are ones directed toward Black-capped Chickadees by other species (Table 7). The Black-capped Chickadee is the only species fitting into Category I (true leader) in the areas studied. Though a great majority of following actions in these flocks were thus directed, occasional actions were noted in late summer that were extremely complicated and perhaps atypical of usual situations. The phenomenon

TABLE 5. Interspecific leading and following in flocks—Louisiana.

Species Leading	Species Following															Total
	Downy Woodpecker	Red-cockaded Woodpecker	Carolina Chickadee	Tufted Titmouse	Brown-headed Nuthatch	Brown Creeper	Golden-crowned Kinglet	Ruby-crowned Kinglet	White-eyed Vireo	Orange-crowned Warbler	Myrtle Warbler	Pine Warbler	Total	Total	Total	
Downy Woodpecker.....	X															1
Red-cockaded Woodpecker.....		X														
Carolina Chickadee.....	3	2														98
Tufted Titmouse.....	4		29	X												134
Brown-headed Nuthatch.....		1			X											20
Brown Creeper.....						X										
Golden-crowned Kinglet.....					5		X									
Ruby-crowned Kinglet.....							X									
White-eyed Vireo.....								X								
Orange-crowned Warbler.....									X							
Myrtle Warbler.....										X						
Pine Warbler.....											X					
Total.....	7	3	30	12	29	1	12	69	1	1	65	32	262			

TABLE 6. Interspecific leading and following in flocks—Maryland.

Species Leading	Species Following															Total
	Red-bellied Woodpecker	Yellow-bellied Sapsucker	Downy Woodpecker	Carolina Chickadee	Tufted Titmouse	White-breasted Nuthatch	Red-breasted Nuthatch	Brown Creeper	Golden-crowned Kinglet	Ruby-crowned Kinglet	Myrtle Warbler	Total	Total	Total	Total	
Red-bellied Woodpecker.....	X															
Yellow-bellied Sapsucker.....		X														
Downy Woodpecker.....	2		2		X											
Carolina Chickadee.....				53	X											24
Tufted Titmouse.....			3		X	7										107
White-breasted Nuthatch.....						X	4									
Red-breasted Nuthatch.....							X	16								2
Brown Creeper.....								X	5							
Golden-crowned Kinglet.....									X	20						2
Ruby-crowned Kinglet.....										X	1					1
Myrtle Warbler.....	2	2	5	53	8	4	20	7	32	2	1	X				136
Total.....																

of chickadees following the parasitic Brown-headed Cowbird, for instance, appeared to result from the chickadees being attracted by the loud notes made by young cowbirds being fed by adult Black-throated Green Warblers, the latter species being one that in turn often followed the chickadees. Occasionally, other species joined family groups of warblers, whose young were still begging loudly. Significantly, Black-throated Green Warblers, Blackburnian Warblers, and cowbirds all fit into Category III (secondary leaders) (Fig. 2).

In winter, insufficient evidence on interspecific joining and following activities was gathered to

assign members to particular categories based on the criteria used above, partly because of the overwhelming predominance of Black-capped Chickadees in the flocks at this season (Table 4). Six of the 49 flocks tallied (12.2%) contained only Black-capped Chickadees. However, observations of winter flocks suggested that the roles filled by the species found (list of species in Table 4) were similar to those that they occupied during the late summer. The Black-capped Chickadees thus would be the only species belonging in Category I (true leaders), with the possible exception of the rarely encountered Boreal Chickadee. White- and Red-breasted nuthatches and

TABLE 7. Interspecific leading and following in flocks—Maine in summer.

Species Leading	Species Following																						
	Hairy Woodpecker	Downy Woodpecker	Black-capped Chickadee	Red-breasted Nuthatch	Brown Creeper	Winter Wren	Golden-crowned Kinglet	Ruby-crowned Kinglet	Red-eyed Vireo	Black-and-white Warbler	Parula Warbler	Yellow Warbler	Magnolia Warbler	Myrtle Warbler	Black-throated Green Warbler	Blackburnian Warbler	Chestnut-sided Warbler	Oven-bird	Yellow-throat	Canada Warbler	American Redstart	Brown-headed Cowbird	Total
Hairy Woodpecker.....	X																						
Downy Woodpecker.....		3																					
Black-capped Chickadee.....			X																				
Red-breasted Nuthatch.....				5																			
Brown Creeper.....																							
Winter Wren.....																							
Golden-crowned Kinglet.....																							
Ruby-crowned Kinglet.....																							
Red-eyed Vireo.....																							
Black-and-white Warbler.....																							
Parula Warbler.....																							
Yellow Warbler.....																							
Magnolia Warbler.....																							
Myrtle Warbler.....																							
Black-throated Green Warbler.....																							
Blackburnian Warbler.....																							
Chestnut-sided Warbler.....																							
Oven-bird.....																							
Yellow-throat.....																							
Canada Warbler.....																							
American Redstart.....																							
Brown-headed Cowbird.....																							
Total.....	3	6	9	47	1	3	2	9	1	13	7	2											

TABLE 7. Interspecific leading and following in flocks—Maine in summer (cont.).

Species Leading	Species Following										
	Magnolia Warbler	Myrtle Warbler	Black-throated Green Warbler	Blackburnian Warbler	Chestnut-sided Warbler	Oven-bird	Yellow-throat	Canada Warbler	American Redstart	Brown-headed Cowbird	Total
Hairy Woodpecker.....											
Downy Woodpecker.....		7									
Black-capped Chickadee.....		1									
Red-breasted Nuthatch.....			4								
Brown Creeper.....				14							
Winter Wren.....					5						
Golden-crowned Kinglet.....						1					
Ruby-crowned Kinglet.....							1				
Red-eyed Vireo.....								5			
Black-and-white Warbler.....									2		
Parula Warbler.....										6	
Yellow Warbler.....										6	
Magnolia Warbler.....											1
Myrtle Warbler.....											4
Black-throated Green Warbler.....											9
Blackburnian Warbler.....											10
Chestnut-sided Warbler.....											133
Oven-bird.....											2
Yellow-throat.....											2
Canada Warbler.....											1
American Redstart.....											1
Brown-headed Cowbird.....											163
Total.....	9	4	15	9	5	2	2	6	2	6	133

TABLE 8. Percentages and numbers (in parentheses) of individuals belonging to flocking and nonflocking species—Louisiana and Maryland.

Geographic Area	Category	Coniferous		Mixed		Deciduous	
		%	Mean No./100 Acres (40 ha)	%	Mean No./100 Acres (40 ha)	%	Mean No./100 Acres (40 ha)
Louisiana	Flocking	79.5	52.4	42.2	96.7	42.5	144.0
Louisiana	Nonflocking	20.5	13.5	57.8	132.5	57.5	194.9
Maryland	Flocking	85.6	82.5	97.5	38.8	93.7	65.2
Maryland	Nonflocking	14.4	13.9	2.5	1.0	6.3	4.4

Golden-crowned Kinglets probably belong in Category IV (usual followers) and the remainder in Category V (absolute followers).

The number of species regularly leading the flocks is small, in each geographic area being comprised of one or two species from the family Paridae. In all but the winter flocks in Maine, these leaders do not make up a large percentage of the flock. In Maine the average number of leaders in winter is higher than in summer, but the winter average is comparable to the combined totals of Carolina Chickadees and Tufted Titmice in Louisiana and Maryland. Hence, the major difference in size of winter flocks in Maine is the result of the difference in numbers of followers rather than leaders.

NUMBERS OF FLOCKING AND NONFLOCKING SPECIES IN THE DIFFERENT HABITATS

Note in Table 8 that the relative abundance (in per cents) of flocking species (Categories I–V of Fig. 2) and species not participating in these groups, computed from censuses of density and composition (Table 9), differed in the study areas in Louisiana. A much higher percentage of individuals belonged to flock-participating species in the coniferous forest, the area of lowest overall bird density, than in the other two areas. In the latter two areas, ones of considerably higher overall density, there is no further sign of a trend.

The data from Maryland (Tables 8 and 10) are comparable to those from Louisiana. The highest percentage of individuals belonging to flock-participating species again appeared in the area of lowest overall bird density, the mixed forest. However, the percentage of nonparticipating species in the area of intermediate overall density, the deciduous forest, was nearly as low. Nonparticipating species in the area of highest overall density, the coniferous forest, were somewhat more common. However, they constituted a smaller percentage of the total avian population than did the nonparticipating species in the area of lowest overall density in Louisiana.

TABLE 9. Density (per 100 acres or 40 ha) of birds in study areas—Louisiana.

Species	Coniferous	Mixed	Deciduous
Red-tailed Hawk.....	—	0.5	—
Sparrow Hawk.....	1.7	—	—
Bobwhite.....	0.3	—	—
Yellow-shafted Flicker.....	0.3	2.9	3.3
Pileated Woodpecker.....	—	2.4	—
Red-bellied Woodpecker.....	3.0	10.0	12.0
Red-headed Woodpecker.....	—	11.0	—
Yellow-bellied Sapsucker.....	0.3	5.7	6.0
Hairy Woodpecker.....	0.3	0.5	2.7
Downy Woodpecker.....	0.3	5.2	9.3
Red-cockaded Woodpecker.....	1.3	—	—
Eastern Phoebe.....	—	3.8	5.3
Blue Jay.....	1.3	4.3	2.7
Common Crow.....	—	0.5	—
Carolina Chickadee.....	4.7	19.0	18.7
Tufted Titmouse.....	7.0	14.0	14.7
White-breasted Nuthatch.....	0.7	—	—
Brown-headed Nuthatch.....	17.2	—	—
Brown Creeper.....	2.3	4.7	5.3
House Wren.....	—	1.0	—
Winter Wren.....	—	1.4	—
Carolina Wren.....	1.7	26.7	26.7
Mockingbird.....	—	2.9	6.0
Catbird.....	—	1.0	—
Brown Thrasher.....	—	4.3	0.3
Robin.....	0.7	6.7	37.3
Hermit Thrush.....	0.3	1.0	2.0
Eastern Bluebird.....	0.7	—	—
Golden-crowned Kinglet.....	1.3	11.9	8.0
Ruby-crowned Kinglet.....	3.7	12.4	14.7
White-eyed Vireo.....	—	1.0	—
Orange-crowned Warbler.....	—	1.4	—
Myrtle Warbler.....	1.0	1.9	49.3
Pine Warbler.....	9.3	9.1	3.3
Yellowthroat.....	—	—	1.3
House Sparrow.....	—	—	1.3
Redwinged Blackbird.....	—	—	20.0
Common Grackle.....	—	—	4.0
Cardinal.....	0.3	16.2	36.7
American Goldfinch.....	0.3	—	—
Rufous-sided Towhee.....	0.3	6.2	—
Bachman's Sparrow.....	4.3	—	—
Slate-colored Junco.....	1.0	—	—
White-throated Sparrow.....	0.3	39.6	46.7
Swamp Sparrow.....	—	—	1.3
Totals.....	65.9	229.2	338.9

No data were gathered in Maine in late summer, because the density and composition of bird populations were constantly shifting due to progressive disappearance of summer residents and appearance of migrants. Furthermore, some indi-

TABLE 10. Density (per 100 acres or 40 ha) of birds in study areas—Maryland.

Species	Coniferous	Mixed	Deciduous
Yellow-shafted Flicker.....	0.6	—	—
Red-bellied Woodpecker.....	2.3	3.4	4.8
Yellow-bellied Sapsucker.....	—	0.4	—
Hairy Woodpecker.....	—	1.0	2.8
Downy Woodpecker.....	4.9	1.4	3.2
Blue Jay.....	4.9	0.4	—
Common Crow.....	0.6	—	—
Carolina Chickadee.....	28.6	11.6	18.0
Tufted Titmouse.....	6.0	5.4	12.0
White-breasted Nuthatch.....	0.9	2.4	4.8
Red-breasted Nuthatch.....	21.5	2.0	0.8
Brown Creeper.....	3.4	1.6	2.0
Carolina Wren.....	1.4	0.6	1.2
Golden-crowned Kinglet.....	14.9	9.6	16.8
Cardinal.....	0.6	—	1.2
American Goldfinch.....	—	—	2.0
White-winged Crossbill.....	2.0	—	—
Rufous-sided Towhee.....	0.6	—	—
Slate-colored Junco.....	2.3	—	—
White-throated Sparrow.....	0.9	—	—
Totals.....	96.4	39.8	69.6

viduals held territories at the beginning of the study, then gave them up and joined flocks later in the summer.

Neither were these censuses conducted during the winter in Maine. Nevertheless, it is apparent that the frequency of nonparticipating species then is extremely low, probably lower than in Maryland.

TENDENCIES FOR POTENTIALLY FLOCKING SPECIES TO BE FOUND IN FLOCKS

Individuals of species that participate in flocks are not always found with these groups. In Louisiana and Maryland I attempted to determine whether tendencies of individuals to participate differed in the habitats studied.

On as many field trips as possible tallies were kept of each individual or group of individuals in Category IV (usual follower) and Category V (absolute follower) seen in and away from flocks. Individuals in Categories I (primary leader) and II–III (secondary leader) were not included in this tabulation, since they almost invariably would be found in the center of a mixed group. The relative frequency of observations made in flocks (expressed as a percentage of the total number of observations) appears in Figs. 3 and 4 for each species tallied five or more times in each habitat. No attempt is made to distinguish between individuals and small groups of a species. Hence, any observation might denote a single individual of a species or two or more individuals of that species found together.

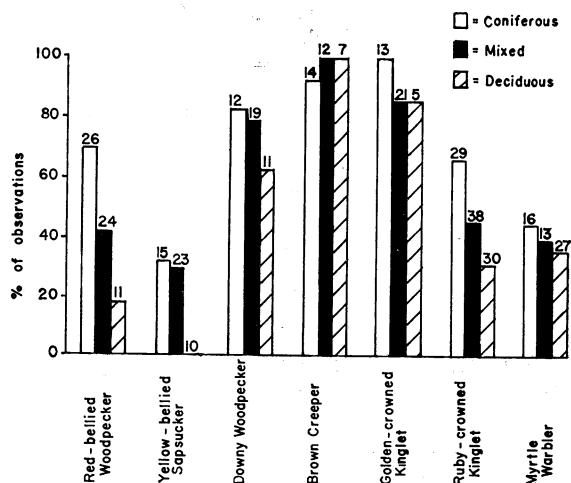


FIG. 3. Percentages of time that observations of species were made while in flocks—Louisiana. Total number of observations appears above each habitat for each species.

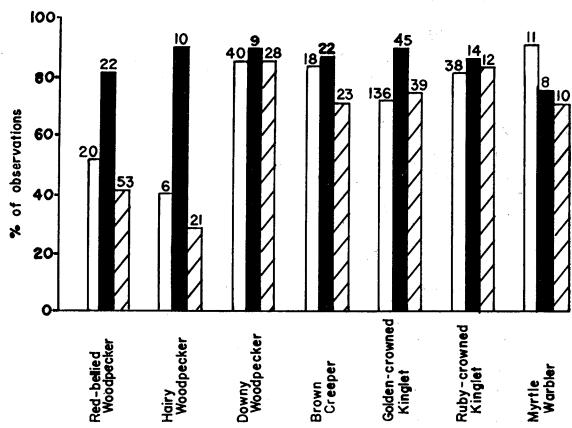


FIG. 4. Percentages of times that observations of species were made while in flocks—Maryland. Total number of observations appears above each habitat for each species. Habitats coded as in Fig. 3.

In most species trends toward an inverse correlation were noted between the tendency of individuals to participate in flocks and the total density of birds found in a habitat (Tables 9 and 10). In Louisiana, a comparison of the three habitats (Table 15) in a Friedman two-way analysis of variance indicates significant differences in these tendencies ($X_r^2 < 0.02$). Only one exception to the general trend was noted, that being the Brown Creeper, which in all habitats displayed a very high tendency to participate in flocks.

In Maryland, the data are not as clearly cut, but in six of seven species the tendency to participate in flocks was highest in the habitat with the lowest overall density of birds (mixed forest) (Fig. 4). The Myrtle Warbler, not normally one of the more conspicuous elements of these flocks,

constituted the sole exception. A Friedman two-way analysis of variance indicates that the groups differ significantly in this regard ($X_r^2 < 0.05$). Differences between tendencies to participate in coniferous and deciduous forests are equivocal.

In a majority of cases where the tendencies of a species to participate in flocks in the two geographic areas were compared, these tendencies were more marked in Maryland, this relationship appearing in four of the six species common to both areas. The two species for which this relation does not hold are the Golden-crowned Kinglet and Brown Creeper. Both are sporadic winter residents in the southern part of Louisiana (Lowery, 1960), and there is a possibility that in unfamiliar habitats an increased tendency to participate may exist. Two other pieces of information support such an explanation. Brown-headed Nuthatches were rare in the mixed forest area studied in Louisiana. All three times that they were seen there they were participating in flocks, while in their accustomed habitat, the longleaf pine forest, they frequently appeared away from mixed flocks (Morse, 1967b). Similarly, all three times that Pine Warblers were seen in the deciduous forest in Louisiana, which is several km from any pine forest, their usual habitat, they were participating in mixed flocks. While usually seen with flocks in the other habitats they were not infrequently found away from them.

Though data from Maine during the winter do not permit detailed comparison, the trend suggests that tendencies to participate in mixed flocks are no higher in the species common to the other areas (Downy Woodpecker, creeper, Golden-crowned Kinglet) than in Maryland. Such information was not gathered in Maine during the summer due to the constant change in flock compositions.

Since I did not sample foliage and stomach contents intensively, it was impossible usually to verify directly tendencies to participate in flocks with level of food supply. However, a bumper crop of longleaf pine seeds occurred during the winter of 1964-65 in Louisiana, and limited collections of flocking species were made for stomach analysis two or more km away from the study area. Of the flock members in the longleaf pine forest (Table 1), only the Brown-headed Nuthatch upon occasion fed nearly exclusively on pine seeds. This was verified both by foraging observations and by stomach contents (Table 11), the vegetable elements being almost totally composed of pine seeds. During the period of maximum seed abundance, Brown-headed Nuthatches demonstrated a considerably reduced tendency to par-

TABLE 11. Percentage of vegetable matter (by volume) in stomachs of species collected in longleaf pine forest in Louisiana during fall and winter of 1964-65.

Species	23 Oct.	21 Nov.	16 Dec.	11 Jan.	7 Feb.
Carolina Chickadee	—	50 (1)*	85 (2)	—	40 (4)
Tufted Titmouse	—	40 (1)	85 (3)	85 (3)	40 (2)
Brown-headed Nuthatch	50 (1)	99 (5)	90 (3)	75 (6)	65 (6)
Pine Warbler	0 (1)	25 (4)	—	45 (5)	5 (5)

*The number of specimens examined is enclosed in parentheses.

ticipate in mixed flocks (Morse, 1967b); a tendency was not observed in other species at this time.

HOSTILE INTERACTIONS

Hostile interactions, including supplanting attacks (Hinde, 1952) chases, and fights, were recorded whenever observed. Data from separate habitats in each geographic area are lumped in most cases.

One point emerging from these data in each geographical area and in each season is that the majority of all such interactions occur among individuals of the same species, from 56.9% intra-specific encounters in Louisiana to 85.9% intra-specific encounters in Maryland (Tables 12-15), with the range being wider among different populations of a single species. If all species occurred in equal numbers in flocks, one might expect more interactions with other members of a species than with members of any other species, since the members of that species, if monomorphic, are usually thought to forage more like each other than like individuals of other species. [This premise may not always be entirely valid; it has been shown by Kilham (1965), Ligon (1968), and Morse (1968) that different sexes of relatively monomorphic species may forage in rather different parts of the habitat. Also, individual variation in foraging has not yet been adequately explored, though I am currently investigating this subject.] If we do accept the assumption, an individual in a flock would have a greater opportunity of meeting another member of its species than an individual of any other species in a flock, unless spacing is exaggerated within the species. However, even in the case of a species seldom occurring in high numbers and thus probably meeting other species more often than other individuals of its species (e.g., Black-and-White Warbler) more intraspecific encounters occurred than with any other single species, suggesting that the data obtained were the result of more specific relationships than random meeting. In the majority of instances the number of intraspecific hostile inter-

TABLE 12. Hostile interactions in flocks—Louisiana.

Species Attacked	Species Attacking														Total
	Red-bellied Woodpecker	Yellow-bellied Sapsucker	Downy Woodpecker	Carolina Chickadee	Tufted Titmouse	White-breasted Nuthatch	Brown-headed Nuthatch	Brown Creeper	Golden-crowned Kinglet	Ruby-crowned Kinglet	Orange-crowned Warbler	Myrtle Warbler	Pine Warbler		
Red-bellied Woodpecker.....	1														2
Yellow-bellied Sapsucker.....		1													2
Downy Woodpecker.....		1	1												2
Carolina Chickadee.....				29											39
Tufted Titmouse.....					19	4									21
White-breasted Nuthatch.....					1	1									4
Brown-headed Nuthatch.....						6									14
Brown Creeper.....							3	3							3
Golden-crowned Kinglet.....								3							22
Ruby-crowned Kinglet.....									5						6
Orange-crowned Warbler.....										16					0
Myrtle Warbler.....	2	2								4					13
Pine Warbler.....					4						1				16
Total.....	3	1	2	33	30	6	14	3	5	20	2	13	12	144	

TABLE 13. Hostile interactions in flocks—Maryland.

Species Attacked	Species Attacking														Total
	Red-bellied Woodpecker	Hairy Woodpecker	Downy Woodpecker	Carolina Chickadee	Tufted Titmouse	White-breasted Nuthatch	Red-breasted Nuthatch	Brown Creeper	Golden-crowned Kinglet	Ruby-crowned Kinglet	Orange-crowned Warbler	Myrtle Warbler	Pine Warbler		
Red-bellied Woodpecker.....				1											1
Hairy Woodpecker.....				2											2
Downy Woodpecker.....		1													4
Carolina Chickadee.....				3											109
Tufted Titmouse.....			1			99	4								21
White-breasted Nuthatch.....						21									16
Red-breasted Nuthatch.....					1										14
Brown Creeper.....				7			3								7
Golden-crowned Kinglet.....			2				12								71
Ruby-crowned Kinglet.....							16								4
Myrtle Warbler.....	1	2	5	107	27	23	13	4	55	9	2				248

actions of a species was greater than its interactions with the rest of the species combined. This represents a disproportionately high frequency of intraspecific encounters, since any species usually represented a relatively small percentage of a flock, with the exception of chickadees in winter flocks in Maine.

Since I did not observe each hostile interaction that occurred during a particular period of time in a flock, I have evaluated the frequency of this behavior by calculating the number of interactions observed per foraging observation. Numbers of foraging observations thus serve as an index of

the relative amount of time spent observing a species. Tables 16–19 give the number of intra- and interspecific hostile interactions per foraging observation of species that in Tables 12–15 tallied 5 or higher in the horizontal totals column. Foraging data were not gathered during all field trips in Louisiana; hence, Table 16 is incomplete in this regard.

The data from Louisiana (Table 16) reveal a tendency for the leaders of flocks to direct a high percentage of their actions toward members of their own species, and for those actions directed at other species to be largely in the nature of sup-

TABLE 14. Hostile interactions in flocks—Maine in summer.

Species Attacked	Species Attacking											
	Hairy Woodpecker	Downy Woodpecker	Black-capped Chickadee	Red-breasted Nuthatch	Brown Creeper	Winter Wren	Golden-crowned Kinglet	Red-eyed Vireo	Black-and-white Warbler	Parula Warbler	Yellow Warbler	Magnolia Warbler
Hairy Woodpecker.....	—	—	—	—	—	—	—	—	—	—	—	—
Downy Woodpecker.....	—	—	—	—	—	4	—	—	—	—	—	—
Black-capped Chickadee.....	—	—	1	—	—	—	—	—	—	—	—	—
Red-breasted Nuthatch.....	—	—	—	—	—	—	—	—	—	—	—	—
Brown Creeper.....	—	—	—	—	—	—	—	—	—	—	—	—
Winter Wren.....	—	—	—	—	—	—	—	—	—	—	—	—
Golden-crowned Kinglet.....	—	—	—	—	—	—	—	—	—	—	—	—
Red-eyed Vireo.....	—	—	—	—	—	—	—	—	—	—	—	—
Black-and-white Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Parula Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Yellow Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Magnolia Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Myrtle Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Black-throated Green Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Blackburnian Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Bay-breasted Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
Yellowthroat.....	—	—	—	—	—	—	—	—	—	—	—	—
Canada Warbler.....	—	—	—	—	—	—	—	—	—	—	—	—
American Redstart.....	—	—	—	—	—	—	—	—	—	—	—	—
Total.....	1	5	177	127	1	1	1	4	8	4	67	11

TABLE 14. Hostile interactions in flocks—Maine in summer (cont.).

Species Attacked	Species Attacking											
	Yellow Warbler	Magnolia Warbler	Myrtle Warbler	Black-throated Green Warbler	Blackburnian Warbler	Bay-breasted Warbler	Yellow throat	Canada Warbler	American Redstart	Total		
Hairy Woodpecker.....	—	—	—	—	—	—	—	—	—	—	—	—
Downy Woodpecker.....	—	—	—	—	—	—	—	—	—	—	8	—
Black-capped Chickadee.....	—	3	—	—	1	—	—	—	—	—	187	—
Red-breasted Nuthatch.....	—	—	—	—	—	—	—	—	—	—	130	—
Brown Creeper.....	—	—	—	—	—	—	—	—	—	—	5	—
Winter Wren.....	—	—	—	—	—	—	—	—	—	—	1	—
Golden-crowned Kinglet.....	—	—	—	—	—	—	—	—	—	—	16	—
Red-eyed Vireo.....	—	—	—	—	—	—	—	—	—	—	—	—
Black-and-white Warbler.....	—	2	—	—	—	—	—	—	—	—	29	—
Parula Warbler.....	—	—	—	—	—	—	—	—	—	—	14	—
Yellow Warbler.....	—	3	—	—	—	—	—	—	—	—	5	—
Magnolia Warbler.....	—	—	—	2	—	—	—	—	—	—	14	—
Myrtle Warbler.....	—	—	—	—	1	—	—	—	—	—	1	—
Black-throated Green Warbler.....	6	—	—	10	—	—	—	—	—	—	38	—
Blackburnian Warbler.....	—	—	2	—	—	—	—	—	—	—	11	—
Bay-breasted Warbler.....	—	—	1	—	—	2	—	—	—	—	3	—
Yellowthroat.....	—	—	—	—	—	—	—	—	—	—	—	—
Canada Warbler.....	—	—	—	—	—	—	—	5	—	—	7	—
American Redstart.....	—	—	—	—	—	—	—	—	—	—	7	—
Total.....	6	8	2	19	7	2	8	14	8	476	—	—

TABLE 15. Hostile interactions in flocks—Maine in winter.

Species Attacked	Species Attacking						Total
	Downy Woodpecker	Black-capped Chickadee	Boreal Chickadee	White-breasted Nuthatch	Red-breasted Nuthatch	Golden-crowned Kinglet	
Downy Woodpecker.....	3	—	—	—	—	—	3
Black-capped Chickadee.....	1	36	—	1	4	—	42
Boreal Chickadee.....	—	2	—	—	—	—	2
White-breasted Nuthatch.....	—	—	—	1	—	—	1
Red-breasted Nuthatch.....	—	2	—	—	1	—	3
Golden-crowned Kinglet.....	—	2	—	—	—	7	9
Total.....	4	42	—	2	5	7	60

planting attacks. This combination of characters was possessed by no other species in the area, and this low level of interspecific hostility may be related to the "attractiveness" of these species to others.

The data from Maryland (Table 17) are consistent with those from Louisiana and indicate further that the total overall frequency of hostile interactions initiated by leaders is low. White-breasted and Red-breasted nuthatches also have a high percentage of intraspecific encounters, and hostile interactions with other species usually take the form of supplanting attacks. However, the frequency of hostile interactions initiated by these species is considerably higher than by chickadees and titmice. Golden-crowned Kinglets initiate a low frequency of hostile interactions, with all of these being intraspecific. Hence the three most common members of flocks in Maryland (chickadee, titmouse, kinglet) displayed a low frequency of interactions initiated, with few of them being of an interspecific nature, and those largely being supplanting attacks.

Much higher levels of hostile interactions occurred in Maine during the late summer, especially interspecifically (Table 18), with a larger percentage of them being fights or chases than in the winter studies. This situation probably is due to three factors: formation of flocks, remnants of territoriality of some local birds that participate in flocks, and the constantly changing makeup of flocks that occurs in a system that contains many transients. Many migrants participated in these flocks, probably for only limited periods of time. The primary leader, the Black-capped Chickadee, possessed a low level of interspecific actions, as did the Golden-crowned Kinglet. However, a greater percentage of interspecific encounters of

chickadees were fights or chases than was the case for the leading species in Louisiana or Maryland.

Data gathered in the winter in Maine (Table 19) were similar to those from other geographic areas. The level of hostile interactions of Black-capped Chickadees was comparable to that of Carolina Chickadees in Maryland, as was the percentage of supplanting attacks. Interestingly, the percentage of intraspecific fights and chases was lower than for Carolina Chickadees in either Louisiana or Maryland and much lower than that occurring in the late summer, suggesting strongly that the high level of hostility in the chickadees at that time was related to the then-existing conditions accompanying flock formation.

Thus, though the frequency and nature of hostile behavior differed among the study areas, the leaders of flocks and one other key member, the Golden-crowned Kinglet, exhibited a relatively low frequency of interspecific hostile encounters (Tables 16-19) in each of the areas studied. Also notable was the low frequency of interspecific fights and chases initiated by them, simple supplanting attacks being the usual mode of hostilities. For several other species for which adequate observations were obtained, interspecific hostile attacks were more frequent, and/or the percentage of fights and chases was higher (Tables 16-19).

In addition to a disproportionately higher percentage of contact with other members of a species, the nature of the hostile interactions between species and among members of a species differed. Regardless of the overall general nature of interactions, the intraspecific interactions usually were more overtly aggressive than the interspecific interactions; thus, proportionately more chases and fights and less supplanting attacks were of an intraspecific nature than interspecific. The one exception was the Ruby-crowned Kinglet in Louisiana and Maryland. The difference can be traced directly to its interactions with Golden-crowned Kinglets, which almost invariably are attacked more vigorously than are members of its own species.

In Maryland, where both censuses of population density were made and frequencies of hostile interactions computed, these frequencies were calculated by habitat also (Table 20) for the two species (Carolina Chickadee and Golden-crowned Kinglet) in which large numbers of intraspecific interactions were observed. A much lower level of hostilities was obtained in the mixed forest (the one with the lowest density of birds, but largest average flock sizes) than in the other two. A gen-

TABLE 16. Analysis of hostile interactions initiated—Louisiana.

Species Attacking	Intraspecific			Interspecific		
	Total No. of Interactions Initiated	% Fights & Chases	% Supplanting Attacks	Total No. of Interactions Initiated	% Fights & Chases	% Supplanting Attacks
Carolina Chickadee.....	29	82.8	17.2	4	25.0	75.0
Tufted Titmouse.....	19	52.6	47.4	11	9.1	90.9
White-breasted Nuthatch.....	0	—	—	6	100.0	0.0
Brown-headed Nuthatch.....	3	66.7	33.3	11	45.5	54.5
Ruby-crowned Kinglet.....	4	75.0	25.0	16	87.5	12.5
Myrtle Warbler.....	13	100.0	0.0	2	50.0	50.0
Pine Warbler.....	15	66.7	33.3	7	57.1	42.9

TABLE 17. Analysis of hostile interactions initiated per foraging observation—Maryland.

Species Attacking	Total Foraging Observations	Total Frequency of Hostile Interactions Initiated; N in ()	Intraspecific			Interspecific		
			Frequency	% Fights & Chases	% Supplanting Attacks	Frequency	% Fights & Chases	% Supplanting Attacks
Downy Woodpecker.....	345	.014 (5)	.009 (3)	66.7	33.3	.005 (2)	0.0	100.0
Carolina Chickadee.....	5610	.019 (107)	.018 (99)	51.5	48.5	.001 (8)	12.5	87.5
Tufted Titmouse.....	799	.034 (27)	.026 (21)	71.4	28.6	.008 (6)	16.7	88.3
White-breasted Nuthatch.....	316	.073 (23)	.050 (16)	62.5	37.5	.023 (7)	0.0	100.0
Red-breasted Nuthatch.....	104	.125 (13)	.115 (12)	58.3	41.7	.010 (1)	0.0	100.0
Golden-crowned Kinglet.....	2236	.025 (55)	.025 (55)	58.2	41.8	.000 (0)	—	—
Ruby-crowned Kinglet.....	69	.130 (9)	.043 (3)	66.7	33.3	.087 (6)	100.0	0.0

TABLE 18. Analysis of hostile interactions initiated per foraging observation—Maine in summer.

Species Attacking	Total Foraging Observations	Total Frequency of Hostile Interactions Initiated; N in ()	Intraspecific			Interspecific		
			Frequency	% Fights & Chases	% Supplanting Attacks	Frequency	% Fights & Chases	% Supplanting Attacks
Downy Woodpecker.....	148	.034 (5)	.027 (4)	100.0	0.0	.007 (1)	0.0	100.0
Black-capped Chickadee.....	3283	.054 (177)	.049 (160)	66.3	33.7	.005 (17)	58.8	41.2
Red-breasted Nuthatch.....	1117	.115 (128)	.093 (108)	84.5	15.5	.022 (25)	32.0	68.0
Golden-crowned Kinglet.....	968	.008 (8)	.007 (7)	100.0	0.0	.001 (1)	0.0	100.0
Black-and-white Warbler.....	505	.135 (68)	.038 (19)	100.0	0.0	.097 (49)	83.7	16.3
Parula Warbler.....	125	.088 (11)	.064 (8)	100.0	0.0	.024 (3)	0.0	100.0
Yellow Warbler.....	15	.400 (6)	.000 (0)	—	—	.400 (6)	83.3	16.7
Magnolia Warbler.....	168	.048 (8)	.018 (3)	100.0	0.0	.030 (5)	100.0	0.0
Black-throated Green Warbler.....	458	.041 (19)	.022 (10)	90.0	10.0	.019 (9)	88.9	11.1
Blackburnian Warbler.....	198	.035 (7)	.000 (0)	—	—	.035 (7)	85.7	14.3
Yellowthroat.....	38	.210 (8)	.000 (0)	—	—	.210 (8)	87.5	12.5
Canada Warbler.....	86	.163 (14)	.058 (5)	100.0	0.0	.105 (9)	100.0	0.0
American Redstart.....	68	.118 (8)	.074 (5)	100.0	0.0	.044 (3)	100.0	0.0

TABLE 19. Analysis of hostile interactions initiated per foraging observation—Maine in winter.

Species Attacking	Total Foraging Observations	Total Frequency of Hostile Interactions Initiated; N in ()	Intraspecific			Interspecific		
			Frequency	% Fights & Chases	% Supplanting Attacks	Frequency	% Fights & Chases	% Supplanting Attacks
Black-capped Chickadee.....	2676	.016 (42)	.014 (36)	36.1	63.9	.002 (6)	0.0	100.0
Red-breasted Nuthatch.....	93	.054 (5)	.011 (1)	100.0	0.0	.043 (4)	0.0	100.0
Golden-crowned Kinglet.....	605	.012 (7)	.012 (7)	71.4	28.6	.000 (0)	—	—

TABLE 20. Analysis of intraspecific interactions initiated per foraging observation in different habitats—Maryland.

Species	Coniferous		Mixed		Deciduous	
	Frequency of Fights & Chases	Frequency of Supplanting Attacks	Frequency of Fights & Chases	Frequency of Supplanting Attacks	Frequency of Fights & Chases	Frequency of Supplanting Attacks
Carolina Chickadee.....	.012 (33)	.009 (23)	.003 (5)	.008 (13)	.010 (13)	.015 (20)
Golden-crowned Kinglet.....	.028 (22)	.013 (10)	.007 (5)	.003 (2)	.007 (5)	.016 (11)

eral, though not absolute, trend also appeared for the percentage of fights and chases to decrease as the density of birds in the habitat decreased.

DOMINANCE HIERARCHIES AMONG SPECIES

In addition to an intraspecific dominance hierarchy in members of these flocks (see Hamerstrom, 1942), an interspecific dominance hierarchy exists, which may be seen in the relatively unidirectional nature of hostile encounters between most pairs of species (Tables 12–15). Weights of the three commonest species participating in flocks in Maryland (Carolina Chickadee, Tufted Titmouse, Golden-crowned Kinglet) were kindly provided by Mr. Chandler Robbins from his personal data and from those gathered in the Operation Recovery program. They represent birds captured within 50 km of Cedarville and probably serve as an adequate representation of the birds studied at that area. Mean weights in grams with ranges in parentheses are as follows: Carolina Chickadee, 9.8 (9.3–10.1); Tufted Titmouse, 22.4 (20.8–23.6); and Golden-crowned Kinglet, 6.3 (5.5–7.8). While fat conditions show some variation in this sample, there is no overlap in the weights of different species. The direct relationship between mean weight and dominance (from Table 13) suggests a simple basis for the interspecific hierarchy among the commonest species. This statement does not extend to all members observed in flocks, but it will be observed that quite unidirectional relationships obtain between most pairs of important flock members.

INDIVIDUAL DISTANCE

While flocks are concentrations of individuals, overcrowding is not tolerated by the members, and they maintain what Conder (1949) called an individual distance: an area about an individual within which approach of another individual is reacted to either with avoidance or attack. The distance maintained between individuals varies in these flocks, but seldom does it approach the density that is found between members of groupings such as congregations of blackbirds. For the purposes of measuring individual distance, only

distance to nearest neighbor (of the same species) was used, though this probably represents an oversimplification where several individuals may be nearly equidistant. Crook (1961) points out that individual distance may vary with the type of activity being performed by the group. All distances reported were obtained from foraging birds feeding upon dispersed foods. Data were obtained in all areas but Louisiana.

Sufficient data for intraspecific quantitative analyses were obtained in Maryland for the Carolina Chickadee, Tufted Titmouse, and Golden-crowned Kinglet (Fig. 5). They indicate that intrusion within a certain range, which usually varied between 0.67 to 1.5 m, will result in an

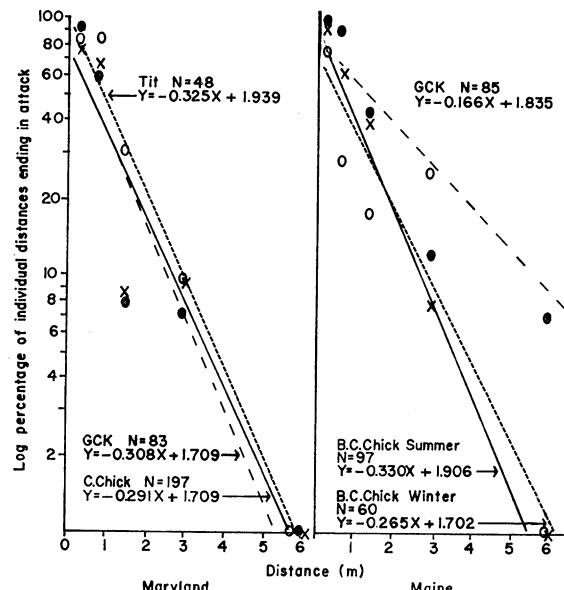


FIG. 5. Percentages of intraspecific individual distances ending in agonistic behavior. B.C. Chick = Black-capped Chickadee, C. Chick = Carolina Chickadee, Tit = Tufted Titmouse, GCK = Golden-crowned Kinglet.

agonistic response on the part of one or both birds. This distance varied directly with the size of the individuals concerned, though the differences are so slight as to be of questionable significance.

In Maine, Black-capped Chickadees and Golden-crowned Kinglets were similarly analyzed during

late summer (Fig. 5). Here the kinglets displayed a markedly greater tendency to respond agonistically at a given distance than did the chickadee, a larger species. Additional information gathered on Black-capped Chickadees during the winter (Fig. 5) indicates a slightly reduced tendency to attack at close range when compared with data from the same species during late summer. Curiously, of the species plotted in Fig. 5, only in this case is an appreciable percentage of hostile actions the result of long-distance attacks, thus resulting in the crossing of regression lines for the two plots of the species. These long-distance attacks could have been the result of attempts to steal food (see Hinde, 1952) but no observations were made that would definitely confirm this statement, and further investigation of the situation is needed.

Insufficient close approaches were obtained to compute curves for interspecific individual distances. In addition to any determined individual distance, preferences of different (though overlapping) centers of concentration for foraging (see below) and other activities automatically predict increased spacing between individuals of different species. The fact that in many instances a change in foraging stations occurred when individuals of different species foraged in each others' presence (see below) suggests strongly, as do the data on hostile interactions (Tables 12-15), that an individual of a given species is by no means oblivious to the presence of individuals of another species.

AREA OCCUPIED BY A FLOCK AT ANY GIVEN INSTANT

I measured the area and volume of space encompassed by a foraging flock at a given time in the deciduous habitat in Maryland (Fig. 6). Only in comparably open habitats could such data be obtained. In order to make an estimate I stood immediately adjacent to the long axis of these roughly elliptical areas and attempted to determine the periphery of the flock at a given instant. By positioning one's self thus, it is usually possible to be within 50 m of all individuals in the flock. The area was calculated by using the equation for an ellipse ($A = \pi ab$).

The results reveal that the larger a flock is, the less space is taken per bird, though the total area is larger than that used by small flocks. Hence, increased crowding will occur unless individuals expand their activities in a vertical plane. It should be noted that members of all flocks were continually foraging when measured. Loud notes uttered by leaders of a flock tend temporarily to

group individuals much more tightly than this, but foraging is limited at such times.

While a tendency toward a smaller area per bird exists as flocks increase in size, an alternative exists for individuals to increase the vertical range in which they forage in large flocks. Since individuals in small flocks will feed from underbrush to treetops also, it is questionable whether individuals in large flocks are able to increase their vertical range enough to offset the two-dimensional differences indicated in Fig. 6. Individuals in all 11 flocks of Fig. 6 were observed foraging

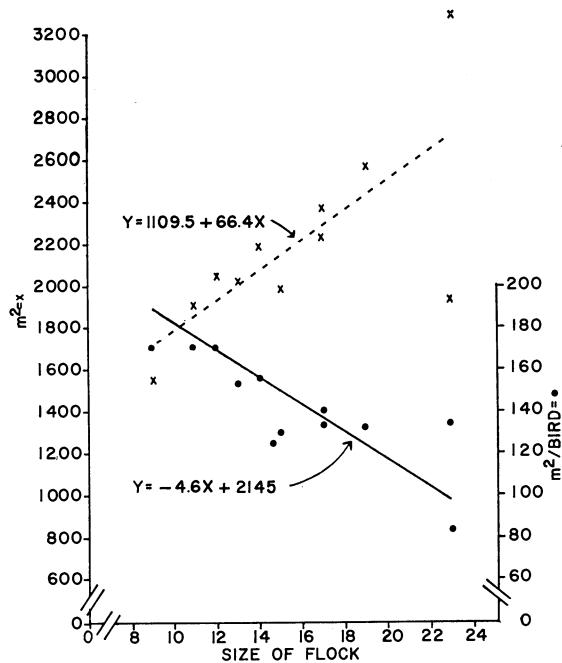


FIG. 6. Area occupied by flocks at a given instant and area available per individual at same time—deciduous forest in Maryland.

from the top to the bottom of the forest; thus, it appears that the volume of space occupied is directly proportional to the area.

Two of the 11 flocks illustrated in Fig. 6 were followed until they entered a nearby grove of Virginia pines. At this point individuals appeared to become considerably more concentrated than they were in the open deciduous forest, though the pine foliage was dense enough to prevent an accurate quantification of the area occupied at such a time. If this impression was correct it suggests that the size of the area occupied is also dependent upon the density of vegetation in the habitat.

SPACING OF THE SPECIES WITHIN THE AREA OCCUPIED

Spacing of individuals within the area occupied by a flock does not have a constant pattern, though

TABLE 21. Estimated size of home ranges of flocks.

Geographic Area	Coniferous			Mixed			Deciduous		
	Census Area in ha	Flocks Seen Census (ave.)	Estimated Range in ha	Census Area in ha	Flocks Seen Census (ave.)	Estimated Range in ha	Census Area in ha	Flocks Seen Census (ave.)	Estimated Range in ha
Louisiana.....	20.0	1.2	16.7	13.2	2.3	5.7	10.0	3.2	3.1
Maryland.....	14.0	2.0	7.0	20.0	1.3	15.4	10.0	0.8	12.5

there is a tendency for at least some leaders to be at one side (leading edge) of this space and for others that follow to fall to the lagging edge upon occasion, particularly when motion is rapid. Upon occasions hyperdispersion was noted among the individuals of a single species in a flock, with individuals of different species displaying closer individual distances than individuals of the same species.

Though no special effort was made to study this aspect of spacing, examples where intraspecific hyperdispersion occurred were seen clearly in flocks observed in Maryland on 17 and 19 November 1967. At both of these times individuals were spaced considerably more closely than usual, and upon several occasions individuals of different species approached to a distance of scarcely over one meter from each other. The observations of 17 November took place at a low level in a mixed forest; three chickadees, two titmice, one creeper, and four Golden-crowned Kinglets were present, and for approximately 10 minutes the majority of the nearest individuals from any given bird appeared to be of a different species. In cases during this period where the distance between pairs of birds recorded was below three meters, 12 were interspecific and 4 intraspecific; in cases where distances were between 3 and 8 meters, 2 noted were interspecific and 8 intraspecific. The probability of obtaining such an extreme difference by chance in the assortment of individuals at the two ranges of individual distances is low ($P = <0.01$ in a Fisher Exact Probability Test). During this period only one hostile attack was noted, with a chickadee supplanting a kinglet. Following this period, both chickadees tended to separate from the immediate vicinity of the other individuals, and two chickadees were seen to supplant other chickadees and three kinglets seen to supplant other kinglets. On 19 November during brief observations in a different part of the forest, six chickadees and five Golden-crowned Kinglets briefly spaced themselves in a similar manner, then the two species separated somewhat, and several intraspecific attacks occurred.

Though not seen again these fragmentary observations are of considerable interest and pos-

sible significance. Since hostile behavior is higher in intraspecific situations than interspecific ones (Tables 12–15), the type of spacing described above would act to decrease the level of aggression (particularly intraspecific) from what would be expected in a one-species situation. Even if only random distribution occurred and only upon occasion, the overall effect would be to separate somewhat conspecifics in space, and presumably lower the level of hostile interactions.

SIZE OF HOME RANGE

The size of home ranges of winter flocks of Black-capped Chickadees has been considered by Butts (1931), Odum (1942), and Batts (1957). The frequencies of appearance of flocks were recorded while winter population censuses were being made in Louisiana and Maryland, thus allowing a rough estimate of range size during the mid-winter period (Table 21). These data indicate that the size of the range varies inversely with the density of birds in the habitat, and that it is comparable to, though usually smaller than, those of flocks of Black-capped Chickadees studied by others to the north.

NATURE OF FORAGING AND ITS ANALYSIS

Procedure

The extent of usage of different parts of each habitat was determined for the different species in the flocks. Habitats were divided into 19 categories, as indicated in Figs. 7–17. Nine separate categories are recognized in both coniferous and deciduous vegetation, and a nineteenth category includes the ground and low herbaceous vegetation (grass, herbs, etc.). Height in the first 18 categories was divided into high and low because of the moderate differences in height of the various forests studied. Since most forests in which I studied averaged between 18 and 20 m in height, 9 m served as the usual line of demarcation between high and low parts. While a forest might be considered coniferous, deciduous trees often occurred in such an area (under 10% of the total volume). Also, most deciduous forests contained occasional conifers. Mixed forests were studied only if the volumes of coniferous and deciduous

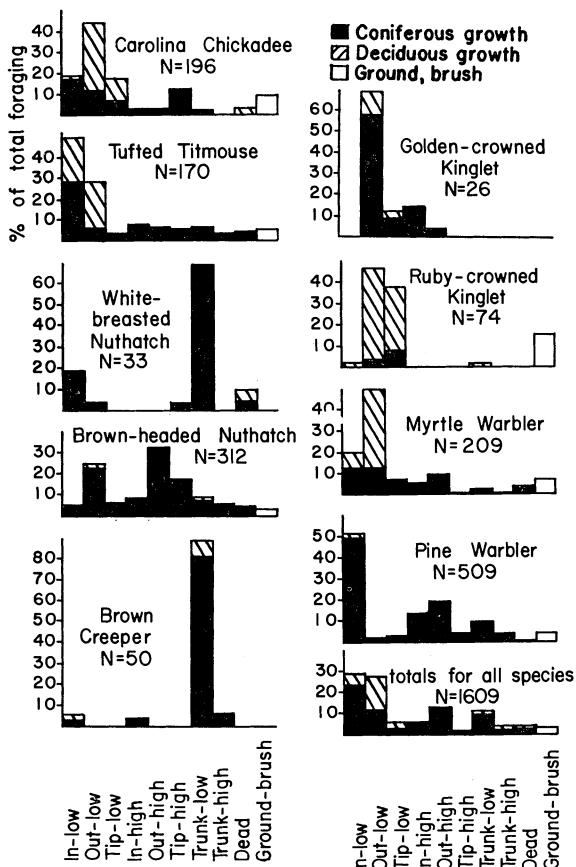


FIG. 7. Frequencies of foraging in different parts of the habitat by flocking species. Data from coniferous forest in Louisiana.

trees were equal or nearly so. Figs. 7–17 contain the foraging data of each common species in the different habitats of the three geographic areas.

Description of Foraging

Members of the flocks treated in this study are typically insectivorous, with none of them apparently being completely independent of insect food over a considerable period of time, even though pine, spruce, fir, oak, sweet gum, or tulip-poplar fruits may form important temporary food sources. These birds possess varied but overlapping foraging preferences, so that almost all parts of the habitat are used by one species or another. While some pairs of species overlap very little in foraging (if at all), each species overlaps to some degree with at least one other species in the flocks. For example, in the mixed forests in Louisiana, the foraging data gathered from Brown Creepers and Golden-crowned Kinglets are exclusive of each other (Fig. 8), yet for the categories considered in the habitat Carolina Chicka-

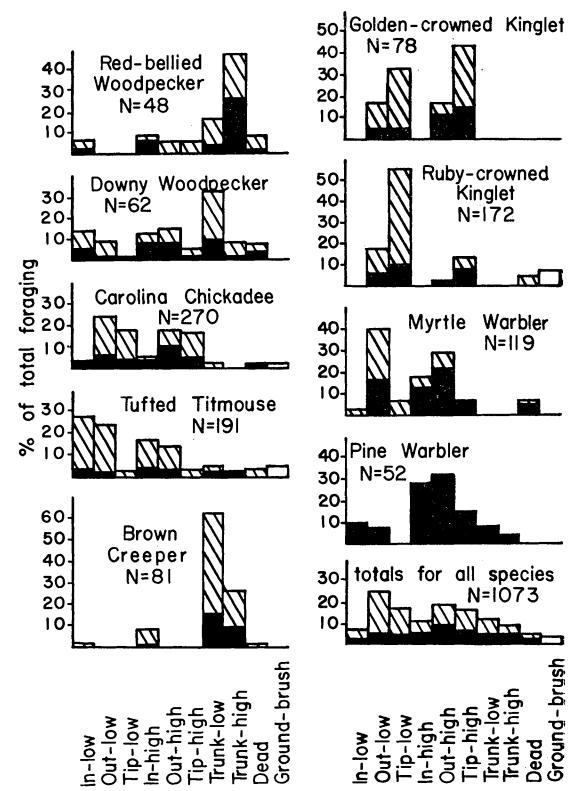


FIG. 8. Frequencies of foraging in different parts of the habitat by flocking species. Data from mixed coniferous-deciduous forest in Louisiana. Foraging stations coded as in Fig. 7.

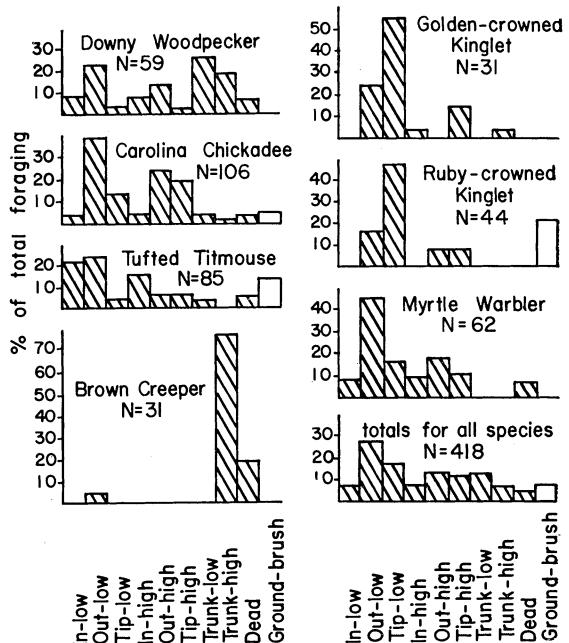


FIG. 9. Frequencies of foraging in different parts of the habitat by flocking species. Data from deciduous forest in Louisiana. Foraging stations coded as in Fig. 7.

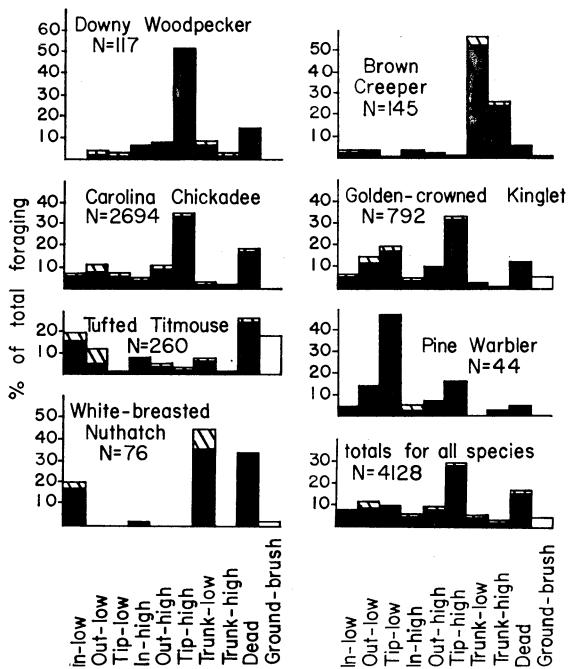


FIG. 10. Frequencies of foraging in different parts of the habitat by flocking species. Data from coniferous forest in Maryland. Foraging stations coded as in Fig. 7.

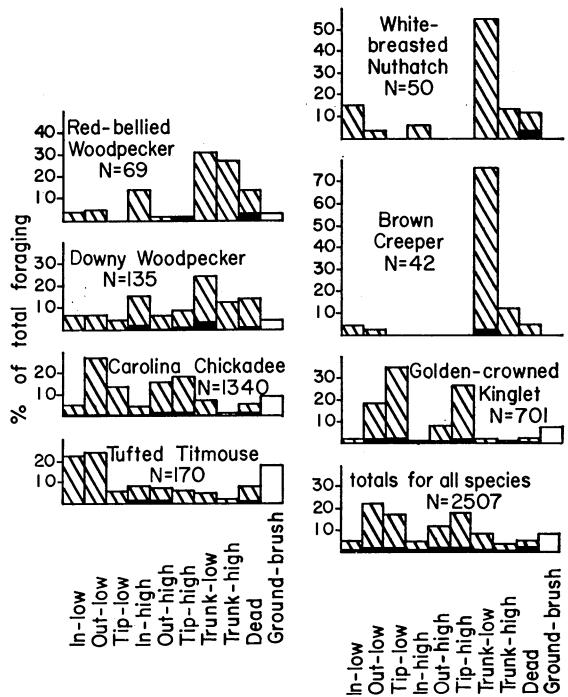


FIG. 12. Frequencies of foraging in different parts of the habitat by flocking species. Data from deciduous forest in Maryland. Foraging stations coded as in Fig. 7.

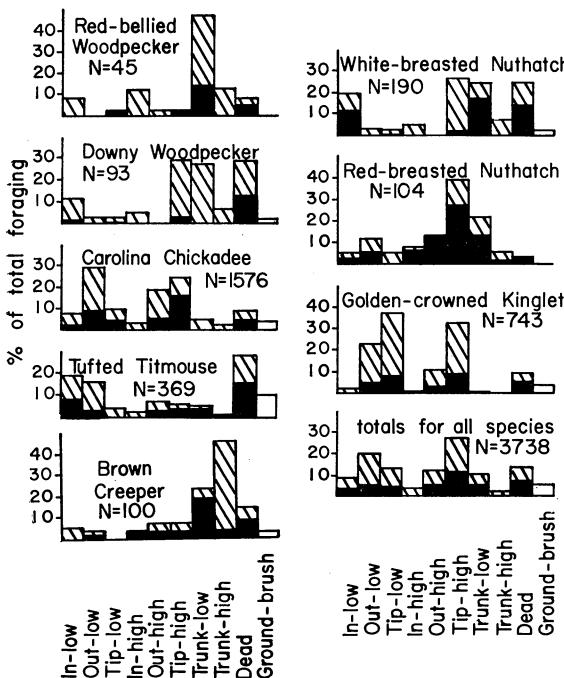


FIG. 11. Frequencies of foraging in different parts of the habitat by flocking species. Data from mixed coniferous-deciduous forest in Maryland. Foraging stations coded as in Fig. 7.

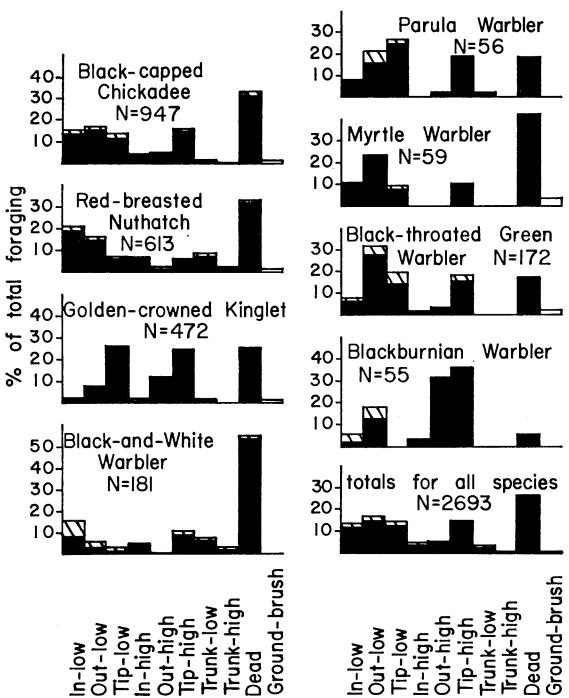


FIG. 13. Frequencies of foraging in different parts of the habitat by flocking species. Data from coniferous forest in Maine in late summer. Foraging stations coded as in Fig. 7.

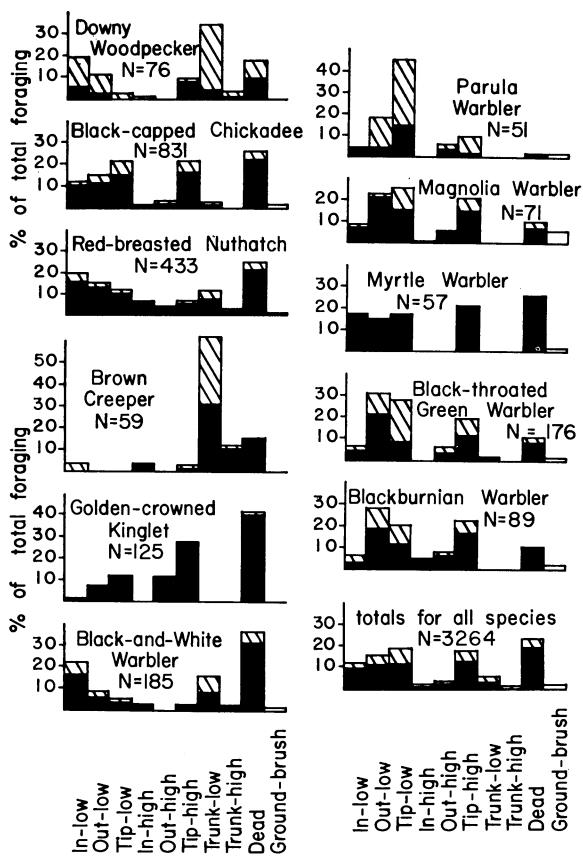


FIG. 14. Frequencies of foraging in different parts of the habitat by flocking species. Data from mixed coniferous-deciduous forest in Maine in late summer. Foraging stations coded as in Fig. 7.

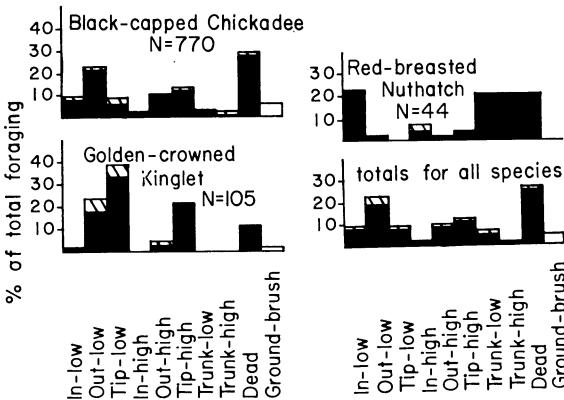


FIG. 15. Frequencies of foraging in different parts of the habitat by flocking species. Data from coniferous forest in Maine in winter. Foraging stations coded as in Fig. 7.

dees overlap broadly both the kinglets and creepers.

Other workers have found preferences of different species of birds for certain species of vegetation within a given habitat (Hartley, 1953; Gibb,

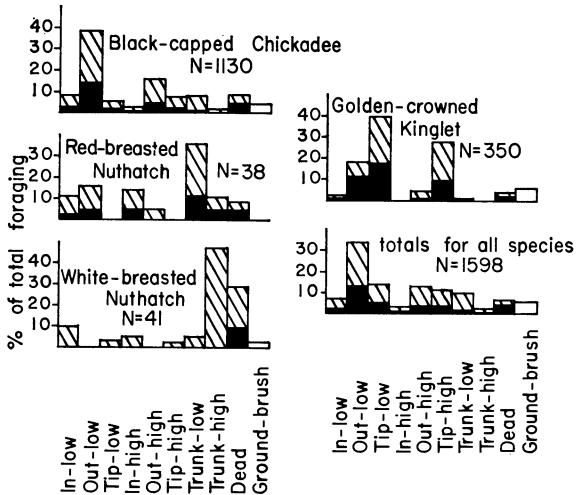


FIG. 16. Frequencies of foraging in different parts of the habitat by flocking species. Data from mixed coniferous-deciduous forest in Maine in winter. Foraging stations coded as in Fig. 7.

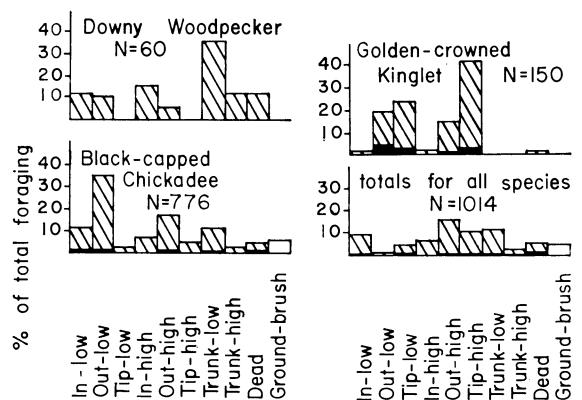


FIG. 17. Frequencies of foraging in different parts of the habitat by flocking species. Data from deciduous forest in Maine in winter. Foraging stations coded as in Fig. 7.

1954). I did not pursue this problem because in each study area containing coniferous species either only one species of conifer was present, or it was vastly more common than any others. The deciduous trees in each case had one or at most a few dominant species. Furthermore, Brewer (1963) found that in Illinois the utilization of comparable species of trees by Black-capped and Carolina chickadees followed closely the relative abundance of these kinds of plants.

Conspicuous seasonal changes in foraging may also occur, though studies were conducted largely within a single part of the year in order to minimize possible variance of this nature. One such fluctuation was displayed clearly by Brown-headed Nuthatches in the longleaf pine forests of Lou-

isiana when an abundant seed crop became available to them (Morse, 1967b). In Maine, the only locality where studies were pursued both in late summer and winter, adequate data from the two seasons for two species. Black-capped Chickadees and Golden-crowned Kinglets, are available for comparison (Figs. 13–16). In the case of the chickadees, there was a stronger tendency to forage on small limbs and on trunks in winter than during the summer. Particularly conspicuous in this regard was the greatly increased tendency to utilize the trunks of deciduous trees, particularly birches, whose papery bark was foraged upon frequently. Golden-crowned Kinglets similarly displayed a less marked tendency to forage on dead limbs and large limbs, though the utilization of large limbs at no time represents a major apparent source for food. The simultaneous trends in the two species may be dependent upon a general shift in the areas where available food occurs in amounts sufficient for convenient utilization. Prey are inactive during the winter and perhaps retreat to some extent from the foliage, if it remains.

While differences in foraging of the commonest species occurred in the various habitats of a geographic area and even between geographic areas, the similarities are marked. The data contained in Figs. 7–17 will be considered further in the section upon indices of foraging.

Indices of Foraging Diversity

Calculation of an index of diversity derived from information theory (Shannon & Weaver, 1949) affords a means of assessing the species' tendency to specialize their efforts within certain foraging stations.

The equation $H' = -\sum_{i=1}^s P_i \log P_i$ is

used, where H' represents the diversity found in the sample, s the number of foraging stations, and P_i the proportion of observations made in category i . All values are expressed as the ratio $J' = H'/H'_{max}$ (see Pielou, 1966), where H'_{max} represents a situation in which utilization of all foraging stations is equal. Thus a specialist would receive a low value of J' (evenness). It must be emphasized for these calculations that separation of the habitat into a certain number of foraging stations is an arbitrary one, and that higher or lower values of foraging diversity might be obtained if any category were divided or group of categories lumped; what can be seen in the indices is simply a consistent measure of behavior. Such techniques may produce a artificial smoothing that could conceivably obscure some important dif-

TABLE 22. Indices of foraging diversity. N 's as in Figs. 7–17.

Species	Geographical Area	Habitat		
		Coniferous	Mixed	Deciduous
Carolina Chickadee	Louisiana	0.73	0.79	0.60
Tufted Titmouse		0.71	0.74	—
Brown-headed Nuthatch		0.63	—	—
Ruby-crowned Kinglet		—	0.55	—
Myrtle Warbler		0.72	0.70	—
Pine Warbler		0.55	—	—
Downy Woodpecker	Maryland	0.58	—	0.82
Carolina Chickadee		0.73	0.85	0.74
Tufted Titmouse		0.73	0.87	0.72
White-breasted Nuthatch		—	0.74	—
Red-breasted Nuthatch		—	0.79	—
Brown Creeper		0.53	0.71	—
Golden-crowned Kinglet		0.71	0.70	0.61
Black-capped Chickadee	Maine-summer	0.68	0.86	
Red-breasted Nuthatch		0.68	0.88	
Golden-crowned Kinglet		0.57	0.51	
Black-and-White Warbler		0.60	0.79	
Black-throated Green Warbler		0.69	0.78	
Black-capped Chickadee	Maine-winter	0.71	0.81	0.70
Golden-crowned Kinglet		0.61	0.70	0.59

ferences; however, any remaining differences should be real ones. Foraging diversity of a species only was calculated when 100 or more observations had been made for that species in the habitat considered (N 's used for all measures from information theory appear in Figs. 7–25). Hence, the number of cases for which indices were calculated is rather small (Table 22).

The diversities obtained from the mixed habitat are with three exceptions higher in a given species than for either coniferous or deciduous habitats. Since the assigned stations contained both coniferous and deciduous categories, where both occurred in considerable volume one would predict a higher index of diversity, since as a tendency toward equal usage of all categories increases (as would be predicted in a mixed habitat of 50% coniferous and 50% deciduous, if no marked preference for one or the other occurred), a value of 1 is approached. Only in a strong specialist would a contrary pattern or lack of change be predicted; in fact, a contrary pattern would suggest that the species involved was seeking out one part of the habitat where a choice occurred, and that it was further restricting its range of foraging stations here. While definite preferences for coniferous or deciduous growth may be detected in several species, in no instance was one type or the other chosen exclusively in a mixed forest. The diversity for all species combined in the mixed forests is significantly higher than in either coniferous or deciduous forests ($P = 0.001$ in a sign test). Since the power of these informa-

tion theory measures is not clearly understood only certain nonparametric statistics are used.

Two of the three exceptions were by Golden-crowned Kinglets, in Maryland and in Maine in the summer. This species appears basically adapted to existence in coniferous forests (Morse, 1967a), though it utilizes deciduous foliage in many situations. However, its choice of stations in deciduous foliage in Maryland was more limited than in coniferous foliage (Figs. 10–12) and in Maine (summer) it showed little disposition to forage on deciduous foliage when the opportunity was present (Fig. 14). In Maine in winter no exception obtained with this species, though the index from the coniferous forest was slightly greater than for the deciduous forest.

In the third case, the Myrtle Warbler, in Louisiana, a slightly greater diversity was obtained in coniferous than in mixed forest. In all probability this exception was related to the differences in numbers of this species appearing in flocks in the two habitats. In several instances large numbers of this species (up to 50) appeared to spread widely through virtually the entire habitat in the longleaf pine forest, presumably as a result of their own high density. Though numbers of this size seldom remained long with the mixed flocks, they did upon occasions move for considerable distances with them. In no other instances did a single species in flocks attain such high numbers that a comparable situation was readily apparent.

No overall significant differences in indices of diversity were noted between coniferous and deciduous habitats ($P = 0.227$ in sign test). Considering individual species, Carolina Chickadees in Louisiana foraged more selectively in deciduous than in coniferous foliage, though the species did not follow this pattern in Maryland, where the diversities for deciduous and coniferous forests were nearly equal. This difference probably was responsible for a higher index being obtained in the mixed forests in Maryland than in Louisiana. Adequate data are not available for Tufted Titmice in deciduous forests in Louisiana. If they follow a pattern comparable to that of Carolina Chickadees, however, with which they agree rather closely in the other five indices from Louisiana and Maryland, one might predict a relatively low diversity for this species from the deciduous area. In two instances (Maryland, Maine in winter) Golden-crowned Kinglets displayed lower diversity in deciduous than in coniferous areas, and the data from Maine in summer project a low index there, based upon the indices in coniferous and mixed forests. The only other species allowing such

a comparison is the Downy Woodpecker in Maryland, and the low diversity noted in the coniferous forest is due to this species doing a large percentage of its foraging there on pine cones.

There was no overall difference detectable in diversity of foraging in different geographical areas, with overlaps in the values being substantial in all cases that could be compared. Four species were sampled with enough regularity to permit comparisons between areas (or seasons). In addition to the species discussed immediately above, Black-capped Chickadees were sampled in Maine both in winter and late summer. No studies were made in deciduous forests in the summer for comparison, but the high diversity for the mixed forest in summer resulted in part from a stronger disposition of the species to forage upon a variety of stations on deciduous trees than during the winter. The foliage on the deciduous trees at this season, which frequently had heavy infestations of insects that chickadees and several other species fed upon, doubtless was a major factor contributing to this difference.

Indices of Overlap in Areas Foraged

Differences between species in utilization of the habitat for foraging were quantified by determining indices of overlap (R_o) from information theory (Horn, 1966) for each pair of species studied in each habitat where 100 or more observations were accumulated for both members (Tables 27–29). In this case the equation

$$R_o = \frac{\sum (x_i + y_i) \log (x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

was used, where X and Y equal the total number of observations in samples of foraging X and Y , respectively; x_i and y_i equal the proportion of observations made in the i^{th} foraging category in samples X and Y , respectively.

The data indicate that while identity in foraging categories is seldom approached between two species, in any habitat overlap in most cases is substantial, with a large majority of pairs being assigned an index of 0.50 or greater. In contrast to foraging diversity, a lower level of overlap will be predicted in mixed forests than in coniferous or deciduous forests, since the availability of alternative positions for foraging will be greater, thus facilitating a greater possibility for habitat partitioning. This relationship holds in all cases in Louisiana, but there are four exceptions in Maryland, one in Maine in summer, and one in Maine in winter. This trend is significant

in Louisiana, Maryland, and Maine in summer ($p < 0.001$ in each instance).

Of the four exceptions in Maryland, three were ones where a lower overlap appeared in coniferous than in mixed forests, and one in which a lower overlap appeared in deciduous than in mixed forests. Of the first group, the pairs are Carolina Chickadee-Tufted Titmouse, Carolina Chickadee-Brown Creeper, and Tufted Titmouse-Brown Creeper. The bases for these exceptions appear largely to lie in the substantially increased tendency for creepers to forage in peripheral parts of deciduous trees in the mixed forest, while in the coniferous forest they showed a stronger tendency to remain on trunks (Fig. 10). Secondly, the Chickadees foraged heavily upon the cones of Virginia pines when in the coniferous forest, this activity resulting in a particularly high score for the category of tips of foliage, an area utilized by the chickadees much less frequently in the mixed forest, and not frequently used by the titmouse at any time.

One pair of species had a higher overlap in mixed forests than in deciduous forests, this being the Tufted Titmouse-Golden-crowned Kinglet combination, and being only 0.01 different. While the total sets of data are rather similar, a particularly strong tendency for titmice to forage on the ground in the deciduous area, in large part resulting from picking up fallen acorns, was the major inconsistent change.

In Maine in summer one species pair, Red-breasted Nuthatch and Black-and-White Warbler, displayed a greater overlap in mixed than in coniferous forests. Particularly heavy usage of dead coniferous growth in the spruce forest by the Black-and-White Warblers was in large part responsible for this situation.

In the winter in Maine sufficient data existed to construct these indices for one pair of species, Golden-crowned Kinglets and Black-capped Chickadees. They were 0.79 in coniferous, 0.71 in mixed, and 0.62 in deciduous, thus displaying a greater overlap in mixed than in deciduous forests. This difference appeared to be the result of the earlier mentioned tendency of Golden-crowned Kinglets to be particularly narrowly restricted to the peripheral parts of the vegetation in the deciduous foliage and less so in coniferous, with the chickadees showing a greater tendency to forage on coniferous tips than deciduous ones.

In short, variation from the above-predicted situation that indices will be lowest in mixed forests represented the exception and special conditions where gross deviations appear in one or

a very few foraging stations account for most of them.

Considerable variation in indices of overlap appeared in coniferous and deciduous forests where adequate observations appeared. In Maryland, overlap of Downy Woodpeckers and both Carolina Chickadees and Golden-crowned Kinglets was considerably greater in coniferous than in deciduous areas and again was closely related to the tendency of Downy Woodpeckers to forage extensively in and about peripheral pine cones in the coniferous areas, parts of the habitat utilized by the chickadees and Golden-crowned Kinglets. A considerably higher overlap between Downy Woodpeckers and Tufted Titmice occurred in the deciduous forest than in the coniferous forest, as away from cones Downy Woodpeckers showed a greater tendency to forage on the inner parts of the vegetation, as do titmice to a somewhat lesser extent. A lower overlap in the coniferous forest between Carolina Chickadees and Tufted Titmice and a higher one in coniferous forests between the chickadees and Golden-crowned Kinglets also appear largely the result of heavy utilization of the peripheral cone-bearing parts of pine trees by chickadees. Overlap of titmice and Golden-crowned Kinglets is rather similar in both habitats.

In Maine in winter, the difference in overlap between coniferous and deciduous habitats was substantial in the species pair studied adequately, Black-capped Chickadee and Golden-crowned Kinglet. Since Golden-crowned Kinglets specialized more in deciduous than in coniferous growth, overlap was the greatest in coniferous growth.

In one pair of species it is possible to compare indices of overlap in different geographical areas. They are the Carolina Chickadee and Tufted Titmouse in coniferous and mixed habitats of Louisiana and Maryland (Tables 27-28). Black-capped Chickadees and Golden-crowned Kinglets in Maine in both summer and winter may also be compared (Table 29, text). No consistent pattern arises within either pair.

Combined Foraging

Figures illustrating the combined areas foraged by all regular participants of flocks in each habitat were constructed (Figs. 7-17). Though there are definite areas of foraging preference in each species, sometimes resulting in high values being obtained in a single column (e.g.—Brown Creeper), the cumulative total from each area is one in which no high peaks occur. Furthermore, it will

TABLE 23. Frequencies (in %) of foraging motions other than gleaning—Louisiana.

Species	Habitat	Total No. of Foraging Observations			
			Hover	Hang	Hawk
Red-bellied Woodpecker	Mixed	48	—	2.1	—
Downy Woodpecker	Coniferous	30	—	—	—
	Mixed	62	—	3.2	—
	Deciduous	59	—	8.5	—
Carolina Chickadee	Coniferous	196	—	8.2	—
	Mixed	270	—	6.7	—
	Deciduous	106	0.9	6.6	—
Tufted Titmouse	Coniferous	170	0.6	1.8	—
	Mixed	191	—	1.0	—
	Deciduous	85	—	4.7	—
White-breasted Nuthatch	Coniferous	33	—	—	—
Brown-headed Nuthatch	Coniferous	312	—	1.3	1.0
Brown Creeper	Coniferous	50	—	—	—
	Mixed	81	—	—	—
Golden-crowned Kinglet	Deciduous	31	—	—	—
	Mixed	78	12.8	1.3	—
Ruby-crowned Kinglet	Deciduous	31	19.4	3.2	—
	Coniferous	74	18.9	—	—
	Mixed	172	17.4	—	—
Myrtle Warbler	Deciduous	44	2.3	—	—
	Coniferous	209	1.0	0.5	2.4
	Mixed	119	—	—	6.7
Pine Warbler	Deciduous	62	—	—	6.5
	Coniferous	509	0.2	1.4	4.5
	Mixed	66	—	3.0	—

TABLE 24. Frequencies (in %) of foraging motions other than gleaning—Maryland.

Species	Habitat	Total No. of Foraging Observations			
			Hover	Hang	Hawk
Red-bellied Woodpecker	Mixed	45	—	—	—
	Deciduous	69	—	—	—
Downy Woodpecker	Coniferous	117	—	8.5	—
	Mixed	93	—	2.1	—
	Deciduous	135	—	5.7	—
Carolina Chickadee	Coniferous	2694	0.4	7.5	0.3
	Mixed	1576	0.8	8.7	0.1
	Deciduous	1220	0.9	7.2	—
Tufted Titmouse	Coniferous	260	—	0.4	—
	Mixed	369	3.0	1.3	—
	Deciduous	283	0.7	1.8	—
White-breasted Nuthatch	Coniferous	76	—	—	—
	Mixed	190	0.5	—	—
Red-breasted Nuthatch	Coniferous	289	0.3	11.1	—
	Mixed	104	—	4.8	—
Brown Creeper	Coniferous	145	—	—	—
	Mixed	100	1.0	—	—
	Deciduous	42	—	—	—
Golden-crowned Kinglet	Coniferous	792	12.9	1.0	0.3
	Mixed	743	23.1	3.3	—
	Deciduous	701	15.3	1.0	—
Pine Warbler	Coniferous	44	9.1	—	—

be noted that there is a tendency for the more common members of the flocks to have "flat" foraging profiles in these histograms, resembling somewhat those of the cumulative profiles. The more prominent members of flocks, then, are ones that have considerable overlap in their foraging areas with other species, rather than ones that specialize highly in one or a few stations.

TABLE 25. Frequencies (in %) of foraging motions other than gleaning—Maine in summer.

Species	Habitat	Total No. of Foraging Observations			
			Hover	Hang	Hawk
Downy Woodpecker	Mixed	76	—	2.6	—
Black-capped Chickadee	Coniferous	947	1.3	10.8	—
	Mixed	1831	3.0	12.2	0.6
Red-breasted Nuthatch	Coniferous	643	2.2	1.2	0.9
Brown Creeper	Mixed	59	—	3.4	—
Golden-crowned Kinglet	Coniferous	472	11.4	4.0	1.1
	Mixed	125	15.2	3.2	—
Black-and-white-Warbler	Coniferous	181	1.7	6.1	1.7
	Mixed	185	—	0.5	1.6
Parula Warbler	Coniferous	56	16.1	—	—
	Mixed	51	—	2.0	2.0
Magnolia Warbler	Mixed	71	12.7	—	1.4
Myrtle Warbler	Coniferous	59	1.7	1.7	5.1
	Mixed	57	5.3	5.3	7.0
Black-throated Green Warbler	Coniferous	172	9.3	—	1.2
	Mixed	176	8.0	0.6	4.5
Blackburnian Warbler	Coniferous	55	3.6	3.6	—
	Mixed	89	7.9	3.4	5.6

TABLE 26. Frequencies (in %) of foraging motions other than gleaning—Maine in winter.

Species	Habitat	Total No. of Foraging Observations			
			Hover	Hang	Hawk
Downy Woodpecker	Deciduous	60	—	—	—
Black-capped Chickadee	Coniferous	770	0.5	7.7	—
	Mixed	1130	0.8	5.1	—
	Deciduous	776	0.1	2.4	—
White-breasted Nuthatch	Mixed	41	2.4	—	—
Red-breasted Nuthatch	Coniferous	44	—	2.3	—
	Mixed	40	—	—	—
Golden-crowned Kinglet	Coniferous	105	20.9	—	—
	Mixed	350	19.4	2.3	—
	Deciduous	150	21.3	2.0	—

TABLE 27. Indices of overlap in foraging between pairs of species—Louisiana. *N*'s as in Figs. 7–9.

	Coniferous			Mixed		
	CC	TT	BHN	TT	CC	TT
TT	0.91			TT	0.67	
BHN	0.58	0.52		RCK	0.74	0.41
MW	0.91	0.89	0.55	MW	0.81	0.67
						0.54

CC=Carolina Chickadee, TT=Tufted Titmouse, BHN=Brown-headed Nuthatch, RCK=Ruby-crowned Kinglet, MW=Myrtle Warbler, PW=Pine Warbler.

Methods of Foraging

While spatial overlap may be high among the most important species, those in question nevertheless may forage in rather different manners within areas where overlap occurs, Tables 23–26 illustrating this situation clearly. Both Carolina Chickadees and Golden-crowned Kinglets spend considerable time on the outer extremities of the vegetation; however, the kinglet hovers frequently at tips and feeds simultaneously; the

TABLE 28. Indices of overlap in foraging between pairs of species—Maryland. N's as in Figs. 10–12.

Coniferous					Mixed					Deciduous				
	DW	CC	TT	BC		CC	TT	WBN	RBN	BC		DW	CC	TT
CC	0.90				TT	0.86					CC	0.79		
TT	0.53	0.81			WBN	0.66	0.71				TT	0.77	0.88	
BC	0.53	0.48	0.51		RBN	0.79	0.55	0.57			GCK	0.55	0.90	0.68
GCK	0.84	0.97	0.70	0.39	BC	0.65	0.63	0.75	0.58	0.39				
					GCK	0.87	0.69	0.49	0.62					

WBN=White-breasted Nuthatch, RBN=Red-breasted Nuthatch, BC=Brown Creeper, GCK=Golden-crowned Kinglet. All other symbols as in Table 27.

TABLE 29. Indices of overlap in foraging between pairs of species—Maine in summer. N's as in Figs. 13–14.

Coniferous					Deciduous				
	BCC	RBN	GCK	B&W		BCC	RBN	GCK	B&W
RBN	0.93				RBN	0.88			
GCK	0.90	0.75			GCK	0.88	0.75		
B&W	0.87	0.90	0.69		B&W	0.81	0.93	0.61	
BTG	0.93	0.82	0.84	0.69	BTG	0.91	0.78	0.65	0.62

BCC=Black-capped Chickadee, B&W=Black-and-White Warbler, BTG=Black-throated Green Warbler. All other symbols as in Table 28.

chickadee often forages by hanging upside down on the tips of the vegetation. The frequency of this behavior may in some cases be closely related to the presence of a single food source; hence, in Maryland where pine seeds were available, chickadees showed a strong tendency to forage upon them, thus accounting for the particularly high frequency of hanging upside down in the pine forest. Hawking for insects (flycatching) may also be a relatively important means of foraging for some of these species during certain parts of the year; however, only on occasional warm days of the winter were insects seen in flight, and the overall frequency was thus extremely low.

Specialization

Thus it appears that there are two possible alternatives for specialization in these largely insectivorous species. A species may concentrate heavily upon a small segment of the habitat (tree trunks, etc.) or utilize special foraging mechanisms such as hovering or hanging within a more strongly utilized area. The more common members of the flocks appear to have chosen the latter alternative. Furthermore, among this central group of species, there is a higher frequency of such behavior in the socially subordinate species. Hence, titmouse do not exhibit as high a frequency of such behavior as chickadees and kinglets, though they are also adept at hanging. Chickadees do not exhibit as high a frequency of this behavior as do Golden-crowned Kinglets. Nuthatches do not possess as high a frequency

as the latter two species either, though one might argue that their ability to move about upside down should be considered an adaptation comparable to those listed in Tables 23–26. Lastly, temporary members of flocks in Maine in late summer displayed a high tendency to utilize these motions (Table 25), particularly hawking for insects, a motion usually only useful during relatively warm parts of the year.

EFFECTS OF OTHER MEMBERS OF FLOCKS UPON FORAGING OF A SPECIES

Procedure

Since each species has a characteristic pattern of foraging, I hoped to determine whether these patterns changed in the presence of other species, or, whether essentially the same patterns held. A striking example of the first alternative in one pair of flock members has already been reported (Morse, 1967b). In the presence of Brown-headed Nuthatches, Pine Warblers foraged more frequently on the inner parts of trees than when the nuthatches were absent; when Pine Warblers were present, the nuthatches would forage more frequently in the outer parts of the tree than when the Pine Warblers were absent.

Data of a species were divided depending upon whether 0, 1–2, or 3–3+ individuals of an other species were present, and analyses were performed when 100 or more observations were available in two or more categories. For example, separate tallies would be made of the foraging of Carolina Chickadees where Golden-crowned Kinglets were absent in a flock, in numbers of 1–2, and numbers of 3 or more. In turn the same analysis would be made upon kinglets when chickadees were absent, present in numbers of one or two, or present in numbers of three or more. Separate tallies were made for each habitat in the different geographical areas (Figs. 18–25). Data were not adequate to test the effect of more than one species upon another at a time, and only in the cases of some of the commonest species was a complete

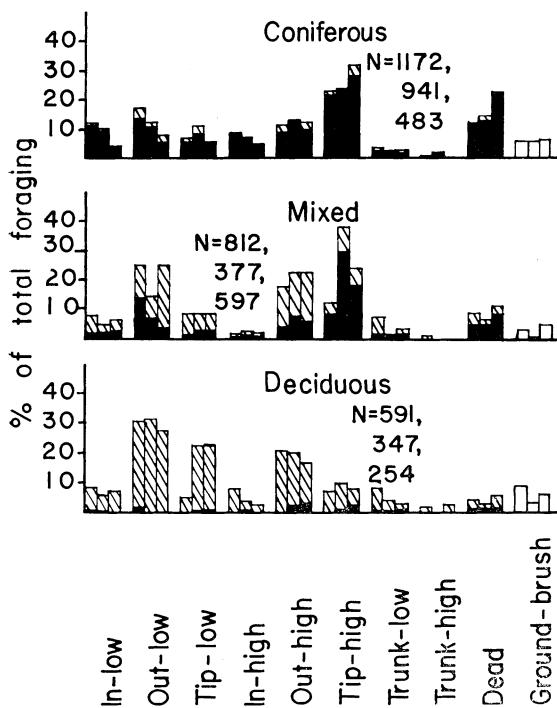


FIG. 18. Frequencies of foraging in different parts of the habitat by Carolina Chickadees in the presence of 0 (left part of triad), 1-2 (center part of triad), and 3-3+ (right part of triad) Tufted Titmice in Maryland. Foraging stations coded as in Fig. 7.

analysis between a pair of species ever possible. In several instances, if present a species occurred in large numbers. For instance, Carolina Chickadees were almost always found in any groups studied in Maryland and characteristically occurred in numbers larger than two. Analyzing the effect of the chickadees upon Golden-crowned Kinglets, insufficient observations were made of kinglets in the presence of one or two chickadees for comparison, and only a nearly minimum number of observations of kinglets foraging away from chickadees was available (Fig. 21). Because of the extreme gregariousness of the group of species studied, it seldom was possible to study individuals apart from all other species.

TWO-SPECIES ANALYSES IN MARYLAND

In coniferous and mixed habitats in the presence of Tufted Titmice, Carolina Chickadees foraged higher and more peripherally than in their absence (Fig. 18). Also, in the coniferous forest a tendency for chickadees to forage more heavily in dead branches was noted when titmice were present. A slight tendency to move peripherally (though not higher) was noted in the presence of titmice in the deciduous forest. In several cases the above-mentioned changes in foraging of Caro-

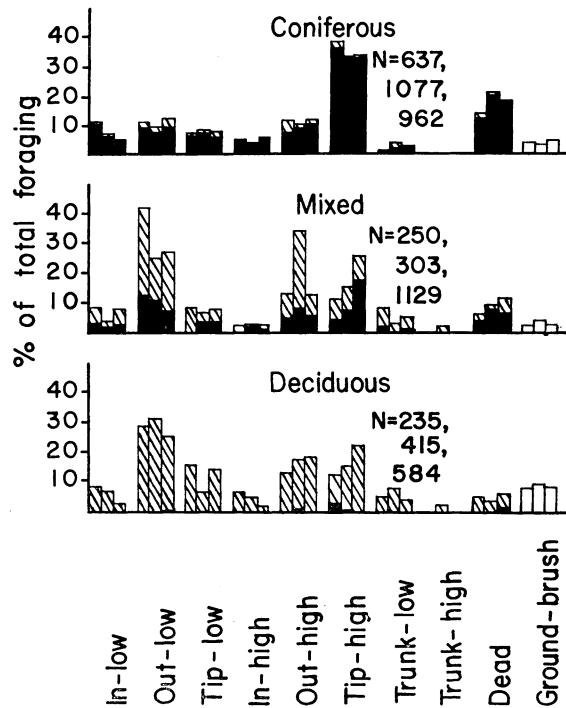


FIG. 19. Frequencies of foraging in different parts of the habitat by Golden-crowned Kinglets in the presence of 0, 1-2, and 3-3+ Tufted Titmice in Maryland. Foraging stations coded as in Fig. 7, triads coded in Fig. 18.

lina Chickadees became progressively stronger as numbers of titmice rose.

Some slight but consistent differences occurred in the foraging of Golden-crowned Kinglets in the presence of titmice; that is, the kinglets were displaced peripherally in the presence of increasing numbers of titmice (Fig. 19). There appeared also to be a slight tendency for kinglets to forage lower when in the presence of titmice in deciduous forests. In the mixed forest there was a slight increase in the tendency to use deciduous foliage in the presence of titmice. Figs. 10-12 indicate that the kinglets employed on the whole a more peripheral foraging pattern than did chickadees, hence a lesser effect of titmice on kinglets than upon chickadees would be predicted.

Activities of titmice in the presence of chickadees are not amenable to analysis in this manner because chickadees were nearly always present in large numbers (3 or more) when titmice were observed. Out of 951 standard foraging observations made upon titmice in Maryland, only 79 were made in the presence of no chickadees or only 1-2 chickadees.

Since chickadees usually were found in large numbers (3 or more), data upon the foraging of Golden-crowned Kinglets permitted analysis only

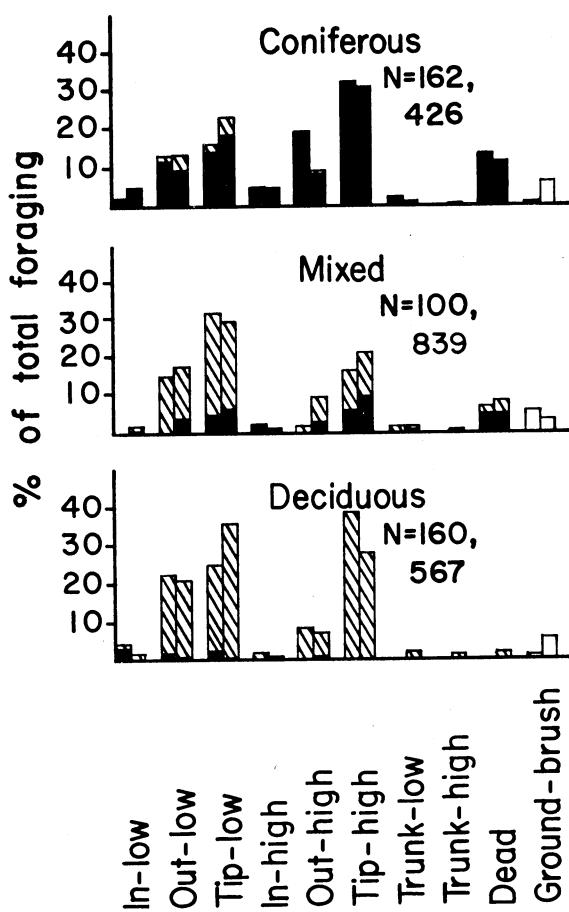


FIG. 20. Frequencies of foraging in different parts of the habitat by Golden-crowned Kinglets in the presence of 0 (left half of diad) and 3-3+ (right half of diad) Carolina Chickadees in Maryland. Foraging stations coded as in Fig. 7.

when chickadees were absent and when present in numbers of 3 or more (Fig. 20). In each habitat a marked increase occurred in the tendency for kinglets to work on the tips of foliage, particularly by hovering, when chickadees were present. Also, a tendency toward increased utilization of low peripheral areas (rather than high ones) existed when chickadees were present, except in the mixed forest. There, an increased tendency to utilize coniferous foliage was noted.

Sufficient data were not obtained on the foraging of titmice in the presence of Golden-crowned Kinglets to allow any firm predictions. In the one situation (deciduous forest) that approached the minimum number of observations for detailed analysis (80 observations when no kinglets were present, 98 where 1-2 kinglets were present, and 121 when 3 or more were present), no systematic variance was noted in numbers of observations in any foraging station. In mixed and coniferous

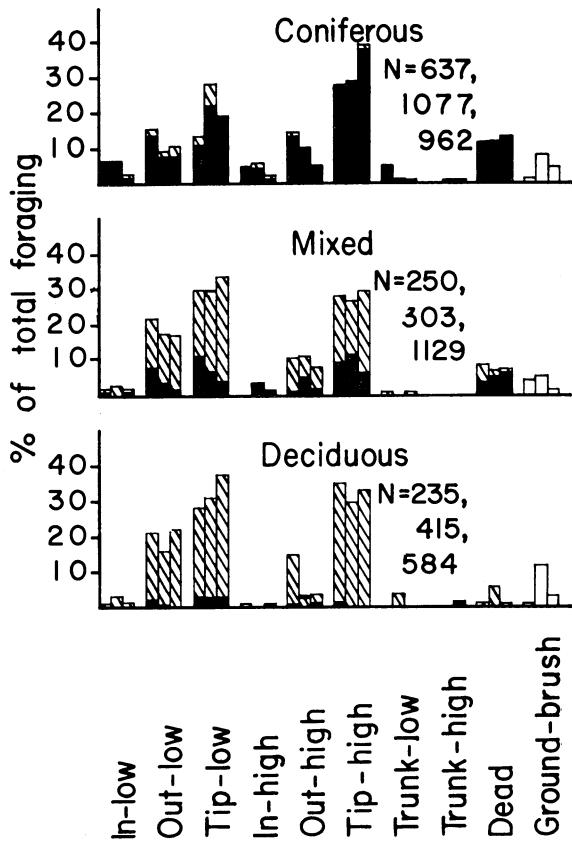


FIG. 21. Frequencies of foraging in different parts of the habitat by Carolina Chickadees in the presence of 0, 1-2, and 3-3+ Golden-crowned Kinglets in Maryland. Foraging stations coded as in Fig. 7, triads coded as in Fig. 18.

forests, substantial numbers of observations of titmice were made only in the presence of 3 or more kinglets, precluding such comparisons. The small number of observations in certain categories probably is the result of the strong attraction to the titmice by the kinglets.

Analysis of chickadees foraging in the presence or absence of the kinglets (Fig. 21) failed to reveal any consistent pattern of change as did the data on chickadees in the presence of titmice, suggesting that any variations appearing in the results were caused by factors other than the presence of the kinglets.

Two-Species Analyses in Maine

The presence of Red-breasted Nuthatches in the mixed forest resulted in a tendency for Black-capped Chickadees to move toward the inner parts of the vegetation and also to increase their utilization of coniferous growth (Fig. 22). However, no clearcut pattern of this sort was noted in the coniferous forest. The nuthatch appeared to be

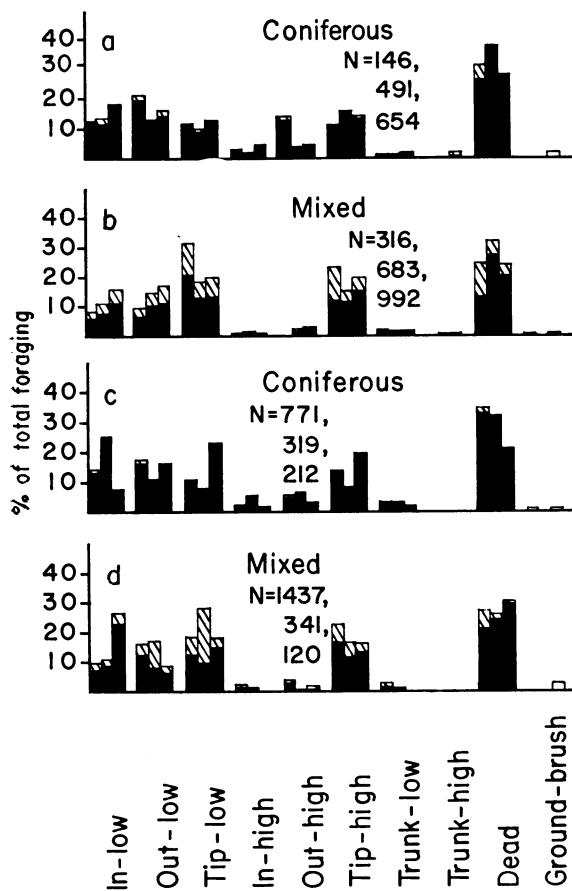


FIG. 22. Frequencies of foraging in different parts of the habitat by Black-capped Chickadees in the presence of 0, 1-2, and 3-3+ Red-breasted Nuthatches in Maine in summer (a & b); frequencies of foraging in different parts of the habitat by Black-capped Chickadees in the presence of 0, 1-2, and 3-3+ Golden-crowned Kinglets in Maine in summer (c & d). Foraging stations coded as in Fig. 7, triads coded as in Fig. 18.

somewhat dominant to the chickadee, but this relationship was not a unidirectional one (Table 14).

Black-and-White Warblers often are prominent members of these late summer flocks, though in low numbers (Table 3). This species displays a high level of aggressiveness at this season (Table 18). It is adapted to a nuthatch-like existence and usually is socially dominant to chickadees (Table 14). Since the foraging of Red-breasted Nuthatches and Black-and-White Warblers show many similarities, one might predict that their effects upon a third species would be comparable. In the coniferous forest chickadees foraged more peripherally when Black-and-White Warblers were present than when they were absent, and in the mixed forest chickadees used deciduous foliage more often when Black-and-White Warblers were

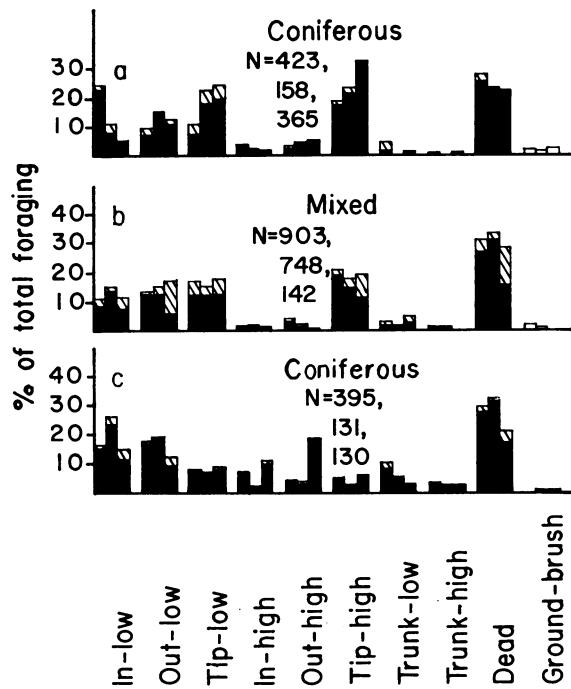


FIG. 23. Frequencies of foraging in different parts of the habitat by Black-capped Chickadees in the presence of 0, 1-2, and 3-3+ Black-and-White Warblers in Maine in summer (a & b); frequencies of foraging in different parts of the habitat by Red-breasted Nuthatches in the presence of 0, 1-2, and 3-3+ Golden-crowned Kinglets in Maine in summer (c). Foraging stations coded as in Fig. 7, triads coded as in Fig. 18.

present (Fig. 23). When present, the Black-and-White Warbler exerted the strongest effect on any species studied upon the foraging of chickadees. Analyses of flock composition during the late summer indicated that from flock formation in mid-July until 10 August if the number of Red-breasted Nuthatches in a flock was above the mean number per flock, the number of Black-and-White Warblers tended to be below it, and vice versa; after this time no such difference was noted.

Thus, frequently when the Red-breasted Nuthatches were absent early in the season, Black-and-White Warblers were present, exerting a stronger pressure on the chickadees than the Red-breasted Nuthatches and tending to force the chickadees toward the outer parts of the vegetation. Hence, when the effect of Red-breasted Nuthatches was lightest, the overall pressure in this direction was apt to be heaviest. As a result, demonstration of any relationship between Red-breasted Nuthatches and Black-capped Chickadees may be obscured. This problem potentially arises at any time when there are several common species in a flock and doubtless is a major reason why relationships are not more clearly cut in

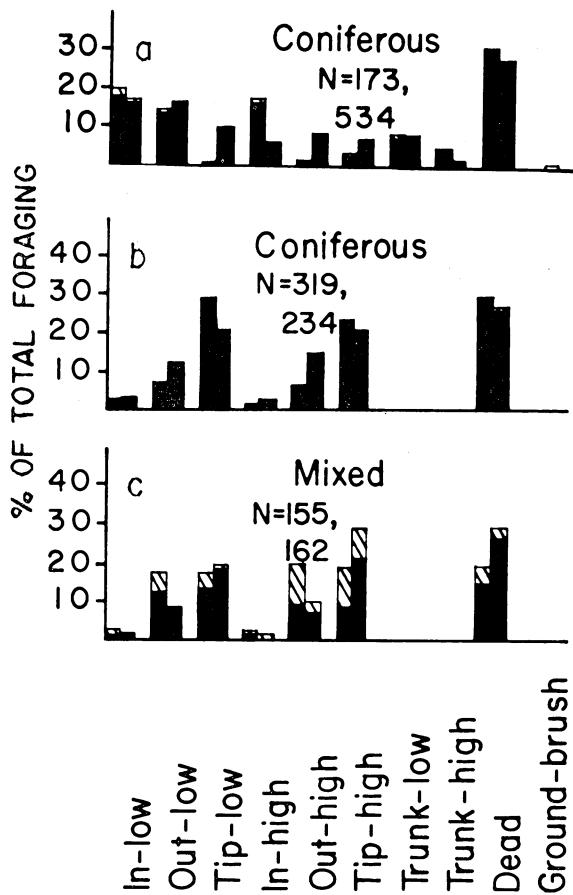


FIG. 24. Frequencies of foraging in different parts of the habitat by Red-breasted Nuthatches in the presence of 0 and 3-3+ Black-capped Chickadees in Maine in summer (a); frequencies of foraging in different parts of the habitat by Golden-crowned Kinglets in the presence of 0 and 3-3+ Black-capped Chickadees in Maine in summer (b & c). Foraging stations coded as in Fig. 7, diads coded as in Fig. 20.

these two-species comparisons. The particular pattern described above appears to be related to the territoriality of the Black-and-White Warblers, which breaks down in early August, resulting in a considerable lessening of hostile behavior of the species and perhaps accounting for the cessation of this reciprocal effect.

No clearcut pattern existed in the foraging of Black-capped Chickadees in the presence of Golden-crowned Kinglets, a clearly subordinate species (Fig. 22). A comparable situation was described from Maryland with Carolina Chickadees and Golden-crowned Kinglets (Fig. 21) and appears typical of the foraging of a dominant in the presence of a subordinate.

The relationship between foraging of Red-breasted Nuthatches and the other two common species (Black-capped Chickadee and Golden-

crowned Kinglet) is more obvious than in the case of Black-and-White Warblers. With both the nuthatch and kinglet, no opportunity existed for obtaining large numbers of observations on foraging behavior in the presence of one or two chickadees, since the latter species is so highly gregarious. As the nuthatch almost always was found with the chickadees when in mixed forests, nearly all the data represent situations where three or more chickadees were present, and analysis therefore is not possible. No strong differences occurred when Red-breasted Nuthatches forage in or away from chickadees in coniferous forests, though a consistent tendency to move peripherally in the presence of the chickadees may be noted (Fig. 24). This may be related to the slightly greater tendency for the chickadees to forage nearer to the trunk when Red-breasted Nuthatches were present in large numbers. This shift of both species may be similar to the situation that I observed between Brown-headed Nuthatches and Pine Warblers in Louisiana, where there was not a clearcut dominance relationship between the two species (Morse, 1967b). No consistent differences were noted in the foraging of the nuthatches in the presence of different concentrations of Golden-crowned Kinglets, a clearly subordinate species (Fig. 23). Sufficient data for this calculation were obtained only in the coniferous forest.

In the coniferous forest, Golden-crowned Kinglets in the presence of increasing numbers of chickadees displayed a moderate tendency to forage more frequently in the extremities of the vegetation (Fig. 24), a tendency that was also noted in chickadees when in the presence of Red-breasted Nuthatches. Since both chickadees and Red-breasted Nuthatches were usually present in a flock, this tendency may have been related to the effects of the Red-breasted Nuthatches on chickadees. In the mixed forest a tendency was noted for Golden-crowned Kinglets in the presence of chickadees to move outward and to forage more extensively in the coniferous elements, particularly the dead vegetation. In the presence of Red-breasted Nuthatches the same general pattern held as for the analysis with chickadees (Fig. 25); however, the tendency to forage in coniferous vegetation became almost absolute, and the tendency to forage in dead vegetation more enhanced when Red-breasted Nuthatches were present than was the case when the analysis dealt with chickadees.

Analyses of foraging in late summer flocks are further complicated by the large number of other

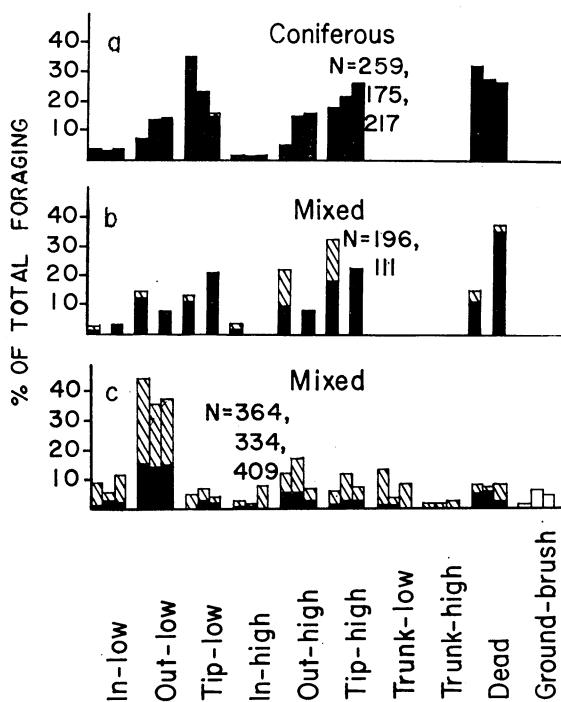


FIG. 25. Frequencies of foraging in different parts of the habitat by Golden-crowned Kinglets in the presence of 0, 1-2, and 3-3+ Red-breasted Nuthatches in Maine in summer (a & b); frequencies of foraging in different parts of the habitat by Black-capped Chickadees in the presence of 0, 1-2, and 3-3+ Golden-crowned Kinglets in Maine in winter (c). Foraging stations coded as in Fig. 7, triads coded as in Fig. 18.

species that participate from time to time in the flocks (Table 3). Several of these species are doubtlessly socially dominant to Golden-crowned Kinglets (Table 14) and their combined effects may be at least equal to that of as common a species as the Black-capped Chickadee.

In Maine during the winter it was possible to analyze the effect of Golden-crowned Kinglets upon Black-capped Chickadees in the mixed forest. It reveals no marked trends (Fig. 25), being consistent with the results of the comparable analysis of the late summer (Fig. 22).

Predicted and Realized Patterns of Foraging

Any attempt to draw general conclusions about foraging where three divisions are present (Species A in the presence of 0, 1-2, and 3-3+ individuals of Species B) is not a simple one. If we propose a situation where Species B has an increasing effect upon the distribution of species A in the foraging stations as its (B) numbers grow, we would ideally expect the middle category (foraging of Species A with 1-2 individuals of Species B) to have an intermediate value. On the other hand, if Species B has no effect on the distribution

of Species A, we would ideally expect no differences in the three categories.

The situations studied bear varying resemblances to this model. The model assumes that only two species are involved, and in few cases is such a situation obtained in the observations. The more species are involved, the more complicated will be the relationships, especially in species at the bottom of an interspecific hierarchy. Interaction obviously exists; in the relationship between Black-capped Chickadees, Red-breasted Nuthatches, and Golden-crowned Kinglets in Maine in the summer there was strong suggestion of this. Studies were made during a relatively short period of a season to minimize variability, but it is again an oversimplification to assume that no changes occurred during that time or from year to year. Sample sizes in some cases tested were small, and an N of 100 foraging observations may not be entirely comparable to that of a considerably larger one. All these factors would tend to obscure both a situation of stepwise progression and one of no difference.

However, a consistent difference was noted between foraging frequencies where subordinates were tested in the presence of dominants, and dominants tested in the presence of subordinates. Considering the histograms in Figs. 18-25, in the first case (subordinates in the presence of dominants) the middle category (foraging of Species A in the presence of 1-2 individuals of Species B) was more frequently of an intermediate value than the alternatives (foraging of Species A in the presence of 0 or 3-3+ individuals of Species B). When data from histograms were combined, the tendency for the middle category to have an intermediate value was shown to be significant ($P = 0.006$ in a binomial test). In the second case (dominants in the presence of subordinates) the middle category seldom was the most frequent of the alternatives. In fact, upon testing the reciprocal of the first hypothesis (the middle category was the least frequent of the alternatives), $P = 0.062$.

The independence of the different pieces of data in these tests and the combination of data from different areas may be questioned. Nevertheless, in spite of the variables involved, the tendency for the two groups (dominants) to sort out as they do is of considerable interest.

Indices of Overlap and Diversity

Indices of overlap were also made in Maryland and Maine (summer) between the foraging of a species in the presence of 0 and 1-2 or 3-3+ in-

dividuals of another species (Table 30). In several other cases, data are included when adequate numbers of observations were made only in the presence of 0 and 3-3+ individuals of the other species under consideration. The situation where three sets of data are available facilitates a more sensitive examination than when only two are available, since indices running in a consistent direction lessen the possibility that differences could be the result of difficulties encountered in gathering data. Sample sizes for these calculations appear in Figs. 18-25.

The data from Maryland fit into a quite consistent pattern. In cases run between Carolina Chickadees and Tufted Titmice and between Golden-crowned Kinglets and Tufted Titmice, as the titmice increased in numbers in the flocks the chickadees or kinglets increased their deviation in foraging from what they were when no individuals of the latter species were present. As chickadees foraged in situations with increasingly greater numbers of Golden-crowned Kinglets, remarkably little difference could be seen in the two indices obtained (0 and 1-2, 0 and 3-3+, and these indices were very high, indicating very little change that could be attributed to the effects of Golden-crowned Kinglets. Only one index is available from each habitat for kinglets in varying numbers of chickadees (0 and 3-3+).

Titmice are socially dominant to both chickadees and kinglets, and it appears that the presence of the former results in displacement of the latter two species. Chickadees are socially dominant to kinglets, and the indices change very little, suggesting that the presence of the kinglets has little effect upon the distribution of chickadees in the different foraging stations. If data were available for the foraging of kinglets in the presence of 1-2 chickadees, one would predict that the indices obtained between 0 and 1-2 chickadees would be higher than those obtained between 0 and 3-3+ in Table 30. Foraging observations of titmice were not obtained in adequate numbers to permit such a procedure to be repeated. Since they are dominant to the chickadees and kinglets, one would predict on the basis of the information obtained upon chickadees when in varying numbers of kinglets that the presence of the chickadees and kinglets would have little effect upon them.

In Maine (summer) several pairs of species could be compared. In cases where the foraging of Black-capped Chickadees was compared with both Red-breasted Nuthatches and Golden-crowned Kinglets, an interesting pattern obtained,

with the index between 0 and 1-2 greater than the one between 0 and 3-3+. This situation may be the result of the overall social dominance of Black-and-White Warblers that was described earlier. The relationship among the indices of this pair of species (foraging of chickadees in the presence of varying numbers of Black-and-White Warblers) is similar to that seen in titmice and Carolina Chickadees (dominant and subordinate). This explanation would allow the possibility that any interactions between Black-capped Chickadees and Red-breasted Nuthatches and between Black-capped Chickadees and Golden-crowned Kinglets would be masked by the interactions between Black-capped Chickadees and Black-and-White Warblers.

Indices consistent with the pattern seen in species socially subordinate to another species in Maryland appeared in the foraging of Golden-crowned Kinglets in the presence of Red-breasted Nuthatches. However, this effect was reciprocal. It may be related to the overall high level of hostilities and complex multi-species interrelationships at this season, but the specific basis for it is unknown. Comparison of the data from Maryland and Maine suggest the degree of complications that can be expected in a complex multi-species group.

Further reference to Table 30 indicates that while trends may appear, one cannot predict whether presence of a dominant will or will not decrease its foraging diversity. The subordinate species might either decrease its diversity of foraging or seek different areas. Willis (1966a) has discussed in detail the options open to a species in such a situation.

MODIFYING ENVIRONMENTAL FACTORS

Though this study has not been primarily concerned with the effects of climatological modifications on flocks, it is germane to consider briefly evidence obtained, since it will bear strongly upon the relevance of the observations I have made to the total energetic problem facing the birds throughout the periods of study. Despite their tendency to forage as indicated in earlier parts of the paper, members of flocks possess considerable adaptability to deal with a variety of environmental situations.

Snow and Ice

Accumulations of snow or ice that cover part of the foliage naturally will restrict the areas available for foraging, simply because individuals will not be able to reach them, at least without an

TABLE 30. Indices of overlap and diversity in foraging of a species (A) in the presence of varying numbers of another species (B). N's as in Figs. 18-25.

Species (A) foraging	In presence of (B)	Habitat	Overlap		Diversity		
			No. sp. B vs 1-2 sp. B	No. sp. B vs 3-3+sp. B	No. sp. B	1-2 sp. B	3-3+sp. B
Carolina Chickadee	Tufted Titmouse	Coniferous-Maryland	0.98	0.96	0.73	0.70	0.67
Carolina Chickadee	Tufted Titmouse	Mixed-Maryland	0.93	0.91	0.87	0.78	0.84
Carolina Chickadee	Tufted Titmouse	Deciduous-Maryland	0.93	0.92	0.71	0.68	0.74
Carolina Chickadee	Golden-crowned Kinglet	Coniferous-Maryland	0.97	0.97	0.73	0.70	0.71
Carolina Chickadee	Golden-crowned Kinglet	Mixed-Maryland	0.97	0.97	0.82	0.82	0.86
Carolina Chickadee	Golden-crowned Kinglet	Deciduous-Maryland	0.97	0.93	0.73	0.70	0.71
Golden-crowned Kinglet	Carolina Chickadee	Coniferous-Maryland	—	0.95	0.64	—	0.71
Golden-crowned Kinglet	Carolina Chickadee	Mixed-Maryland	—	0.92	0.67	—	0.74
Golden-crowned Kinglet	Carolina Chickadee	Deciduous-Maryland	—	0.92	0.57	—	0.56
Golden-crowned Kinglet	Tufted Titmouse	Coniferous-Maryland	0.94	0.92	0.71	0.69	0.65
Golden-crowned Kinglet	Tufted Titmouse	Mixed-Maryland	0.94	0.82	0.75	0.79	0.68
Golden-crowned Kinglet	Tufted Titmouse	Deciduous-Maryland	0.93	0.83	0.56	0.58	0.53
Golden-crowned Kinglet	Red-breasted Nuthatch	Coniferous-Maine (summer)	0.92	0.96	0.68	0.58	0.69
Black-capped Chickadee	Red-breasted Nuthatch	Mixed-Maine (summer)	0.89	0.94	0.77	0.77	0.79
Black-capped Chickadee	Golden-crowned Kinglet	Coniferous-Maine (summer)	0.85	0.92	0.64	0.62	0.70
Black-capped Chickadee	Golden-crowned Kinglet	Mixed-Maine (summer)	0.94	0.94	0.80	0.74	0.66
Black-capped Chickadee	Black-and-White Warbler	Coniferous-Maine (summer)	0.90	0.88	0.73	0.70	0.65
Black-capped Chickadee	Black-and-White Warbler	Mixed-Maine (summer)	0.98	0.92	0.77	0.71	0.81
Red-breasted Nuthatch	Black-capped Chickadee	Coniferous-Maine (summer)	—	0.93	0.68	—	0.71
Red-breasted Nuthatch	Golden-crowned Kinglet	Coniferous-Maine (summer)	0.96	0.88	0.70	0.65	0.80
Golden-crowned Kinglet	Black-capped Chickadee	Coniferous-Maine (summer)	—	0.96	0.55	—	0.60
Golden-crowned Kinglet	Black-capped Chickadee	Mixed-Maine (summer)	—	0.88	0.81	—	0.69
Golden-crowned Kinglet	Red-breasted Nuthatch	Coniferous-Maine (summer)	0.96	0.93	0.52	0.58	0.59
Golden-crowned Kinglet	Red-breasted Nuthatch	Mixed-Maine (summer)	—	0.73	0.79	—	0.59
Black-capped Chickadee	Golden-crowned Kinglet	Mixed-Maine (winter)	0.88	0.90	0.78	0.83	0.84

TABLE 31. Frequency (in %) of foraging on ground in Maryland.

Species	No Snow			Snow		
	Total Foraging Observations	% on Ground	No. of Observations on Ground	Total Foraging Observations	% on Ground	No. of Observations on Ground
Carolina Chickadee.....	4830	0.6	29	780	6.4	50
Tufted Titmouse.....	595	5.9	35	204	9.8	20
Golden-crowned Kinglet.....	1936	1.2	24	300	4.0	12

excessive expenditure of work. Snow usually falls quickly from trees, often knocked from them by the birds, and appears seldom to be an important factor unless it crusts heavily. However, infrequent ice storms doubtlessly result in a potentially critical period for the birds involved. In Maryland it was possible to observe the effect of a ground cover of snow on members of the flock. While under snowless conditions the use of the ground by members of flocks is low, with a cover of snow usage increases in some species (Table 31) and appears to be the result of the conspicuousness of fresh potential food items that have fallen from the trees against a conspicuous white background. At this time food sources lying on the ground prior to the cover are apparently unavailable; no individuals were observed digging in the snow. All observations in Maine during the winter were made while a cover of snow existed. Hartley (1953) and Gotshen (1960) have

also commented upon the effect of snow on foraging by flock members.

Wet Foraging Areas

The vast majority of foraging observations were taken when the foliage was dry. Subjectively, rain itself (if not particularly heavy) appears not to result in a marked change in foraging stations utilized, though it quickly wets the foliage, introducing a second variable. The effect of wet vegetation was assessed by studying flocks on overcast days while foliage was literally dripping as a result of recent rain. Fig. 26 illustrates the foraging of Carolina Chickadees on 13 December 1965 in a wet coniferous forest in Maryland. This species utilized heavily the available dead limbs on pine trees and showed an overall tendency to avoid the wet foliage. Few observations were made on deciduous trees (without foliage at this season) in this predominantly coniferous forest, but these

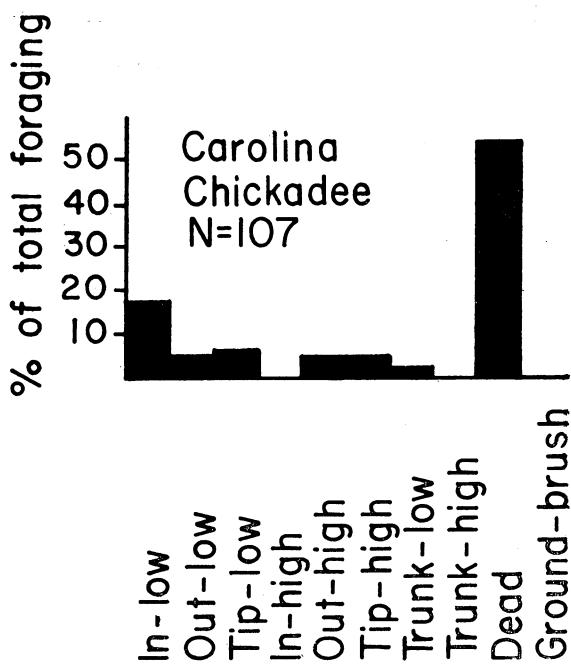


FIG. 26. Frequencies of foraging of Carolina Chickadees in different parts of a coniferous forest in Maryland. Data obtained while foliage was wet. Foraging stations coded as in Fig. 7.

were similar to those observed at other times. Since the flocks observed on this day contained over three Tufted Titmice and three Golden-crowned Kinglets, Fig. 26 should be compared with the one for the corresponding situations existing when the vegetation was dry (Figs. 18 and 21). The index of diversity in the wet foliage was considerably lower (0.52) than in dry foliage, where it was 0.67 with titmice, 0.71 with kinglets.

Wind

Wind of high velocity presents a confounding picture to the study of these groups. Less activity is observed at such times, but this cannot be separated clearly from the reduced conspicuousness of individuals caused both by the movement of foliage and the masking of their vocalizations to the observer. While observations for direct comparison with relatively windless conditions are virtually impossible to make under these circumstances, field work at such times suggests strongly that the members for the most part forage lower than on days when no wind or only a moderate wind (up to 15 Kph) is blowing. On several occasions individuals were observed nearly to be blown from exposed perches. This tendency to compress their stratification in the vegetation action will either crowd the individuals or force them to spread out horizontally.

Temperature

Some observations of distribution within the forests were noted that could probably be attributed to the effects of temperature. Upon occasions at low temperatures certain individuals would be noted in the early morning in locations where they would be exposed to the sunlight, a phenomenon noted by Lawrence (1958) in Black-capped Chickadees and other species. Under these situations they might remain stationary for a few minutes at a time. Carolina Chickadees and Golden-crowned Kinglets were noted performing in such a manner upon several occasions; this behavior might result in a tendency to follow with foraging activity in an immediately adjacent area; however, this matter was not investigated further. Johnston (1942) noted that unseasonably warm weather hastened flock dispersal.

Season

There was a decrease in the tendency for birds to participate in flocks as spring approached. On the basis of the flexibility of the foraging of flock members, depending upon the composition of flocks, one might anticipate a resultant change of foraging to occur concurrently. For this reason, observations on winter flocks reported in this paper do not extend beyond 31 January in Louisiana and 15 February in Maryland. Continuation of this investigation into the breeding season would constitute another interesting study.

RATES OF MOVEMENT

One characteristic of flocks is that they are almost constantly on the move, rather than remaining in a single area for extended periods foraging upon a localized food source. Typically they move briskly through their collective range, foraging while under way. Rapid movements through what appear to be unfavorable areas (openings in the forests, patches of different habitat) also occur, but are not combined with data on movements of flocks presented in this paper. By choosing carefully the habitat in which flocks were to be studied, this problem was minimized.

Rates of movement of several flocks were obtained in both Louisiana and Maryland (Fig. 27). In Louisiana, large flocks moved through the habitat more rapidly than did small ones, though individual variability was high. The data from Maryland are not as easily interpreted, though in large part they appear consistent with those from Louisiana.

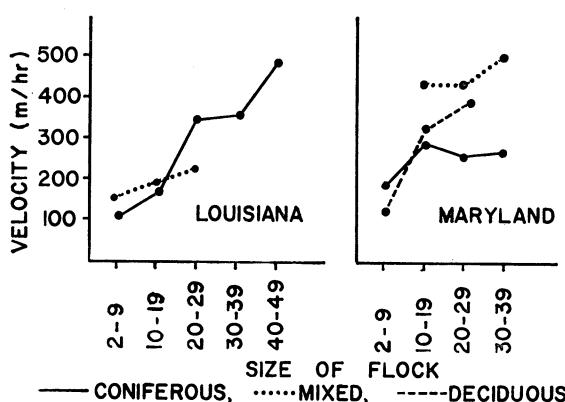


FIG. 27. Rates of horizontal movement in flocks of different sizes. Numbers on plot indicate number of flocks measured. Standard deviations: Louisiana (coniferous)—0 (2-9), 51 (10-19), 98 (20-29), 42 (30-39), 165 (40-49). Louisiana (mixed)—35 (2-9), 85 (10-19), 47 (20-29). Maryland (coniferous)—131 (2-9), 101 (10-19), 8 (20-29), 0 (30-39). Maryland (mixed)—237 (10-19), 138 (20-29), 108 (30-39). Maryland (deciduous)—19 (2-9), 164 (10-19), 64 (20-29).

In Louisiana, an average flock in the longleaf pine forest (area of lowest bird density) moved faster than one in the mixed forest; however, it was also larger (Table 1), and flocks of small size moved at quite comparable rates in the two habitats, though there was a marked difference between rates of movement of the largest flocks of the mixed forest and similar-sized ones of the longleaf pine forest. In Maryland, rates of movement obtained in the mixed forest (area of lowest bird density) were larger than for the two others, and in any given size range a considerable difference existed as well. One possible discrepancy appears in the medium-sized flocks of the coniferous forest, which show a peak in rate of movement, with a slight decrease in rate seen in the larger ones. However, this difference in rate is not large, and the sample size of the large flocks is small, so no definite conclusions about this part of the curve probably should be drawn.

Two general trends thus appear; first, for large flocks to move faster than small ones, and second, for flocks in areas of low densities of birds to move faster than in areas of high density. The second factor may or may not be independent of the first factor.

The densities may serve as an estimate of the mean carrying capacities of the areas studied. The assumption is frequently made that such a correspondence exists (see Lack, 1954), though precise data on this problem are few. However, Gibb (1960), working largely with populations in England similar to the ones studied in this investi-

gation, established a close correlation between densities of birds and their stocks of food in the winter. If we assume that population density serves as an indicator of the availability of resources, then we find that flocks are largest and move fastest where resources are in minimum supply. In these areas flocks are also widely spaced (i.e., hold large home ranges), as indicated in Table 21. Such an overall patterning then apparently is advantageous in depauperate habitats. While such a system does exist, it has definite limits. Only upon rare occasions does one find a flock of over 45 individuals in any of the study areas.

THE ROLE OF PREDATION UPON FLOCKING BEHAVIOR

Among the advantages often attributed to the flocking of small birds is an improved protection from predators. Many flocking species possess characteristic vocalizations that are given when predators are observed, and they react to such signals given by individuals of their own or other species. Birds within hearing range thus are more effectively apprised of danger than are single birds, which may produce and respond to such stimuli, but often are too scattered to obtain this advantage.

The main purpose of this section is to describe the responses to predators of birds in flocks and to comment upon the frequency of these actions. Different responses are usually accorded to flying predators on one hand and to perched avian predators or potential nonavian predators on the other. When perched a winged predator often will elicit a different response than when in flight, commonly referred to as mobbing and comparable to the response that potential nonavian predators usually elicit.

Mobbing Actions

Members of mixed-species flocks participate strongly in mobbing actions, though these tendencies are shared by many other species. The behavior is particularly conspicuous when a flock responds, due to the large number of individuals involved. Frequently this commotion will attract other species in the immediate area, which will participate also. Carolina Wrens, Mockingbirds, and Cardinals were particularly prone to participate in these groups in Louisiana and Maryland.

Most often this behavior was directed at the observer when he approached too close to the group; hence, in order to study undisturbed birds it was advantageous to remain some distance (25 m or more) from members of the flock. Hinde

TABLE 32. Types of flying predator calls given by chickadees in responses/hr, with N in parentheses. Includes responses to winged predators, inappropriate stimuli, and cases where cause not known.

Species	Locality	Sibilant (<i>tsee</i>) call	Nonsibilant (<i>chit-chit-chit</i>) call	Chorus (Pri- marily Sibilant (Calls)	Total hr that Flocks were Observed
Carolina Chickadee.....	Louisiana	.024 (12)	.002 (1)	.002 (1)	500
Carolina Chickadee.....	Maryland	.003 (2)	.020 (11)*	.003 (2)	650
Black-capped Chickadee.....	Maine (summer)	.008 (6)	.005 (4)	.001 (1)	750
Black-capped Chickadee.....	Maine (winter)	.013 (2)	.013 (2)	0 (0)	150

*In four cases sibilant notes immediately followed initial nonsibilant notes.

(1952) and Erard (1960) have commented upon the tendency of other flocks of titmice to mob human beings. In the present study, Black-capped Chickadees in the late summer were particularly sensitive to human observers.

Few such responses appeared to be directed at other organisms during the periods of study, though they are known to be given to a variety of birds and mammals (Hinde, 1952). Mobbing responses given to known objects other than humans consisted of two directed at Red Squirrels (*Tamiasciurus hudsonicus*) in Maine and one to a perched Barred Owl in Louisiana. Responses to human beings are not included, since they were so dependent upon the actions of the observer.

Description of Calls

Some members of flocks possess two distinctive vocalizations that are involved in responses given in the presence of winged predators. Odum (1942) named them *warning* and *alarm* notes in the Black-capped Chickadee, but I will refer to them as *sibilant* and *nonsibilant* calls, respectively, in order to avoid any possible connotations of function. The term *flying predator call* will be used as a general category to include all calls given in apparent response to a predator in flight. Again, any intent of function should be avoided when using this term. Two vocalizations comparable to those of the Black-capped Chickadee are given by Carolina Chickadees. I noted only one type of flying predator call in the few other species that I heard giving a distinctive vocal response of this nature. In both species of chickadees, the sibilant call is of extremely high frequency, described by Odum in the Black-capped Chickadee as a thin, very high-pitched "*tsee*," and in my experience usually repeated in phrases of three or more notes by both species of chickadees. The nonsibilant calls appear similar to other vocalizations of the species in frequency, described in the Black-capped Chickadee by Odum as "*chit-chit-chit*," and very similar in the Carolina Chick-

adee. The only note that I heard from Tufted Titmice involved in defensive activities was a high-pitched "*seeet*." Brown-headed Nuthatches gave a series of "*see-see-see*" notes very similar to other notes of their repertoire. When such situations arose, several species of warblers gave sibilant "*tsit*" notes rather similar to other notes given by them outside the breeding season. Since I heard only a single type of flying predator call from titmice, nuthatches, and warblers, they are not classified as either sibilant or nonsibilant calls. No other species appeared to give flying predator calls in the flocks that I studied. It remains quite possible, however, that other members use similar calls upon occasion, since the presence of flying predator calls is widespread (see Marler, 1955).

Frequently chickadees give only sibilant calls, but sometimes nonsibilant ones follow. At other times nonsibilant calls may be the first vocalizations heard. Regardless of the nature of the first vocalization, individuals dived quickly for cover, scattered, or froze—actions that have been noted by several other workers (Sharpe, 1905; Hindwood, 1937; Odum, 1942; Hinde, 1952; Morley, 1953). In every observation made of this evasive behavior in the present study, if the stimulus was identified it proved to be a predator in flight or another species of bird.

My observations suggest that a geographical difference exists in the tendency to give both sibilant and nonsibilant calls in the Carolina Chickadee (Table 32), sibilant notes being given relatively more frequently in Maryland and nonsibilant relatively more frequently in Louisiana. Both of these differences are significant ($P < 0.005$ in a Fisher Exact Probability Test).

A *chorus* (a series of call notes given simultaneously by many birds from scattered locations) occasionally follows initial notes (Table 32). In their studies upon Common Bushtits Grinnell (1903) and Miller (1922) referred to comparable vocalizations as *confusion choruses*. In the Black-

TABLE 33. Stimuli accompanying flying predator calls of mixed flocks.

Locality	Number of Attacks	Stimulus		
		to Winged Predator	Inappropriate Stimuli	Cause Not Known
Louisiana.....	0	7	2	4
Maryland.....	0	3	2	8
Maine (summer).....	0	2	5	3
Maine (winter).....	0	3	0	1

capped and Carolina Chickadees choruses consisted of infrequent single, high frequency notes, similar to the *tsee* note, given by many or all the individuals of the species in the flock. I was unable to determine whether any other species participated in choruses.

Responses of Regular Flock Members to Predators or Unknown Causes

Though infrequent in each area studied, responses to winged predators by mixed-species flocks were seen most often in Louisiana (Table 33). All observations of evasive activities in the presence of a predator by members of mixed-species flocks there were made in the longleaf pine forest, where these birds responded to several wintering American Sparrow Hawks. In four other cases (pine and mixed forests) this behavior was observed when no specific stimulus was seen. Although no hawk was observed actively attacking individuals in the flocks, sometimes they flew repeatedly over the trees at a low altitude, landed in trees or circled over the flocks, occasionally calling loudly. During these periods members of flocks emitted vocalizations nearly continually. With rare exception vocalizations were commenced by Carolina Chickadees, which characteristically gave series of sibilant notes initially. They then dived into the scattered underbrush, where they frequently continued to give sibilant notes, sometimes in the form of a chorus. Carolina Chickadees fed heavily in the sparse deciduous understory during the winter (Fig. 7) habitat in which they probably were most vulnerable.

Other members of the flocks in Louisiana responded in various ways. Though they also foraged frequently in the exposed deciduous understory, actions of Tufted Titmice at such a time were less predictable than those of the chickadees, the titmice displaying a less pronounced tendency than chickadees to move into thicker cover of the understory when sibilant or nonsibilant notes were given, at times remaining nearly motionless at the point where they were

foraging. Upon three occasions titmice were observed to fly distances over 30 m in the open bushes of the understory directly after a pass by a hawk. Brown-headed Nuthatches and Pine Warblers decreased their movements considerably, though seldom did they cease activity completely under these circumstances. They remained in the pine trees, the area in which both foraged almost exclusively. Upon one occasion that an American Sparrow Hawk flew over an unmixed flock of Brown-headed Nuthatches, these birds gave loud calls that closely resembled their normal loud *see-see-see* notes. Activity diminished considerably at this time, though it did not completely cease. Upon two occasions individuals of this species flew considerable distances in the open following a pass by the hawk. Red-cockaded Woodpeckers appeared not to modify their activities under these circumstances, calling regularly and continuing their activities after the chickadees' note had been given. Most of this woodpecker's activities were conducted upon exposed pine trunks.

After such vocalizations activity returned toward normal as soon as Carolina Chickadees began calling with usual quality chick-a-dee notes and commenced to move about in the low vegetation where they had sought cover. Usually these notes were given between 2 and 10 min after the initial vocalizations. Myrtle Warblers and Ruby-crowned Kinglets also were seen to emerge from low vegetation following sibilant calls of chickadees on different occasions, and they probably sought cover at this level. They frequently foraged in the exposed parts of the deciduous understory.

One might question whether the American Sparrow Hawk is an effective predator upon members of mixed flocks, and thus whether members respond to it as a true predator, especially since the individuals that I studied were not actually observed to attack members of the flock. While this species does not usually prey as heavily upon small birds as do some of the small species of the genus *Accipiter*, it not infrequently feeds upon songbirds, especially when other food is scarce (Bent, 1938). Responses by potential prey species to American Sparrow Hawks were similar to those given Sharp-shinned Hawks upon the occasional instances that the latter were seen outside the study areas. Thus, the above observations probably represent usual reactions to a flying predator.

The actions accompanying flying predator calls of flocks studied in Maryland were comparable to those observed in Louisiana; but in two cases

Tufted Titmice gave the first calls. However, in only three cases were potential predators seen during these observations (Table 33). Carolina Chickadees feeding in Virginia pines worked principally on the outer parts of foliage and often scattered when sibilant or nonsibilant calls were given, this movement resulting in a retreat to a less vulnerable position. They usually remained high in the trees at this time. When calls were given at a time that birds were vulnerably located high in a defoliated tree, they remained still. Choruses, in which vocalizations of Carolina Chickadees were identified, followed the flying predator calls twice. As in Louisiana, *chick-a-dee* notes of the Carolina Chickadees signalled a return to previous activities.

Black-capped Chickadees in Maine gave flying predator calls that were similar to those of the Carolina Chickadees. If these vocalizations were given when a chickadee was located in a defoliated tree, the bird remained motionless in that position, otherwise they scattered. Choruses were also recorded in which only Black-capped Chickadee vocalizations were definitely identified, these notes being extremely similar to those of the Carolina Chickadees. *Chick-a-dee* notes (also reported by Odum, 1942) resulted in a return to usual activities.

Responses of Temporary Associates to Predators or Unknown Causes

Small groups of Eastern Bluebirds, Slate-colored Juncos, and Chipping Sparrows occasionally followed mixed flocks in the pinelands of Louisiana for short periods of time. The juncos and sparrows usually foraged on the ground, while the bluebirds frequently flew down to it from low limbs in order to pick up objects of food. None of these species regularly utilized foraging areas of the members of mixed flocks. Small birds probably were most vulnerable on the ground because of the sparse grassy undergrowth in these areas. All three species responded strongly to the flying predator calls of the Carolina Chickadees, usually scattering simultaneously and alighting in the lower limbs of the pines. A similar tendency of Slate-colored Juncos to follow mixed flocks was noted in the study areas in Maryland. Several openings with young deciduous second growth and slash provided suitable habitat for these birds. When mixed flocks foraged about the openings juncos frequently moved with them. Occasionally they even followed the flocks into the deep forest, and almost any junco seen away from the edge was accompanying a mixed flock.

Nature and Frequency of Attacks by Predators

Probably the most important potential predator of small woodland birds in eastern North America is the Sharp-shinned Hawk. Occasional observations of this species in all three geographic areas where studies were conducted and along a migratory pathway at Kent Island, Queen Anne's Co., Maryland, in the fall of 1965 indicated that these birds usually hunted for small birds by flying just over and through the treetops, a characteristic commonly attributed to this species and close relatives (Bent, 1937). In this manner they remained relatively obscure until an instant before the prey was attacked. Sharp-shinned Hawks also perched frequently inside the foliage of the trees in that forest. The closely-related Cooper's Hawk (Bent, 1937) and European Sparrow-hawk (L. Tinbergen, 1946; Rudebeck, 1950), as well as the Northern Shrike (Cade, 1962), all potential predators of members of parid flocks in the Northern Hemisphere, also take advantage of stealth in hunting.

In seven years of intensive field work studying flocks in three separate geographical areas, I have seen only infrequent instances of predation or attempted predation by winged raptors on woodland birds, whether within flocks or without. During periods in which I tallied the observations found in Table 33, I recorded no attempts at predation by those birds, and my observations at other times further suggest an overall low frequency of predation.

In many parts of the northern coniferous forests of North America few if any diurnal avian predators of small birds are present in the winter. The scarcity of such a type of predator is especially noticeable in heavily wooded areas, where the sporadic Northern Shrike is infrequent. Sharp-shinned and Cooper's hawks, the major bird-hunting hawks in these areas, do not regularly remain in the northern part of their range during the winter season. Though I have observed three sets of responses from Black-capped Chickadees to Goshawks, this uncommon species feeds principally upon larger prey (Bent, 1937).

However, all of my other studies have been conducted within the seasonal geographic range of one or more species of hawks that feed principally upon small birds. The frequency of observations of these hawks has been low, as has been the number of attacks or attempted attacks on small birds. Six winter bird population censuses conducted in areas where flocks were studied indicated that a very low density of predators was present, and an extremely high ratio of small

potential prey birds to predators (Tables 9-10). The only species of predator observed more than once during these six censuses was the American Sparrow Hawk. A survey of relevant literature reveals that quantitative information upon frequencies of attacks and/or captures of flock members by predators is particularly rare.

There is no evidence to suggest that the absence of observations upon predators noted in Table 33 could be explained by the conspicuousness of the observer to shy predators. The techniques used in studying flocks necessitated long periods of stationary observations, during which interference with the flocks was virtually nonexistent. Still, it is not yet possible to eliminate unequivocally the possibility that predators and flock members did not respond identically to my presence.

Responses to Inappropriate Stimuli

Responses may be given to an inappropriate stimulus (Table 33). In the Satsuma, Louisiana, study area, Mourning Doves that flew at a low level over trees containing Carolina Chickadees elicited sibilant calls from them. With one exception no members of flocks studied in Louisiana or Maryland reacted to Turkey Vultures or Black Vultures flying overhead. In that case a flock in Maryland responded to a nonsibilant call of a Carolina Chickadee when a Turkey Vulture soared at a height of about 15 m over the pine trees that the members occupied. None of the vultures observed ever flew at a height substantially lower than 15 m over the trees.

Observations made on 31 July 1962 at Hog Island, Maine, illustrate another case. A mixed flock containing Black-capped Chickadees and several species of warblers was foraging in the crown of a white birch when a Black-billed Cuckoo suddenly flew into the tree and silently alighted in its midst. A flying predator call was given, and the birds immediately dived for cover. Shortly, they congregated in a nearby white birch and continued foraging. After a few minutes the cuckoo alighted in this tree, causing repetition of the response. Mixed flocks on Hog Island did not respond to Common Loons, Double-crested Cormorants, Great Black-backed Gulls or Herring Gulls when these species flew over the trees at a low level. With one exception, no reaction to Great Blue Herons was observed. At that time the heron flew unusually low among the tops of the tallest trees. The two responses to the Osprey that I noted also occurred when individuals flew among the treetops rather than well over them. Neither did these flocks respond to the presence of Blue

Jays; however, the jays were extremely noisy at these times and moved rather deliberately, seldom making a silent abrupt move.

In 18 of the 41 flying predator responses that I observed in the course of the studies, no predator or other possible stimulus for a response was noted (Table 33). It is impossible to say how many of these responses were caused by an undetected predator, but the low frequency of predators noted suggests that many of these reactions occurred in their absence. Responses to inappropriate stimuli have been reported by several investigators. In addition to my observations, Hinde (1952), Morley (1953), and Gibb (1960) observed English flocks of tits giving responses to Wood Pigeons, and Hinde further mentioned that Blackbirds at times caused such a reaction. Scrub Jays may cause Common Bushtits to produce this response (Miller, 1921).

In short, highly developed systems exist in mixed flocks that may warn members of the presence of predators. They were infrequently used in this way during the study and occasionally were set off by other stimuli.

DISCUSSION

Tendencies of Species to Participate in Flocks in Different Habitats

Considerable variation existed in the densities of bird populations wintering in study areas that were censused (Tables 9-10). Lack (1954) has proposed a direct correspondence between population density and food supply. During most winters the food supply in the longleaf pine forests, the area of lowest population density in Louisiana, is known to be exceedingly low. This species of tree supports an extremely low density of insects (Wahlenberg, 1946). The mixed forest was the area of lowest population density in Maryland. Upon 15 occasions flocks that had been foraging for one hour or more in deciduous forests adjacent to mixed forests were observed to fly almost directly through several hundred meters of mixed forest, scarcely stopping to forage in transit. Upon reaching deciduous forest again, the birds began to forage as before. Never was the opposite tendency (to forage in mixed forests and to fly directly through deciduous forests) noted. This behavior suggests that more advantageous foraging conditions exist in the deciduous forest than in the mixed forest. Thus, while extensive sampling of vegetation was not performed to quantify differences in food abundance or availability, the indirect data permit tentative acceptance of Lack's correlation of population density and food supply.

Further, Gibb's (1960) data on some parid flocks in England demonstrate a close correspondence between these two factors.

A considerable amount of evidence suggests strongly that participation in flocks is an effective adaptation to difficult environmental conditions. Hinde (1952) points out that if the food supply and environmental conditions permit, territoriality may be held through the winter in some species of the genus *Parus*. If conditions are not favorable, there is a tendency for individuals to stay near the formerly held territory and to participate in flocks. These comments are based principally upon European titmice. In Japan, Ogasawara (1965) noted marked seasonal differences in participation of several species, as did Gotshen (1960) in Russia, which may be associated with changes in availability of resources.

Table 8 points out that an inverse relationship existed between the overall density of birds and the percentage of the total that belonged to flock-participating species. Lastly, most flock-joining species showed the highest tendency to participate in flocks where the lowest population density existed (Figs. 3-4). When a temporarily superabundant food source of the Brown-headed Nuthatch (pine seeds) became available in the longleaf pine forest of Louisiana, that bird demonstrated a marked decrease in flock participation (Morse, 1967b). This information suggests that individuals in flocks obtain advantages related to the securing of food by participating in these groups.

It must be pointed out that well-developed flocks are found in the tropical forests (Bates, 1864; Moynihan, 1962), areas well-known for their abundance of life, including birds. However, the vast majority of tropical areas demonstrate some sign of seasonality (Richards, 1952), so it is probable that fluctuations in food availability occur. Smythe's recent work (in press) on Barro Colorado Is., Canal Zone, demonstrates a marked fluctuation in seasonal fruit fall there, accompanied by fluctuations in the cycles of species associated with this food chain. Thus, it appears premature to assume that an abundance of resources is always available in areas that support high densities of animals. If food is short in supply at certain times the above-mentioned rationale for flocking would exist.

Foraging of Different Members of Flocks

All species studied concentrated their activities in certain parts of a habitat; furthermore, foraging stations were used in different ways by dif-

ferent species. A tendency to specialize strongly was least marked, however, in the commonest and most frequent species of the flocks studied (chickadees, titmice, kinglets, etc.). These species also displayed high indices of foraging overlap, suggesting that a premium exists for species with similarities in foraging to be together.

The Effect of Other Species upon Foraging

The data indicate that individuals modify their areas of foraging in the presence of socially dominant species, but that a reciprocal effect is not well developed or is absent. If such a situation obtains, one might ask why subordinate species show a marked tendency to participate in flocks. Indeed, one could alternatively hypothesize that if these groupings modified the foraging of an individual as indicated, that individual would demonstrate a marked tendency to avoid them, rather than to participate in them. Hence, the observed condition requires explanation.

Since different species utilize particular parts of the environment with varying frequencies, they reduce the probability of meeting by chance other species at very close range. With the increasing displacement noted in foraging stations as certain species appear in higher numbers, the frequency of close contacts should remain at a low level. When individuals meet at sufficiently close range, interactions usually occur (Fig. 5). Hence, movement into alternate feeding stations should act to keep the number of hostile encounters at a low level.

Modifications of habitat utilization in response to another species should occur with minimal disturbance among individuals that are regularly in contact, rather than ones that only occasionally meet (*i.e.*, are not flock members). The importance of individual recognition in the organization of intraspecific hierarchies has been stressed by many workers, who have also reported relatively low levels of overt aggression in these groups. In particular, Hamerstrom (1942) found these conditions in winter flocks of Black-capped Chickadees. Initially, high levels of hostile interactions may be directed at strange individuals (Hamerstrom); regular participation of members may maintain them at a low frequency. It appears reasonable that participation of individuals in groups of more than one species would facilitate a low level of aggression. The low level of interspecific hostile interactions and high degree of integration noted in flocks suggest that strong interspecific organization exists. Where a habitat is frequented by species with overlapping require-

ments this condition should allow the individual a maximally advantageous use of resources with a minimal amount of interruption. Though avoidance of flocks offers subordinates the opportunity of using the entire habitat occasionally, this option was not regularly utilized. Species that do not join flocks almost always are ones that share few similarities in foraging to members of these groups. Though the Brown Creeper is a narrow specialist, considerable overlap in foraging occurs with nuthatches and woodpeckers.

In the presence of socially dominant species subordinate species modified their foraging in a direction that facilitated increased use of their special foraging adaptations. For example, Golden-crowned Kinglets demonstrated an increased tendency to forage in the outer extremities of the foliage, often hovering at tips, when socially dominant species were present. Thus, it may be maximally advantageous for kinglets to be opportunistic and to make heavier use of the inner parts of trees if these areas are not being exploited by other species, but to retire to their area of specialization if the inner area is being exploited by dominants, even if the subordinates cannot gather food as rapidly in the outer area as in the inner area in the absence of dominants. Variation occurred in numbers of a species; for instance, some flocks in Maryland appeared not to contain titmice at any time during the winter. Ability to exploit a variety of foraging stations allows a flexibility lacking if adaptation occurred for marrow specialization to a largely exclusive part of the habitat. In such variable and unpredictable environments selection for opportunism doubtless occurs, as well as selection for specialization. If dominant species that use these stations are present, then it is probably most advantageous for the subordinates to forage in the area where they are highly adapted to feed, rather than to encounter a high frequency of hostile interactions toward the parts of the habitat frequented by dominants. If available, the latter areas may provide a superior foraging source for the subordinate. When Brown-headed Nuthatches encountered a temporarily superabundant food source in the longleaf pine forest in Louisiana, they changed their pattern of spatial utilization. This modification exposed them to a high level of hostile interactions with Pine Warblers, which might not have been tolerable if an unlimited food supply had not been available (Morse, 1967b).

This high degree of opportunism obviously does not exist in all situations. Several species of wood warblers nesting in the northeastern spruce forests

demonstrate very little flexibility in their foraging regimes during the breeding season, a period of more predictable stability (Morse, MS).

Socially dominant species might also profit from participation in flocks because other species in their presence would have a lower tendency to forage in the stations most frequently used by these dominants than if they were absent. This situation might insure them of a larger proportion of the food supply from a station than they would realize if they or other species avoided the flocks. It would also act to lower interspecific hostilities.

Movement of Flocks

The fact that groups almost always show a tendency to move constantly may allow them to glean the most readily available food at any given time. In the two areas analyzed in this regard, occasional to frequent periods occur during the winter that are mild enough that insects are in flight. Then there will probably be a redistribution of these animals, resulting in some becoming available that previously were located in inaccessible areas. It is likely that many prey are vulnerable only at certain times, and thus constant movement and maximally superficial gleaning by the birds would result in a superior method of harvesting this food source. Other factors may modify a habitat in such a way that new items constantly become available. Wind, rain, snow, and other animals produce modifications of the habitat and consequent changes in accessibility of invertebrates when it is too cold for them to move by themselves. This was shown clearly in February, 1966, in Maryland when following an ice and snow storm members of flocks fed frequently on the snow cover among debris that had fallen from the trees. In Louisiana there were even occasional winter spells warm enough to permit the hatching of some arthropods. The potential of sources of food becoming available during the winter season, either by active or passive means, appears somewhat underestimated in the literature. Even during mid-winter in Maine signs of insect movement occasionally were evident. Perhaps the most striking was noted on 29 December 1967, when the temperature was 4°C and approximately 30 cm of snow lay on the ground. In a sheltered area of a white pine grove a number of small dipterans were noted in flight, including several in the vicinity of chickadees at that time.

To date other studies suggest that seldom does an absolute lack of food exist, though upon occasions high percentages of individual prey species might be removed (MacLellan, 1958; Gibb, 1960;

L. Tinbergen, 1960). Limited sampling of foliage that I performed intermittently during this study to estimate the size of the food store did not point to an absolute lack of food. However, an absolute lack of food is not the relevant biological limiting factor, but whether accessible food exists, and if so, in quantities sufficient that an adequate amount may be obtained in the time available. Gibb's (1960) calculations indicate that a small insectivorous bird must find prey items with considerable rapidity in order to survive during the winter. In this situation it would appear that a premium for skimming would exist.

Large flocks usually moved faster than small ones, though with considerable variance existing (Fig. 27), an observation also made by Gibb (1960). Since each bird maintains an individual distance about itself, and the area available per individual in a flock decreases as these groups become larger (at least in the one area sampled, Fig. 6), individuals in large flocks will have to forage on the average in a smaller space at any given foraging station than do individuals in small flocks, and will have to fly farther on the average in large flocks in order to reach a new foraging station if an area is to be found that is not occupied by another individual. Crowding of the individuals into proportionately small areas at any given time will also increase the possibilities of hostile interactions. Further, if an individual did remain a similar amount of time in both large and small stations, it would be forced to forage more intensively in the small one if basic food demands were to be met. Flocks on the average also were larger in areas of low population density and moved faster, this tendency of speed per unit size varying with the habitat in Maryland, though not clearly so in Louisiana. If food stores are sparser in areas of low bird density, as we have postulated, then at each foraging station of similar size fewer food items would be readily available. To obtain the same number of items as found where stores are richer we would predict more rapid movement, as appears in Maryland. The home ranges of flocks also increased as the density of birds per unit area decreased. This pattern of movement facilitates regular patrol of a home range, and in a situation where the range is large one might predict rapid movement, which would facilitate regular visits, and regular cropping of resources.

Thus, the rate of movement that usually occurs in large flocks appears explainable. However, if large flocks necessitate rapid movement, then one might question their utility and ask why tendencies exist (particularly in the poorest foraging

area) for the flocks to become progressively larger rather than smaller and proportionately more frequent.

If, as Miller (1922) and Short (1961) believe, flocks improve efficiency of foraging by lessening duplication of effort, then large flocks may be maximally efficient in this way. In a habitat containing a low density of food, pressure should be maximum in such a direction. It is also patent that there would be an optimal balance between moving long distances rapidly (and obtaining the most conspicuous food items) and remaining at a foraging station for a longer period (and obtaining less conspicuous items). When abundant sources of food exist, there is a trend toward the slower motions; at this time adequate items are easily obtained. Brown-headed Nuthatches exploiting temporarily superabundant longleaf pine seeds in Louisiana often remained for relatively long periods in a single tree (Morse, 1967b). The potentialities of increase in flock size would probably be limited by the amount that it was convenient for flocks to increase their rate of movement. As pointed out earlier, flocks seldom are seen that consist of over 45 individuals. Selective pressures also probably operate in preventing flocks on the average from becoming as large as this. The advantages of smaller areas have been commented upon by others: in a small area knowledge of the features of the habitat is better (Dixon, 1949), and more individuals would be able to remain maximally close to their breeding territories, which apparently is a matter of considerable importance in reclaiming these areas successfully in some species when spring arrives (Hamerstrom, 1942; Odum, 1942; Hinde, 1952).

Predation

Both flocking and a solitary existence potentially bestow certain advantages upon individuals in protecting them from predators. Flocks under attack supposedly benefit from a confusion effect when they move in concert (Allee, 1938), in which the grouping and flocking behavior of the prey species make it difficult for a predator to single out an individual. This statement is supported by the experimental work of Welty (1934) on *Daphnia*, using goldfish (*Carassius auratus*) as the predator. Experimental proof in a flock of birds would indeed be difficult to obtain. While N. Tinbergen (1953) noted that flocking in flight, as performed by Starlings against strongly flying raptors, has definite survival advantage, such an advantage probably can be discounted in flocks of woodlands because of their extremely loose nature.

These flocks may, however, obtain the benefit of greater total alertness than can solitary individuals, with several pairs of eyes being available to spot a predator, rather than a single pair. The combined watch, plus their special calls, doubtless results in a greater awareness of predators than exists in solitary individuals.

Rudebeck (1950) gives some data on the relative success of European Sparrow-hawks attacking single and flocked prey, observations from woodland and open country being combined. Of 190 attacks on suitable bird prey, 23 were successful. 60 of these attacks were on flocks, 5 of them being successful. While the success in capturing lone birds was higher than with flock members, the difference in a chi-square test was not statistically significant ($P > 0.20$). The data thus fail to show that once an attack is initiated, significant differences in vulnerability exist between flocked and solitary individuals. However, these data are only from one species of raptor (though a major predator of small birds), and groups in which a flying predator call has already been sounded are not treated separately. If added alertness for predators decreased the frequency of attacks, a selective advantage would be apparent. Moynihan (1962) even suggested that the very presence of birds in flocks might discourage predators. Unfortunately, no quantitative data of either sort apparently exist, unless the lack of attacks in the present study provide indirectly information of this nature. The occasional association of certain species that show few similarities in foraging to flock members (Eastern Bluebirds, Slate-colored Juncos, and Chipping Sparrows) may be the result of the improved alertness that they gain from the flying predator calls of aboreal flocks. Significantly, Marler (1956) noted that sometimes it was more common for the Chaffinch, another gregarious species that frequently feeds on the ground, to be warned of danger by the calls of tits high in the trees than by others of its own species. Rudebeck (1950, 1951) states that when the intended victim is sufficiently warned of the danger seldom does the predator capture it, this statement holding true for encounters involving small birds and both the European Sparrow-hawk and the Pigeon Hawk. These raptors take advantage of any objects in the landscape that obscure them from the intended victim while they approach. Thus by their hunting methods these predators minimize the advantage of increased awareness that prey obtain by participating in flocks.

Although flocking birds possess a mechanism that aids in protection from attack, their combined constant group movement also calls attention to their presence, and they also produce a considerable amount of sound *en masse*. The factor of movement appears to be of particular importance to some predators. Conspicuous individuals run a high risk of being captured by European Sparrow-hawks (L. Tinbergen, 1946). Constant movement by several individuals would result in increased exposure to such species. Birds in a flock also are auditorily more conspicuous than lone individuals because of their concentrated vocalizations. When in a flock each individual usually produces considerably more sound than it would if solitary because of the constant "contact notes" (Odum, 1942) that are uttered while in flocks, the loud aggressive notes given when hostile behavior is exhibited, and the loud notes produced by several species when they become somewhat separated from the group. Loudly calling birds temporarily displaced from a flock appear particularly vulnerable in this respect, because of the number of vocalizations being given and because of the lack of any defensive system of the group at that moment. Loud vocalizations were given regularly by temporarily displaced Black-capped and Carolina chickadees and Red-breasted and Brown-headed nuthatches; furthermore, these calls usually were given from exposed positions. All these activities increase conspicuousness and likely serve to counter the advantages of predator protection gained by flocking. Thus the overall protective value of flocking is open to question.

Gregarious tendencies could develop if flocking allowed additional and even more important advantages than protection from predation for the individuals that began this practice. If maximally effective pursuit of other activities (such as foraging) were the principal advantage of flocking, the definite importance of an effective response to flying predators is nevertheless apparent. Individuals in groups with no such response would likely be preyed upon disproportionately heavily, since they would be conspicuous and would not have that compensatory means of protection. Thus a high degree of selection would exist for evolution of effective flying predator calls or some other comparable mechanism if predation upon a group of individuals were heavy. Even if selective pressures were not particularly high, a system could develop over a period of many generations. On an evolutionary basis, only a very slight selectivity in predation needs to be postulated to ac-

count for the strong development of such a trait (see Fisher, 1930).

While many have commented upon predation by winged raptors, the particular attention paid to the phenomenon may be partly attributable to the spectacular nature of attacks rather than to frequent observations, and many such observations have been made in open country or forest edge. The lack of specific information suggests that in many areas predation by raptors is currently an uncommon occurrence.

The possibility exists that the danger of winged predators to small birds was more severe in the immediate past than it is at present, particularly in settled areas. Though no accurate comparative figures are available, the numbers of winged predators in settled areas of North America probably have dropped considerably more sharply than have those of songbirds over the last 150 years, as a result of control programs, indiscriminate shooting, and other factors. Such subjective interpretations of change in density occur for species after species in Bent (1937, 1938). More recently, much evidence suggests that further decreases have occurred, in part the result of the increased use of insecticides (see Moore, 1967).

Other observations suggest indirectly that the level of predation by hawks has declined markedly of late. Otherwise, activities such as flying considerable distances in the open in the presence of predators should be rapidly selected against. While several avian predators seldom catch birds on the wing (see Rudebeck, 1950, 1951; Cade, 1962), flying at such a time adds greatly to the conspicuousness of the potential victim. Rudebeck indicated that most actions of an individual that are different from the usual ones of its species in the presence of a predator would result in an abnormally high mortality among the individuals performing those actions. Further, the low degree of response to flying predator calls by some species in Louisiana may be correlated with an apparent low density of predators present at the time. These data all suggest a possible relaxation of selection at this time.

Frequent responses in the absence of a predator are wasteful of both time and energy to potential prey species. Thus habituation to loons, cormorants, herons, vultures, and gulls is probably advantageous where those species are particularly common. Responses to Great Blue Herons and Ospreys out of the usual context, as well as to Black-billed Cuckoos and Mourning Doves, indicate, however, that flying predator calls may be given in response to a variety of stimuli. Most of

these reactions share the characteristic of being set off by sudden or surprising stimuli, rather than particular-shaped ones. Accipiters regularly fly at treetop level or lower while foraging, thus presenting a comparable pattern of stimuli to the ones that most often produce inappropriate responses. As Thorpe (1944) pointed out, most animals are subject to a great variety of dangers, and a specific instinctive response to every danger usually is out of the question. In at least some species the individual initially possesses a disposition to respond to a wide variety of stimuli and narrows this variety by habituation (Schleidt, 1961).

The tendency for birds to give and respond to flying predator calls in inappropriate situations even under inclement conditions easily might be selected against if the total system did not possess at least a moderate degree of protective advantage, suggesting that either it currently has advantage or did until quite recently. The almost continuous foraging of some species in the winter time, such as Gibb's (1960) Goldcrests, which foraged nearly 100 per cent of their waking time at that season, suggests that constant attention to foraging activities may be of critical importance at times. Hence the presence of responses to flying predator calls under such conditions suggests that it has (or had) an overall positive selective value.

The existence of two distinct flying predator calls in some species suggests further that at least a moderate degree of selective pressure has been exerted upon the individuals for development of this characteristic. The sibilant calls of chickadees and titmice in flocks that I observed were more distinct from other vocalizations of the species than were nonsibilant calls. However, sibilant calls of many species bear marked resemblances to each other (Marler, 1957). Sibilant calls are more difficult to locate than other notes in the repertoire of the species that give them, and therefore would be of advantage in dangerous situations (Marler, 1955). Choruses, such as those noted by Grinnell (1903) and Miller (1922) in Common Bushtits, and that I observed in chickadees, presumably aid further in obscuring the direction from which a single sound originates, increasing the difficulty of separating out an individual for the predator. While flying predator calls are found in nonflocking species, choruses probably are of advantage primarily in flocks. Nonsibilant calls bore considerable resemblance to other notes of the repertoire; for instance, the nonsibilant calls of the Black-capped Chickadee closely resembled one that Odum (1942) indicated was used as a "scold-

ing" note, and Brewer (1961) indicated that the comparable call in the Carolina Chickadee was similar to the Black-capped Chickadee's in form and function. The flying predator call of the Brown-headed Nuthatches was very similar to other notes of their repertoire. In spite of their apparent similarity, however, they signify a markedly different context.

In summary, it appears that the incidence of predation on mixed-species flocks in woodlands by raptors is presently often of low frequency, though it may differ between flocks. The apparent discrepancy between presence of well-developed alarm systems and low levels of predation could be explained at least in part by the apparent recent decrease in density of predators. The lax nature of responses in several species in Louisiana might represent the action of selective forces moving toward a new equilibrium.

Function of Flocks

The subject of the function of such assemblages has long been a matter of considerable interest, though no truly satisfactory answer has yet appeared. Many workers have proposed a single function, though Moynihan (1962) clearly points out that advantages can vary strikingly in different flocks.

As indicated, some protective function, at least in the evolutionary background of the species concerned, is strongly suggested by the presence of signals and responses that serve as an effective alarm from predators, particularly winged ones. This, coupled with a well-developed tendency on the part of members of flocks to respond to a number of stimuli implies that some premium in this direction exists or has recently existed. The fact that wasteful false alarms may be as frequent as responses to an actual predator suggests in itself that we are dealing with a factor that *in toto* possesses or has recently possessed a marked selective advantage. Nevertheless, several years of field work suggest a low frequency of these predators in the study area.

What appears to be a more important explanation for the advantages gained by these flocks is an ability for their species to exploit available resources in a maximally effective manner, given that other species with overlapping spectra of habitat utilization are present and utilizing common resources. Any absence or rarity of individuals of a species within the home range of a flock could result in exploitation of an otherwise unused part of the habitat by other species. Under erratically fluctuating environmental condi-

tions, selection would undoubtedly exist for such adaptability.

Relation to Some Other Nonreproductive Social Groupings

Other types of mixed-species groupings of vertebrate animals are prominent in addition to the mixed-species foraging flocks described here. They may be separated into categories and commented upon in light of the information obtained above.

Recent papers by Recher (1966) and Recher and Recher (1969) on groups of migrant shorebirds indicate some similarities with the flocks reported upon in this paper. A wide overlap exists in the foraging of different species found in these groups, and their patterns of aggression parallel those of the parids and their associates. However, they are temporary, change constantly in composition, and usually feed on abundant food sources, rather than dispersed stocks.

Rand (1954) suggests that assemblages of several species of seabirds may be similar in function to insectivorous flocks, though no data apparently exist to support or refute this proposition. In this paper Rand also presents a review of mixed assemblages of birds.

Ant-following aggregations have been studied in the neotropics most recently by Willis (1966a, b). Birds are attracted to the presence of army ants by food items flushed by these insects, which represent a clearly extrinsic factor; thus, these groupings should be considered aggregations rather than flocks. The potential prey items flushed presumably account for the existence of these groupings, which break up when the cyclical ants are not swarming. Hence, while a definite energetic advantage doubtless exists from exploiting the readily obtained items of prey flushed, this grouping is of a different nature than that of mixed flocks that I studied. However, the situation bears some resemblance to the beating function advocated by Swynnerton (1915) and others for flocks in the tropics. Willis has noted a definite social hierarchy and temporal displacement in some situations, similar to the one described in this paper and by Morse (1967b). Hence, certain ecological and behavioral aspects of the two types of groups are similar.

Large mixed or unmixed groups of icterids and fringillids may be seen in various parts of the world outside of the breeding season. These groupings often tend to be more or less nomadic and to exploit temporarily superabundant food sources. That this type of organization and the flocks described in this paper need not be con-

sidered exclusive of each other is shown by the behavior of the Myrtle Warbler, particularly in Louisiana, which showed strong tendencies to participate in mixed flocks, but also a marked predilection to wander in large flocks of its own species. Also, the tendency for Slate-colored Juncos to move about with insectivorous members of flocks suggests a functional relationship between the two types of groups, which in this case is most likely explained by an increased awareness of predators for this species. Others (Marler, 1956, Erard, 1960) have reported tendencies of fringillids to join mixed insectivorous flocks.

Mixed herds of antelope have been reported from the African plains (Lamprey, 1963). While they have not been studied in great detail in this regard, it is apparent that marked differences in foraging exist among the species in these groups, and that studies of the temporal aspects of this foraging similar to the ones employed in the present study might be expected to generate interesting information regarding their exploitation patterns. Here again, we can visualize a potential multi-purpose function of these groupings, since large predators abound in this region and alarm systems are well-developed in the herbivores.

Lastly, while unmixed schools of fishes appear to be better known, mixed ones exist as well (see Breder, 1959). Furthermore, Breder (1967) states emphatically that all fish schools are not similar structures and that they cannot be encompassed into a single formulation. This situation appears analogous to the one existing in birds and makes it hazardous to attempt to draw detailed parallels between schools and flocks at this time.

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Appendix: Scientific Names of Birds Mentioned in Text

American Goldfinch	Downy Woodpecker
American Redstart	Double-crested Cormorant
American Sparrow Hawk	Eastern Bluebird
Bachman's Sparrow	Eastern Phoebe
Baltimore Oriole	European Sparrow-hawk
Barred Owl	Goldcrest
Bay-breasted Warbler	Golden-crowned Kinglet
Black-billed Cuckoo	Goshawk
Blackbird	Great Black-backed Gull
Blackburnian Warbler	Great Blue Heron
Black-capped Chickadee	Hairy Woodpecker
Black-throated Green Warbler	Hermit Thrush
Black Vulture	Herring Gull
Black-and-White Warbler	House Sparrow
Blue Jay	House Wren
Bobwhite	Magnolia Warbler
Boreal Chickadee	Mockingbird
Brown Creeper	Mourning Dove
Brown-headed Cowbird	Myrtle Warbler
Brown-headed Nuthatch	Northern Shrike
Brown Thrasher	Orange-crowned Warbler
Canada Warbler	Osprey
Cardinal	Ovenbird
Carolina Chickadee	Parula Warbler
Carolina Wren	Pigeon Hawk
Catbird	Pileated Woodpecker
Chaffinch	Pine Warbler
Chestnut-sided Warbler	Red-bellied Woodpecker
Chipping Sparrow	Red-breasted Nuthatch
Common Bushtit	Red-cockaded Woodpecker
Common Crow	Red-eyed Vireo
Common Grackle	Red-headed Woodpecker
Common Loon	Red-tailed Hawk
Cooper's Hawk	Redwinged Blackbird
	Robin
	Ruby-crowned Kinglet
	Rufous-sided Towhee
	Scrub Jay
	Sharp-shinned Hawk
	Slate-colored Junco
	Starling
	Swamp Sparrow
	Tufted Titmouse
	Turkey Vulture
	White-breasted Nuthatch
	White-eyed Vireo
	White-throated Sparrow
	White-winged Crossbill
	Winter Wren
	Wood Pigeon
	Yellow-bellied Sapsucker
	Yellow-shafted Flicker
	Yellowthroat
	Yellow Warbler
	<i>Spinus tristis</i>
	<i>Setophaga ruticilla</i>
	<i>Falco sparverius</i>
	<i>Aimophila aestivalis</i>
	<i>Icterus galbula</i>
	<i>Strix varia</i>
	<i>Dendroica castanea</i>
	<i>Coccyzus erythrophthalmus</i>
	<i>Turdus merula</i>
	<i>Dendroica fusca</i>
	<i>Parus atricapillus</i>
	<i>Dendroica virens</i>
	<i>Coragyps atratus</i>
	<i>Mniotilla varia</i>
	<i>Cyanocitta cristata</i>
	<i>Colinus virginianus</i>
	<i>Parus hudsonicus</i>
	<i>Certhia familiaris</i>
	<i>Molothrus ater</i>
	<i>Sitta pusilla</i>
	<i>Toxostoma rufum</i>
	<i>Wilsonia canadensis</i>
	<i>Richmondena cardinalis</i>
	<i>Parus carolinensis</i>
	<i>Thryothorus ludovicianus</i>
	<i>Dumetella carolinensis</i>
	<i>Fringilla coelebs</i>
	<i>Dendroica pensylvanica</i>
	<i>Spizella passerina</i>
	<i>Psaltriparus minimus</i>
	<i>Corvus brachyrhynchos</i>
	<i>Quiscalus quiscula</i>
	<i>Gavia immer</i>
	<i>Accipiter cooperii</i>
	<i>Dendrocopos pubescens</i>
	<i>Phalacrocorax auritus</i>
	<i>Sialia sialis</i>
	<i>Sayornis phoebe</i>
	<i>Accipiter nisus</i>
	<i>Regulus regulus</i>
	<i>Regulus satrapa</i>
	<i>Accipiter gentilis</i>
	<i>Larus marinus</i>
	<i>Ardea herodias</i>
	<i>Dendrocopos villosus</i>
	<i>Hylocichla guttata</i>
	<i>Larus argentatus</i>
	<i>Passer domesticus</i>
	<i>Troglodytes aedon</i>
	<i>Dendroica magnolia</i>
	<i>Mimus polyglottos</i>
	<i>Zenaidura macroura</i>
	<i>Dendroica coronata</i>
	<i>Lanius excubitor</i>
	<i>Vermivora celata</i>
	<i>Pandion haliaetus</i>
	<i>Seiurus aurocapillus</i>
	<i>Parula americana</i>
	<i>Falco columbarius</i>
	<i>Dryocopus pileatus</i>
	<i>Dendroica pinus</i>
	<i>Centurus carolinus</i>
	<i>Sitta canadensis</i>
	<i>Dendrocopos borealis</i>
	<i>Vireo olivaceus</i>
	<i>Melanerpes erythrocephalus</i>
	<i>Buteo jamaicensis</i>
	<i>Agelaius phoeniceus</i>
	<i>Turdus migratorius</i>
	<i>Regulus calendula</i>
	<i>Pipilo erythrorynchus</i>
	<i>Aphelocoma coerulescens</i>
	<i>Accipiter striatus</i>
	<i>Junco hyemalis</i>
	<i>Sturnus vulgaris</i>
	<i>Melospiza georgiana</i>
	<i>Parus bicolor</i>
	<i>Cathartes aura</i>
	<i>Sitta carolinensis</i>
	<i>Vireo griseus</i>
	<i>Zonotrichia albicollis</i>
	<i>Loxia leucoptera</i>
	<i>Troglodytes troglodytes</i>
	<i>Columba palumbus</i>
	<i>Sphyrapicus varius</i>
	<i>Colaptes auratus</i>
	<i>Geothlypis trichas</i>
	<i>Dendroica petechia</i>