

COMPOSITION AND TEMPORAL VARIATION OF FLOCKS IN THE SIERRA NEVADA¹

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Abstract. The size and species composition of bird flocks in a mixed-conifer forest of the western Sierra Nevada was nearly identical over three winters. Golden-crowned Kinglets (*Regulus satrapa*), Chestnut-backed Chickadees (*Parus rufescens*), and Red-breasted Nuthatches (*Sitta canadensis*) had the highest number of individuals/flock. Kinglets and nuthatches were the most frequent flock members, although they occurred in only 28% and 20% of all flocks, respectively. Most species formed monospecific flocks, although they more often occurred in mixed-species flocks. Although flock size was significantly greater in early winter than in middle and late winter, the number of species/flock did not vary temporally. No meaningful correlations between flock composition and weather conditions were evident. Differences in flock composition between this and other studies resulted from the relatively high frequency of nuthatches found in our flocks. In addition, flock composition was apparently influenced greatly by habitat. The anti-predator and foraging efficiency models emphasized in the literature are evaluated, and a framework for a more complete testing of causes of flocking discussed.

Key words: Anti-predator models; bird flocks; coniferous forests; flocking behavior; foraging-efficiency models; Sierra Nevada.

INTRODUCTION

The grouping of terrestrial birds into flocks of two or more species is common worldwide; not surprisingly, numerous studies have described flock formation in birds (see reviews by Moynihan 1960; Morse 1970, 1977; also Wing 1941; Smith 1967; Austin and Smith 1972; Powell 1974; La Gory et al. 1984). The ultimate evolutionary reasons for flock formation are multifaceted, but have centered on two models: the anti-predation and the foraging efficiency models. The anti-predation model states that an individual joins a flock to reduce the chances of predation. This model can be subdivided into two hypotheses: the "many eyes" idea whereby an individual benefits from increased vigilance as a consequence of flock membership; or the "safety in numbers" idea whereby an individual uses the other flock members as a buffer to decrease its

chances of predation (e.g., Vine 1971, 1973; Siegfried and Underhill 1975; Treisman 1975). Further, flocks may possess a geometry that may protect them from predator attack (Hamilton 1971, Pulliam 1973). The foraging efficiency model also uses the many eyes idea to emphasize that flock members have an increased likelihood of locating food and/or the ability to spend more time foraging while being less vigilant for predators relative to that of solitary foragers (e.g., Krebs et al. 1972; Krebs 1973; Caraco 1979a, 1979b). It is difficult, however, to separate the anti-predation from the foraging efficiency function of flocking. Recognizing this problem, Berner and Grubb (1985) emphasized experimental methods (e.g., food supplementation) to try to separate these two functions. Nevertheless, the primary ultimate cause(s) of flocking have still not been determined.

We believe that part of the problem surrounding determination of ultimate causes of flock formation involves the failure to consider all of the often interrelated factors that can influence a bird.

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Little attention has been given, for example, to temporal variations in flock size and composition, or to the influence of weather on flocks. Further, other processes influencing birds, such as mate selection, seasonal changes in habitat requirements, and physiological constraints, have not been adequately considered. These considerations are important in understanding the mechanisms controlling flock formation.

Our objectives were to describe flock size and composition within and between years during three winters in the western Sierra Nevada, with attention given to the frequency of occurrence of species in flocks. We also analyzed the possible influence of environmental conditions on flocking behavior, and evaluated results in light of current models of flock formation in birds. We emphasize that the nonexperimental nature of our study renders our examination exploratory and hypothesis generating, rather than hypothesis testing.

STUDY AREA AND METHODS

The study area was the 1,200-ha Blodgett Forest Research Station (University of California, Berkeley), El Dorado County, California. The forest is between 1,200 and 1,500 m elevation in the mixed-conifer zone (Griffin and Critchfield 1972) of the western Sierra Nevada, and is predominated by mature stands of various mixtures of incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), ponderosa (*Pinus ponderosa*) and sugar (*P. lambertiana*) pines, Douglas-fir (*Pseudotsuga menziesii*), and California black oak (*Quercus kelloggii*). The climate is characterized by dry, warm summers and mild, wet winters. Average precipitation is about 168 cm/year with a 22 year range of 58–274 cm. Snow is common from November to April, averaging about 254 cm/year. Average daily maximum temperatures range from 9°C during winter to 27°C during summer (R. C. Heald, pers. comm. from unpubl. data on file at Blodgett Forest). Vegetation of the forest was described by Airola and Barrett (1985) and Morrison et al. (1985, 1986).

Because of a change in study design, two different methods were used to record bird flocks; these methods are outlined below, and further details regarding counting methods and overall study design were given by Morrison et al. (1985, 1986). During winter (late October to mid-March) 1982–1983 and 1983–1984, birds were counted for 5 min in 30-m-radius plots at 40 points in

the forest; each point was visited on four mornings during each winter. Each point was at least 200 m from the next nearest point. All birds were counted, and those in flocks (defined as a group of two or more individuals of the same or a different species apparently moving together) were noted. All members of a flock were counted when any part of the flock entered a count radius. Because flocks were seldom recorded using this method, and flock size did not vary ($P > 0.1$, t -test) between these winters, we combined data to provide larger sample sizes for comparison with data collected during 1984–1985 (see below). This method totalled 27 hr of actual recording time during the two winters.

During winter 1984–1985, several different areas (totaling about 100 ha) were chosen for study. Rather than using specific counting points, observers systematically walked through the areas throughout the day, recording all birds seen and noting flock composition. Possibly the same individuals or flocks were counted repeatedly; however, our intent was to determine average flocking characteristics and not the abundance of birds. About 120 hr during 22 days were spent in observing flocking behavior during winter 1984–1985. Analysis of intraseasonal aspects of flock composition were restricted to 1984–1985 because of the larger sample sizes. All analyses were performed using the SPSSX (SPSS 1983) computer package.

RESULTS

FLOCK SIZE AND COMPOSITION

The overall size and composition of mixed-species flocks were nearly identical between winters (Table 1). Except for the absence of Varied Thrushes (scientific names in Table 1) during winters 1982–1983/1983–1984, the abundance of individuals by species in mixed-species flocks was similar throughout the three winters of study (Spearman's rho [ρ_s] = 0.74, $P = 0.001$, $n = 15$ species). Golden-crowned Kinglets, Chestnut-backed Chickadees, and Red-breasted Nuthatches, in descending order, were the most abundant members of mixed-species flocks; all other species averaged <1.0 individuals/flock (Table 1). Mountain Chickadees, Brown Creepers, Dark-eyed Juncos, and Ruby-crowned Kinglets were moderately abundant in groups averaging 0.1 to 0.7 individuals/flock. The remaining species all averaged ≤ 0.1 individuals/flock.

TABLE 1. Number of individuals per bird species in mixed-species flocks during winter at Blodgett Forest, California.^a

Species	Winter 1982-1983/1983-1984 ^a			Winter 1984-1985 ^b		
	\bar{x}	SD	Range	\bar{x}	SD	Range
Downy Woodpecker (<i>Picoides pubescens</i>)	0.00	0.000	0	0.01	0.070	1
Hairy Woodpecker (<i>P. villosus</i>)	0.00	0.000	0	0.10	0.478	5
White-headed Woodpecker (<i>P. albolarvatus</i>)	0.06	0.308	2	0.04	0.241	2
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	0.00	0.000	0	0.00	0.000	0
Mountain Chickadee (<i>Parus gambeli</i>)	0.65	1.385	6	0.49	1.350	8
Chestnut-backed Chickadee (<i>P. rufescens</i>)	1.44	2.253	11	1.47	2.504	12
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	1.10	1.624	7	1.36	1.477	6
Brown Creeper (<i>Certhia americana</i>)	0.35	0.968	5	0.47	0.847	4
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	3.31	2.790	12	3.69	3.812	25
Ruby-crowned Kinglet (<i>R. calendula</i>)	0.10	0.358	2	0.22	0.577	4
American Robin (<i>Turdus migratorius</i>)	0.04	0.194	1	0.01	0.141	2
Varied Thrush (<i>Ixoreus naevius</i>)	0.00	0.000	0	0.52	1.869	20
Yellow-rumped Warbler (<i>Dendroica coronata auduboni</i>)	0.02	0.139	1	0.02	0.157	2
Dark-eyed Junco (<i>Junco hyemalis</i>)	0.69	2.624	14	0.19	0.831	8
Other	0.21	0.893	6	0.23	0.662	6
Overall						
No. birds/flock	7.96	4.715	3-22	8.78	6.698	2-40
No. species/flock	2.5	0.87	2-7	2.8	1.13	2-8

^a All comparisons between years were not significant ($P > 0.05$, t -test).

^b Range for species is the maximum number of individuals seen in a flock; minimum was always zero. Sample size: 1982-1983 and 1983-1984 combined = 52 flocks; 1984-1985 = 202 flocks.

The four species of woodpeckers seldom joined mixed-species flocks: Pileated Woodpeckers were never seen in flocks; solitary Downy Woodpeckers were seen in flocks during one winter; and up to two White-headed Woodpeckers, usually a male and female (mated pair?), were occasionally observed in flocks. Up to five Hairy Woodpeckers were seen in mixed-species flocks during winter 1984-1985, but none were seen flocking during the previous winters.

Golden-crowned Kinglets (about 28%) and Red-breasted Nuthatches (20%) were the most frequent flock members (Fig. 1). Chestnut-backed Chickadees and Brown Creepers (about 10% each) were the only other species with over 6% frequency in flocks. Together, five species—the two

chickadees (total = 17%), two kinglets (34%), and the nuthatch—were the most common species in mixed-species flocks at Blodgett Forest.

FLOCK TYPE

Most species formed monospecific flocks, although no species did so for more than about one-third of our observation time (Table 2). Ruby-crowned Kinglets were never observed in monospecific flocks; Mountain Chickadees (6%), American Robins (14%), and Pileated Woodpeckers (15%) seldom occurred in such flocks.

Ruby-crowned Kinglets, and Mountain and Chestnut-backed chickadees were usually (>80%) observed in mixed-species flocks; Golden-crowned Kinglets, Brown Creepers, Varied

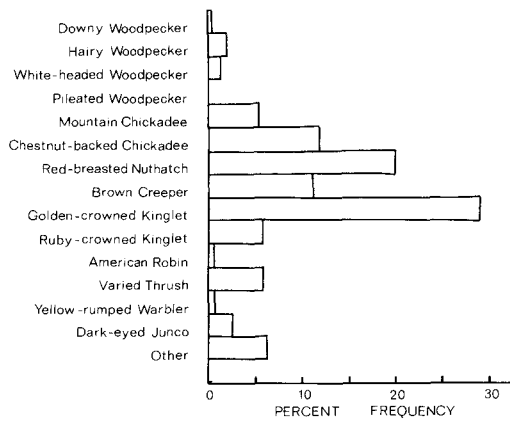


FIGURE 1. The percent of flocks containing various bird species observed at Blodgett Forest, California, during winter 1984–1985.

Thrushes, Red-breasted Nuthatches, and Dark-eyed Juncos occurred in these flocks 50 to 60% of the time. American Robins seldom joined mixed flocks, and Pileated Woodpeckers never did.

Pileated Woodpeckers and American Robins were usually (about 80%) seen as solitary individuals. Hairy and White-headed woodpeckers were observed solitarily in just under 50% of the observations. The remaining species were observed alone in less than 25% of the observations; Chestnut-backed Chickadees were never observed alone (Table 2).

TEMPORAL VARIATION OF FLOCK SIZE

Overall flock size was significantly greater early in winter compared to late winter (Table 3). Only three species analyzed showed temporal variation in the number of individuals/flock: Brown Creepers, Golden-crowned Kinglets, and Ruby-crowned Kinglets had significantly more individuals in each flock early in winter (Table 3). The difference in overall flock size was due to the presence of Golden-crowned Kinglets which contributed 7 to 8 individuals/flock during early winter, accounting for about 59% of all individuals/flock. The number of these kinglets decreased to about 3 individuals/flock during middle and late winter, but still accounted for about 35 to 40% of all individuals in mixed-species flocks at this time.

The mean number of species/flock was similar between time periods, ranging from 2.4 species/flock (SD = 0.74) in late winter to 2.9 species/flock during both early (SD = 1.27) and middle (SD = 1.24) winter.

WEATHER AND FLOCK COMPOSITION

Although we sampled during windy and snowy conditions, over 90% of the flocks were observed when the wind was absent or light and there was no precipitation; not surprisingly, these variables did not help predict flock size ($P > 0.1$). During winter 1982–1983/1983–1984, flock size increased with increasing temperature ($\rho_s = 0.26$, $P = 0.033$), but tended ($P = 0.07$) to decrease

TABLE 2. Percent occurrence of birds in single- and mixed-species flocks, and as solitary individuals, for selected species at Blodgett Forest during winter, 1984–1985.

Species	% occurrence by flocking behavior			n ^a	P ^b
	Single-species	Mixed-species	Solitary		
Hairy Woodpecker	26.1	26.1	47.8	46	ns
White-headed Woodpecker	28.6	28.6	42.9	21	ns
Pileated Woodpecker	15.4	0.0	84.6	13	*
Mountain Chickadee	5.7	85.7	8.6	35	***
Chestnut-backed Chickadee	20.7	79.3	0.0	82	***
Red-breasted Nuthatch	34.1	51.4	14.5	220	***
Brown Creeper	19.6	57.8	22.5	102	***
Golden-crowned Kinglet	37.0	60.6	2.4	254	***
Ruby-crowned Kinglet	0.0	91.7	8.3	36	***
American Robin	14.3	7.1	78.6	14	**
Varied Thrush	26.7	53.3	20.0	60	**
Dark-eyed Junco	34.5	48.3	17.2	29	ns
Other	22.4	31.8	45.8	107	*
Overall ^b	41.9	30.0	28.1	1,019	***

^a Sample size = number of occurrences of species.

^b * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = $P > 0.05$, χ^2 -test.

TABLE 3. Number of individuals per mixed-species flock for bird species at Blodgett Forest within early (November to early January), middle (early February to late February), and late (early March) winter periods, 1984–1985. Sample size indicates the number of flocks observed. Values = \bar{x} (SD).

Species	No. individuals/flock*		
	Early (n = 29)	Middle (n = 11)	Late (n = 62)
Downy Woodpecker	0.00 (0.00)	0.00 (0.00)	0.02 (0.13)
Hairy Woodpecker	0.00 (0.00)	0.15 (0.61)	0.05 (0.28)
White-headed Woodpecker	0.00 (0.00)	0.06 (0.31)	0.02 (0.13)
Pileated Woodpecker	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Mountain Chickadee	0.41 (1.32)	0.65 (1.60)	0.23 (0.66)
Chestnut-backed Chickadee	1.45 (3.28)	1.64 (2.49)	1.18 (2.10)
Red-breasted Nuthatch	1.00 (1.49)	1.37 (1.49)	1.50 (1.45)
Brown Creeper	0.83 (1.28) ^A	0.48 (0.75) ^B	0.29 (0.71) ^B
Golden-crowned Kinglet	7.52 (5.57) ^A	3.10 (3.10) ^B	2.97 (2.87) ^B
Ruby-crowned Kinglet	0.86 (0.79) ^A	0.15 (0.54) ^B	0.05 (0.22) ^B
American Robin	0.00 (0.00)	0.02 (0.19)	0.00 (0.00)
Varied Thrush	0.69 (3.71)	0.52 (1.40)	0.42 (1.27)
Yellow-rumped Warbler	0.00 (0.00)	0.03 (0.21)	0.00 (0.00)
Dark-eyed Junco	0.03 (0.19)	0.30 (1.04)	0.06 (0.51)
Other	0.10 (0.31)	0.24 (0.78)	0.27 (0.55)
Total	12.83 (10.69) ^B	8.70 (5.97) ^A	7.03 (4.49) ^A

* Time periods with different letter superscripts (A, B) denote significant ($P < 0.05$) differences as determined by Duncan's multiple range test.

with increasing cloud cover ($\rho_s = -0.21$). During winter 1984–1985, however, flock size decreased with temperature ($\rho_s = -0.38$, $P < 0.001$) and increased with cloud cover ($\rho_s = 0.21$, $P < 0.001$). The number of species/flock increased with temperature during winters 1982–1983/1983–1984 ($\rho_s = 0.23$, $P = 0.048$), but decreased with temperature during winter 1984–1985 ($\rho_s = -0.22$, $P < 0.001$); cloud cover was not significantly correlated with the number of species per flock.

DISCUSSION

Mixed-species flocks in temperate North America range from 10 to 17 individuals (Morse 1970, Austin and Smith 1972); our findings were thus at the low end of this range. Our flocks differed from previous studies in: (1) containing a lower number of *Parus*, about 5 to 8 individuals/flock (Austin and Smith 1972) vs. roughly 2 individuals/flock in our study; and (2) a much lower frequency of occurrence of *Parus* and *Regulus* in flocks. Flocks summarized by Austin and Smith (1972) contained *Parus* 80 to 90% and *Regulus* 60 to 70% of the time; we saw *Parus* in only 17% and *Regulus* in 34% of the flocks. The flocks at Blodgett often contained Red-breasted Nuthatches (often monospecifically or with several Brown Creepers), which apparently reduced the absolute frequency of *Parus* and *Regulus* in our data.

A tendency toward decreased flock participa-

tion as spring approaches has been documented (Morse 1970). Flock size decreased progressively across winter in our study because of a decreased number of Golden-crowned Kinglets in each flock. We do not know if this reduction in kinglets was due to movement out of the study area, the death of individuals, or dispersion of birds within the area (into more but smaller flocks). Hogstad (1984) also noted a decrease in flock size during winter in Goldcrests (*Regulus regulus*), and concluded that a lowered food supply was responsible.

Some aspect of habitat, whether it be structure, physiognomy, or food supply, plays a role in flock formation. Care must be taken, therefore, when comparing our results with data from areas outside the mixed-conifer zone of the western Sierra Nevada. For example, Morse (1970:table 4) showed (in Maine) that Red-breasted Nuthatches were not found in flocks in deciduous woods, were in one-third of the flocks in mixed-forests, and in three-fourths of the flocks observed in coniferous forests; Red-breasted Nuthatches occurred in one-fifth of the flocks in our study. In contrast, Black-capped Chickadees (*Parus atricapillus*) were found in about 90% of the flocks in all habitat types; chickadees occurred in only 17% of the flocks in our study. As in our study, Morse (1970) found that Hairy and Downy woodpeckers seldom joined mixed-species flocks; again, occurrence in flocks varied with habitat.

In contrast, Berner and Grubb (1985) found (in Ohio) Downy Woodpeckers in about 50% of their flocks. As the absolute density of various species could, of course, influence their frequency of occurrence in flocks, further caution must be introduced when comparing data from different areas.

We could not consistently relate within-season flock formation to weather conditions. Thus, we do not know if interseasonal changes in weather affected flock formation. The inclusion of inclement days in our sampling was at least partially responsible for the few (and low) correlations we found between flocking behavior and weather. The contradictory results we found between seasons (i.e., positive correlation one year, negative the next for the same variables) indicates a high probability of a Type I error (i.e., correlations judged significant when in fact they did not represent a causal relationship). We cannot determine, therefore, if our methods were adequate to evaluate the influence of weather on flocking behavior; more years of study are necessary to see patterns in such relationships. Although Morse (1970) did not intensively study the effects of weather on flocking behavior, he felt that precipitation had only a minor influence on flocking behavior, that wind caused a shifting foraging location, and that temperature probably had some influence on behavior.

Temperature may, of course, primarily influence arthropod prey activity depending upon geographic location. Pulliam et al. (1974) hypothesized that mean flock size in juncos would increase as temperature decreased; such a relationship was later found (Caraco 1979b). Hogstad (1984) showed that flock size in the Goldcrest was inversely related with ambient temperature. He concluded that this was related to the need to reduce predator vigilance to increase feeding time. A difficulty in assessing the role of weather on flocking behavior is that wind, rain, and other factors may reduce the ability of observers to see birds and the conspicuousness of the birds (e.g., moving foliage; see also Morse 1970).

Neither the anti-predation or foraging efficiency models, two constructs commonly employed to explain flock formation in birds, appear to be supported by our data. Although we can only infer the reasons for flock formation because of the observational nature of our data, we see no reason to invoke models that require some com-

mon decision by individuals of various species to seek protection from predators (i.e., through increased predator protection—the many eyes hypothesis). Flock size was generally low (about 7 to 13 individuals/flock; Table 3). Other studies have also shown that, although species of *Parus* and *Regulus* are usually members of flocks, most species spend considerably less time flocking (e.g., Morse 1970, Austin and Smith 1972). Thus, the selfish-herd hypothesis of Hamilton (1971) does not appear to be a necessary and sufficient explanation for flock formation (i.e., protection from predators via buffering by other individuals).

It is further unreasonable to assume that increased foraging efficiency was responsible for flock formation at Blodgett. At Blodgett, the food supply used by the small birds forming flocks is apparently readily available and widely distributed throughout the forest (Morrison et al. 1985). Birds concentrate foraging activities on small (i.e., 10 to 20 cm dbh) incense cedar that are infested with the scale insect, *Xylococcus macrocarpae*; the infestation is at endemic levels. Heavily infested trees are easily identified by a covering of black mold. Incense cedar accounts for about 30% of the basal area of trees in our study area, and scale insects are found at a density of 15 to 20 scales/dm² of bark surface at the beginning of winter (Morrison et al., unpubl.; see also Dahlsten et al. 1986). Most bird species that join flocks feed on this scale (Morrison et al. 1985 and unpubl. data). Thus it does not appear that flocking at Blodgett Forest was a response to a limited and/or patchy food supply.

We feel the general failure to identify the ultimate causes of flock formation is based primarily on two related topics. First, an adequate conceptualization of the possible factors influencing flock formation—in both ultimate and proximate senses—has not been developed. Second, the anti-predation and foraging efficiency models are not truly competing hypotheses that can be readily tested in the field. It is critical to recognize that individuals that may join a flock are influenced by ecological, evolutionary, and physiological constraints that interact along some continuum that produces configurations ranging from solitary behavior to flock membership. Foraging efficiency, mate selection, anti-predator behavior, and thermal protection are all examples of possible critical—and interacting—factors leading to the joining of a flock by an individual.

The anti-predator and foraging efficiency models apparently consider these constraints *within* the framework of each model, but not in regard to how factors other than predation and foraging may impact an individual bird's decision to join a flock. The flocks we observed at Blodgett Forest were varied in time and space with regard to size and species composition, indicating that many factors were responsible for joining a flock and also varied in space and time.

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LITERATURE CITED

- AIROLA, D. A., AND R. H. BARRETT. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. *Condor* 87:205-216.
- AUSTIN, G. T., AND E. L. SMITH. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. *Condor* 74:17-24.
- BERNER, T. O., AND T. C. GRUBB, JR. 1985. An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology* 66:1229-1236.
- CARACO, T. 1979a. Time budgeting and group size: a theory. *Ecology* 60:611-617.
- CARACO, T. 1979b. Time budgeting and group size: a test of theory. *Ecology* 60:618-627.
- DAHLSTEN, D. L., M. L. MORRISON, D. L. ROWNEY, AND S. M. TAIT. 1986. Impact of insectivorous birds on incense cedar scale in the Sierra Nevada of California, p. 663-672. *In Proc. 18th IUFRO Congress. Vol. 2, Division 2. Ljubljana, Yugoslavia.*
- GRIFFIN, J. R., AND W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S.D.A. For. Serv. Res. Pap. PSW-82.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295-311.
- HOGSTAD, O. 1984. Variation in numbers, territoriality and flock size of a Goldcrest *Regulus regulus* population in winter. *Ibis* 126:296-306.
- KREBS, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Can. J. Zool.* 51:1275-1288.
- KREBS, J. R., M. H. MACROBERTS, AND J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* 114:507-530.
- LA GORY, K. E., M. K. LA GORY, D. M. MEYERS, AND S. G. HERMAN. 1984. Niche relationships in wintering mixed-species flocks in western Washington. *Wilson Bull.* 96:108-116.
- MORRISON, M. L., I. C. TIMOSSI, K. A. WITH, AND P. N. MANLEY. 1985. Use of tree species by forest birds during winter and summer. *J. Wildl. Manage.* 49:1098-1102.
- MORRISON, M. L., K. A. WITH, AND I. C. TIMOSSI. 1986. The structure of a forest bird community during winter and summer. *Wilson Bull.* 98:214-230.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* 40:119-168.
- MORSE, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27:332-339.
- MOYNIHAN, M. 1960. Some adaptations which help to promote gregariousness. *Proc. XII Int. Ornithol. Congr.* (1958):523-541.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* 22:501-505.
- PULLIAM, H. R. 1973. On the advantages of flocking. *J. Theor. Biol.* 38:419-422.
- PULLIAM, H. R., K. A. ANDERSON, A. MISZTAL, AND N. MOORE. 1974. Temperature-dependent social behaviour in juncos. *Ibis* 116:360-364.
- SIEGFRIED, W. R., AND L. G. UNDERHILL. 1975. Flocking as an anti-predator strategy in doves. *Anim. Behav.* 23:504-508.
- SMITH, S. M. 1967. An ecological study of winter flocks of Black-capped and Chestnut-backed chickadees. *Wilson Bull.* 79:200-207.
- SPSS, INC. 1983. *SPSSX user's guide.* McGraw Hill, New York.
- TREISMAN, M. 1975. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. *Anim. Behav.* 23:801-825.
- VINE, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* 30:405-422.
- VINE, I. 1973. Detection of prey flocks by predators. *J. Theor. Biol.* 40:207-210.
- WING, L. 1941. Size of bird flocks in winter. *Auk* 58:188-194.