

Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks

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The species that participated in mixed-species foraging flocks in the pine-oak woodlands of western Mexico differed significantly in their foraging microhabitats (plant species and locations within the plants) and foraging movement patterns (average number of moves s^{-1} and average length of a given move). Because the foraging locations and rates of progression while feeding within trees differed among species, some species must be making continual adjustments to match the overall rate of flock progression. These same species may be buying the benefits of flocking at a cost in terms of feeding efficiency.

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Introduction

In the absence of constraints associated with breeding activity, the social organization of bird species often changes dramatically during the nonbreeding season (Pulliam and Millikan 1982). While nesting, bird foraging behavior is essentially an individual endeavor, where patterns of foraging are largely attributable to the location and number of nestlings that need to be fed (Orians and Pearson 1979, Andersson 1981, Biermann and Sealy 1982). In contrast, nonbreeding birds are often associated with large single-species or mixed-species flocks, where the patterns of foraging are constrained principally by the maintenance of group cohesion and, possibly, by competition for food with flockmates. In terms of mixed-species foraging flocks, the evolution of such complex social behavior – like the evolution of any behavior – involves both costs and benefits. Unfortunately, literature on the evolution of flocking has centered around a discussion of which is the most important benefit associated with flock foraging (but see Jones 1977, Ekman and Askenmo 1984), despite the frustrating fact that the favored hypotheses (avoidance of predation and increased feeding efficiency) are not mutually exclusive (Morse 1977).

Although potential predators may detect birds in

flocks more readily than nonflocking birds, flocking birds are likely to enjoy a net benefit in terms of decreased predation rates relative to solitary individuals because of an inevitable increase in the probability of predator detection due to more effective surveillance (Lack 1954, Goss-Custard 1970, Pulliam 1973, Powell 1974, Hoogland and Sherman 1976, Kenward 1978, Lazarus 1979). Once a potential predator is detected, and its needed element of surprise (see numerous references in Powell 1985) is removed, the threat of predation is presumably minor because of the superior agility of a smaller bird. Hence, the avoidance of predation is more than likely a necessary consequence of flocking.

In contrast, flock foragers do not necessarily gain benefits in terms of feeding efficiency as a consequence of group foraging (Rabenold and Christensen 1979). It would seem, therefore, that we might devote more attention to studies of the potential costs associated with group foraging, particularly costs associated with potential competition for food as these birds progress through the woods in such close proximity. After all, in most geographic locations, flocking behavior is most pronounced during the nonbreeding season (Davis 1946, Slud 1960, Moynihan 1962, McClure 1967, Powell 1979, Herrera 1979, Bell 1980), when food availability is presumably at its lowest level of the year and when the

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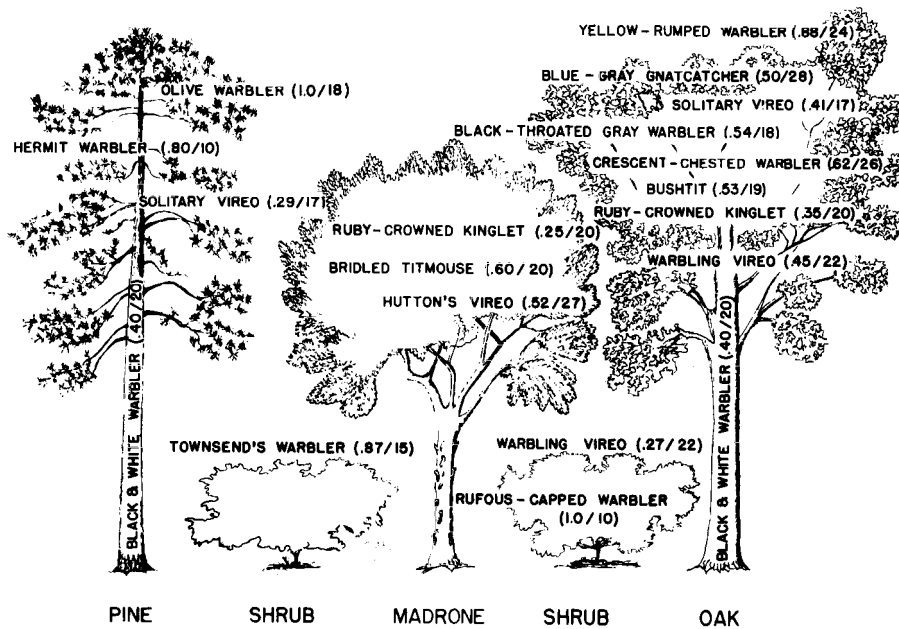


Fig. 1. Diagrammatic representation of the foraging locations of flock participants near Morelia, Michoacán. A given bird species' name appears in the plant species category within which the largest proportion of its observations were recorded. The same species was placed in additional plant species categories until at least 50% of its observations were represented. The relative heights of the names within the plant reflect the average position of that species based on the proportion of observations in the low, middle, and high categories. The total number of observations and the proportion of those recorded in a given plant type are given to the right and left of the slash, respectively.

abundance and diversity of birds in many tropical habitats is higher than it will be at any other time of the year (Hutto 1980, Rappole et al. 1983).

In the present paper, I address the potential costs associated with feeding in flocks by describing patterns in the foraging locations and foraging rates of the participants of a pine-oak woodland flock. My results suggest the hypothesis that group foraging behavior might be energetically costly because it imposes constraints on the individual foraging behavior of flock participants. Although I do not test this hypothesis directly, I believe that its discussion might provide a clearer focus for future research on the evolution of flocking behavior.

Study site and methods

I spent several weeks (1–13 March 1975, 1976) observing the behavior of birds in the pine-oak woodland located 31 km west of Morelia, Michoacán, Mexico (19° 40'N, 101° 20'W). The woodland was dominated by 10- to 15-m tall oaks (*Quercus* spp.), although similar-sized pines (*Pinus* sp.) and madrones (*Arbutus* sp.) were scattered throughout. The understory was composed of grasses and small (1–2 m) bushes.

I recorded the foraging behavior of flock participants in the following manner. Upon encountering a foraging individual within a flock, I started a stopwatch and recorded the number of moves and the total length of travel for as long a period as I was able to observe the bird within a tree. I did not include observations that lasted fewer than 10 s, and I did not include the relatively distant travel between trees as part of these data. I then recorded the category of plant species (pine, oak, madrone, or shrub) within which the bird was observed as well as the category of height (< 2m, 2–5m, > 5m) at

which the bird was first observed. I rotated observations among the various individuals on a given day. Because it was not uncommon to observe as many as 20 species in flocks at this site, it was difficult to accumulate a satisfactory number of observations for each species, given the limited time available. My analyses therefore include only those species for which I was able to accumulate at least 10 observations. A species list of all the flock participants is included, along with the scientific nomenclature, in Appendix I.

Results and discussion

The use of foraging locations by each of the commonly observed species ($N > 10$ observations) was nonuniform among the four plant species categories ($G^2 = 183$, $df = 42$, $P < 0.001$) and among the three foraging height categories ($G^2 = 74$, $df = 28$, $P < 0.001$). These differences are diagrammatically illustrated in Fig. 1. Some species foraged predominantly in the oaks, others in pines, some at the top of the canopy and others in the middle. The feeding behaviors of individual flock participants were, therefore, species specific and "typical" of the way each species forages at other times of the year. The distinctive (and, in many cases, non-overlapping) nature of the foraging behavior of each species in mixed-species flocks has been noted previously (Hindwood 1937, Willis 1966, Vuilleumier 1967, Austin and Smith 1972, Partridge and Ashcroft 1977, Moynihan 1979, Munn and Terborgh 1979, Wiley 1980). Such distinctiveness in the use of space is inconsistent with the idea (Krebs 1973) that the primary selective advantage gained by flock participants is the ability to "copy" the foraging behaviors or locations of individuals of other species (see also Partridge and Ashcroft 1977).

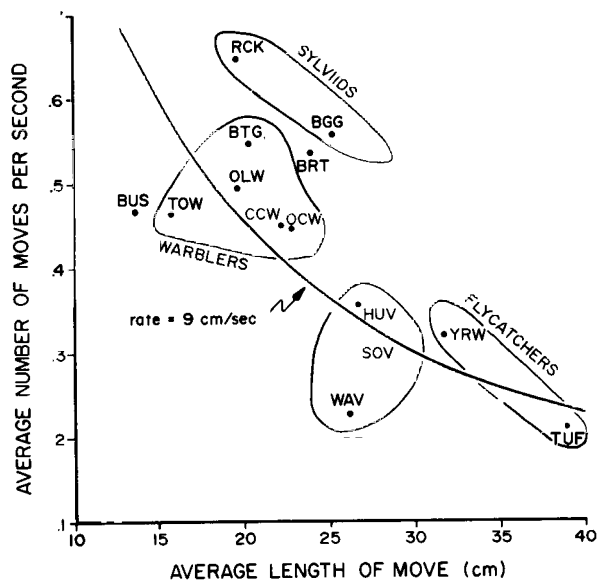


Fig. 2. The foraging movement patterns of some of the *Morelia* flock participants as illustrated by the average number of moves s^{-1} and the average length of a move between perches within a tree. Note how well the different behavioral groups are separated, while still tending to converge on a single rate of progression. Species codes are as follows: BGG = blue-gray gnatcatcher, BRT = bridled titmouse, BTG = black-throated gray warbler, BUS = bushtit, CCW = crescent-chested warbler, HUV = Hutton's vireo, OCW = orange-crowned warbler, OLW = olive warbler, RCK = ruby-crowned kinglet, SOV = solitary vireo, TOW = townsend's warbler, TUF = tufted flycatcher, WAV = warbling vireo, YRW = yellow-rumped warbler. Sample sizes given in Fig. 1.

The foraging movement patterns of the different species were distinctive as well. The species differed in their rate of movement within trees [ANOVA, $F(12, 208) = 24.9$, $P < 0.001$] and average length of a given move within trees [ANOVA, $F(12, 208) = 4.8$, $P < 0.001$]. A plot of the relationship between these two variables (Fig. 2) illustrates the wide range of foraging movement patterns among participants – a range of differences that reflects the participation of a variety of foraging guilds. Some species cover large distances per unit time while foraging (e.g., blue-gray gnatcatcher), while others progress at a much slower rate (e.g., warbling vireo). Although I did not measure the overall rate of movement by flocks at *Morelia*, if we assume for heuristic purposes that flocks there proceeded at the same rate as the flocks at another pine-oak site in western Mexico (about 9 cm s^{-1} ; Hutto 1987), then we could draw that line connecting points of equal rate onto Fig. 2. Two important implications emerge from such an exercise: (1) the line that connects points of equal rate provides an excellent fit to the points on the graph i.e., the points are not scattered randomly throughout the state space; (2) a rate of 9 cm s^{-1} would suggest that the sylviids (which lie above the line and, therefore, move more rapidly than 9 cm s^{-1}) and vireos (which lie below the line and move more slowly) are buying the flock-

associated benefits of reduced predation at an increased cost in terms of foraging efficiency because they would have to make continual adjustments (skip trees, or use a zig zag path between trees) to remain with the flock. Whatever the actual rate of flock movement, because the flock as a whole progresses at a single rate, and because the within-tree movement rates of the different species do not match any single rate, there may be considerable adjustment in the foraging rate parameters by some participants so that they can stay with the flock. Partridge and Ashcroft (1977) reached a similar conclusion after studying some mixed-species flocks in Ceylon. The species that deviate most strongly from the actual rate of flock progression may, on that basis, suffer a relative loss in foraging effectiveness.

The extent to which individuals modify foraging movement patterns or other aspects of behavior (foraging tactics, foraging locations) upon joining a mixed-species flock is, however, unknown. There are several studies whose results suggest that competitively-based changes in behavior do occur (Morse 1970, 1978, Austin and Smith 1972, Alerstam et al. 1974, Greig-Smith 1978, Hogstad 1978, Herrera 1979, Alatalo 1981), but the results of these studies are equivocal because changes in the behavior of color-marked individuals were not observed. Instead, these authors found differences between individuals foraging solitarily and other individuals that were foraging in flocks; the differences could, therefore, have reflected a nonrandom sampling of individuals between groups. Similar kinds of data will be difficult to obtain for the Mexican pine-oak flocks because most participants forage only in mixed-species flocks (Hutto 1987). The strongest evidence that individuals modify their behavior in the company of other individuals comes from studies like those of Ekman and Askenmo (1984), who circumvented these problems through removal experiments involving color-marked birds. They found that the spatial separation of age classes within monospecific willow tit flocks was a product of dominance interactions. Such experimentation remains to be done for interspecific groups.

When possible, the general assumption that the feeding rate of a participant is greater while in vs out of a flock (Krebs et al. 1972, Davies 1976, Greig-Smith 1978, Herrera 1979, Goldman 1980) needs to be tested using the species that are comprised of individuals that do forage both in and out of flocks. There is, in fact, evidence through this approach that color-marked individuals of at least some species forage less rapidly while in flocks (Rabenold and Christensen 1979, J. Shopland, pers. comm.).

The important point is that many flock participants may be suffering disadvantages rather than accruing benefits when it comes to food acquisition in these large mixed-species flocks. In most cases, we still lack the descriptive information necessary to determine whether foraging efficiency increases or decreases as a result of flocking. My results suggest that before we continue

searching for possible mechanisms by which birds gain feeding advantages associated with flocking, we need to devote more attention toward testing the assumption that flock foragers accrue any feeding advantages at all.

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Appendix I. Common and scientific names of flock participants

Common name	Scientific name	Common name	Scientific name
Ladder-backed woodpecker	<i>Picoides scalaris</i>	Warbling vireo	<i>V. gilvus</i>
Northern flicker	<i>Colaptes auratus</i>	Orange-crowned warbler	<i>Vermivora celata</i>
Tufted flycatcher	<i>Mitrephanes phaeocercus</i>	Crescent-chested warbler	<i>Parula superciliosa</i>
Greater pewee	<i>Contopus pertinax</i>	Yellow-rumped warbler	<i>Dendroica coronata</i>
Western flycatcher	<i>Empidonax difficilis</i>	Black-throated gray warbler	<i>D. nigrescens</i>
Buff-breasted flycatcher	<i>E. fulvifrons</i>	Townsend's warbler	<i>D. townsendi</i>
Bridled titmouse	<i>Parus wollweberi</i>	Hermit warbler	<i>D. occidentalis</i>
Bushtit	<i>Psaltriparus minimus</i>	Black-and-white warbler	<i>Mniotilta varia</i>
Spotted wren	<i>Campylorhynchus gularis</i>	MacGillivray's warbler	<i>Oporornis tolmiei</i>
Ruby-crowned kinglet	<i>Regulus calendula</i>	Rufous-capped warbler	<i>Basileuterus rufifrons</i>
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	Olive warbler	<i>Peucedramus taeniatus</i>
Solitary vireo	<i>Vireo solitarius</i>	Hepatic tanager	<i>Piranga flava</i>
Hutton's vireo	<i>V. huttoni</i>		