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FLOCKING AND FRUGIVORY: THE EFFECT OF SOCIAL GROUPINGS ON RESOURCE USE IN THE COMMON BUSH-TANAGER[1]

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Abstract. The Common Bush-Tanager (*Chlorospingus ophthalmicus*) displays flexibility in social behavior and prey choice. Thirty-three marked individuals were observed at Monteverde, Costa Rica over 15 consecutive months to determine the effect of social foraging (single individual, single- and mixed-species flock) on levels of frugivory and insectivory. I quantified the effects of social group composition and size, sex, and seasonality on the proportion of fruits and arthropods consumed by individuals.

Common Bush-Tanagers spent one-third of their time in mixed-species flocks, consuming higher proportions of arthropods than individuals in single-species groups. Flock composition, rather than flock size, was the major factor influencing patterns of fruit and arthropod consumption. This study supports the hypothesis that birds may join mixed-species flocks in order to consume insect prey because when Common Bush-Tanagers participated in mixed-species flocks, they switched from frugivory to insectivory. Hence, the trophic position of species varies with the particular mix of single-species and mixed-species foraging groups available within a community.

Key words: Common Bush-Tanager; mixed-species flock; single-species flock; foraging; frugivory; insectivory; Costa Rica.

INTRODUCTION

Vertebrates may show considerable flexibility both in their use of prey taxa, alternating between insectivory and frugivory, and in their tendency to forage both as solitary individuals and in groups. Foraging in groups may alter the tendency of some vertebrates to forage for insects or fruits, because social foraging may affect the efficiency (Cody 1971) or safety (Powell 1977) with which these different foods are found and consumed. Therefore, the trophic position of species could vary with the particular mix of single-species and mixed-species foraging groups available within a community. For example, Terborgh (1983) found that the diet of South American primates varied depending upon whether individuals foraged in single-species or mixed-species groups. For individuals within avian flocks, Buskirk (1976) found that the behavior when joining mixed-species flocks tended to converge with the nuclear species in that mixed-species flock. Common Bush-Tanagers (*Chlorospingus ophthalmicus*) are highly variable in the extent to which they forage for fruits and arthropods. This variation provides the opportunity to study the conditions under which different interactions and foraging modes are favored (Thompson 1988). Here I ask (1) how the proportion of time spent by Common Bush-Tanagers foraging as single individuals, in single-species flocks, and in mixed-species flocks varies seasonally and diurnally, and (2) how social grouping affects the proportions of fruits and arthropods consumed.

Differences in behavior between insectivorous and frugivorous flocks have been linked to differences in the resource to be exploited: insects are cryptic and difficult to find, whereas fruits are often conspicuous (Morse 1970, Morton 1973, Moermond and Denslow 1985). For insectivores, rates of ingestion do not greatly exceed rates of digestion, resulting in continuous searching activity (Munn and Terborgh 1979, Hutto 1981). In contrast, frugivores can ingest fruit much more rapidly than they can digest it, which results in episodic searching for food (Sorenson 1984, Johnson et al. 1985). Exploitation of these different resources may therefore favor differences in foraging behavior. For an omnivore, balancing the time constraints of insectivory and the spatial constraints of frugivory necessitates compromises in both behavior and diet (Karr 1971, McNab 1980).

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If foraging behaviors for exploiting fruit as a primary resource differ from those for exploiting insects, then flocks containing both insectivores and frugivores should be uncommon (Moynihan 1962, Munn and Terborgh 1979). Nonetheless, frugivorous Common Bush-Tanagers do join the predominantly insectivorous flocks of the mid-elevation neotropical forest (Buskirk 1976, Powell 1979). When not in mixed-species groups, they are highly gregarious, forming intraspecific flocks. This behavioral flexibility allowed me to examine the effect of social group size and composition on prey choice.

STUDY AREA

I studied Common Bush-Tanagers in a Lower Montane Wet Forest (Holdridge 1967) adjacent to the Monteverde Cloud Forest Biological Preserve in Puntarenas Province, Costa Rica. The climate is characterized by little seasonal variation in temperature regime, but much seasonal variation in precipitation and wind. The vegetation has four strata, with an average canopy height of 20 m. Common trees in the canopy are members of the Lauraceae, Sapotaceae, Moraceae, and Symplocaceae, and understory trees include members of the Melastomataceae, Solanaceae, and Urticaceae (Lawton and Dryer 1980). Many shrubs fill in light gaps, and tree trunks are covered with epiphytes and climbing vines. Common Bush-Tanagers forage mostly in understory and second-growth patches, although many home ranges include primary forest. Since bush-tanagers use the heavily fruiting shrubs of second-growth areas, they do not rely on distantly spaced fruiting trees, but forage on their own fruit-bearing territories.

Common Bush-Tanagers are one of the most abundant bird species of the Lower Montane Cloud Forest. Previous work on the mixed-species flocks of Monteverde demonstrated that Common Bush-Tanagers maintain 0.5-ha home ranges and participate in mixed-species flocks only when those flocks pass through their territories (Powell 1977). Individuals consume a wide variety of high-sugar, low-lipid fruit species at Monteverde (Wheelwright et al. 1984). As noisy, understory foragers, banded individual Common Bush-Tanagers are relatively easy to follow. Mixed-species flocks at Monteverde usually include Three-striped Warblers, Slate-throated Redstarts, Spotted Barbtails, and Gray-breasted Wood-Wrens, along with many other species. The only major avian predators of adult birds observed at this site were Barred Forest-Falcons and, on two occasions, a Collared Forest-Falcon.

METHODS

Thirty-three Common Bush-Tanagers were mist-netted and banded during April, May, and June, 1987. Transient birds were not marked, but were tallied in single-species flock counts. Each individual's foraging behavior was recorded at 1-min intervals during 45-min observation periods. Data were collected during every month from March 1987 through June 1988, yielding data from one wet season, two breeding seasons, and one dry season. During each month, each pair or individual bird was observed 3–4 times, with observation periods for each bird staggered to cover the hours of 07:00–17:00 hours. I visited the home ranges of each pair, and I listened and observed until each individual was located. Because pairs often foraged together, either in single- or mixed-species groups, both birds in a given area were often located simultaneously. Social grouping (both flock composition and flock size), type of prey consumed if any was taken (arthropod or fruit), time of day, and the sex of the bird were recorded for each individual at 1-min intervals during an observation period. Group composition was determined as solitary, single-species flock, or mixed-species flock. Flock size was determined from flock counts. A flock was defined, for these purposes, as two or more birds moving in the same direction in fairly close proximity to each other (Winterbottom 1943, Morse 1970). Insects consumed were not identified, but fruits consumed were not identified, but fruits consumed were identified to species when possible. The sex of most birds was initially recorded as unknown, but was subsequently determined on the basis of breeding behavior, or reproductive morphology (presence or absence of incubation patch during the breeding season) upon subsequent recapture. Incidents of predation were recorded as they occurred, noting group type, predator species, and success of the predator.

DATA ANALYSIS

Foraging records included 29,320 observations for 33 Common Bush-Tanagers. I used an ANOVA design to determine the effects of social grouping, flock size, time-of-day, month, and sex on the ratio of fruit to insects consumed. Levels of flock participation and raw numbers of insects

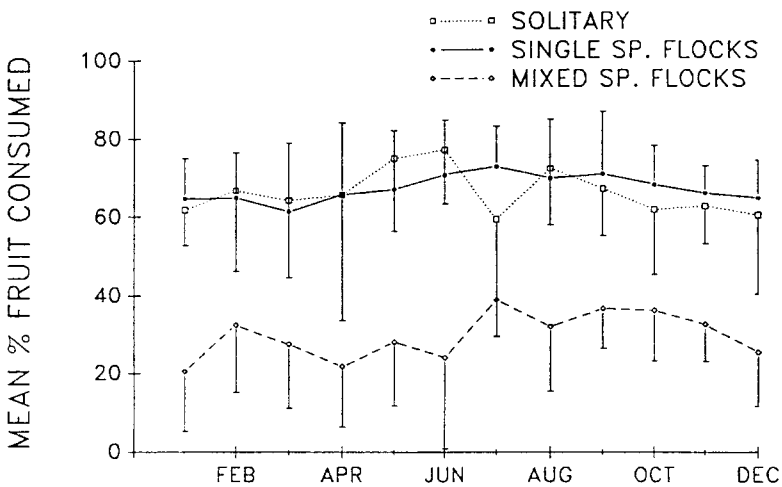

FIGURE 1. Mean percentages of fruit consumed by Common Bush-Tanagers in three social groupings: solitary, single-species flocks and mixed-species flocks over the annual cycle, with SE. Monthly values represent pooled data from 33 individuals over 15 months of observation.

and fruits consumed did not significantly vary among individuals (1-way ANOVA, $P < 0.001$), so data from the 33 individuals were analyzed by individual observation periods. Flock sizes were categorized into groups of 1, 2, 3–8, 9–20, and more than 20 individuals. These groups corresponded to the most common groupings of Common Bush-Tanagers. Time of day was recorded in hours and minutes, and then classified as early (06:30–11:00) or late (11:01–15:30). Data from March 1987 to June 1988 were combined to represent a single annual cycle. The data from months of March through June did not show annual differences relating to social or foraging behavior, and consecutive months did not show autocorrelation. Each month included 90–100 observation periods. All analyses of variance were performed using the GLM procedure of SAS (1985). Data were analyzed for normality and homogeneity of variances using the univariate procedure of SAS (1985). In multiway analyses, Type III sums of squares were used.

RESULTS

The effect of group composition on fruit consumption. Percentages of fruit consumed by individuals per observation period differed significantly between mixed-species and single-species groups (multi-way ANOVA, $F = 66.24$, $P < 0.0001$; Fig. 1), with members of single-species groups averaging 66% fruit as compared with an average of 27.5% for individuals in mixed-species groups. Levels of fruit consumption did not vary over the annual cycle in all social groupings (Fig. 1), despite seasonal fluctuations in availability of particular fruit species.

The effect of group size on fruit consumption. Fruit consumption decreased significantly as flock size increased when flock composition was ignored (one-way ANOVA, $F = 5.08$, $P < 0.0005$, Fig. 2). The most conspicuous decrease occurred at flock sizes of 5–15 birds, therefore data were analyzed most thoroughly for groups of these sizes. It was within this range of flock sizes that the incidence of the two types of flock composition overlapped. When fruit consumption was examined with respect to flock composition, it was clear that the decrease in fruit consumption occurred as a result of a move from a single-species flock to a mixed-species flock (Fig. 3). Levels of frugivory within the flock types remained fairly consistent. Flock composition had a significant effect alone, and also interacted with group size (ANOVA, $F = 7.26$, $P < 0.0001$).

Time allocation to social groupings and effects on frugivory. Single-species flocks were much more common than mixed-species flocks, with 60% of all observations recorded on groups of two or more conspecific birds. Mixed-species flocking accounted for an average of 30% of the bird's day, with only 10% spent in solitary foraging. Over the annual cycle, single-species flocking peaked in May, the height of breeding season. A corresponding annual low in the prevalence of

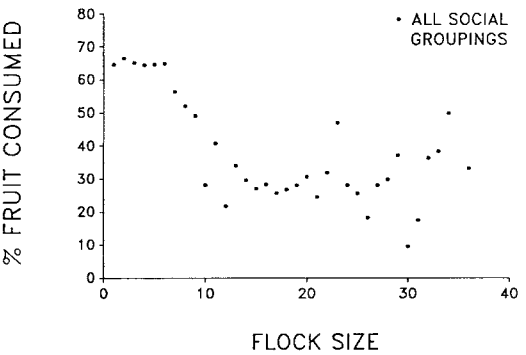

FIGURE 2. Variation in the mean percentage of fruit consumption by Common Bush-Tanagers by flock size for all social groupings combined.

mixed-species flocking occurred during the pre-breeding and breeding season (March through June). Solitary foraging underwent no significant month-to-month fluctuations.

The effects of time allocation and time-of-day on frugivory in different social groupings. Common Bush-Tanagers did not vary in their mean percentage of fruit consumption over the course of the day (multi-way ANOVA, TIME, $F = 0.84$, $P > 0.05$), but spent significantly more time in solitary foraging during the morning hours ($F = 4.73$, $P > 0.01$).

The effect of sex on frugivory in the different social groupings. The sex of an individual did not directly affect frugivory (multi-way ANOVA, $F = 0.55$, $P > 0.05$), but male Common Bush-Tanagers were more likely than females to form large single-species groups during December and January ($F = 2.62$, $P = 0.05$).

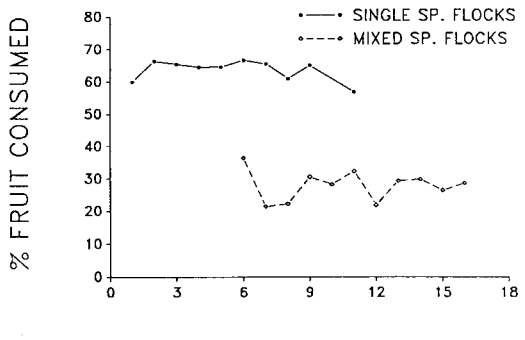

FIGURE 3. Variation in mean percentage by Common Bush-Tanagers by flock size for flocks of 6–16 birds containing both single-, and mixed-species groups.

The effect of predators on birds in the different social groupings. During fifteen months of observation, only eight incidents of predation were observed. Of these incidents, three were directed toward solitary Common Bush-Tanagers, and one was successful. The predator was a Barred Forest-Falcon. The other five predation attempts were directed toward members of mixed-species flocks during the time when bush-tanagers were foraging with the flock. Of these, three were successful: a Collared Forest-Falcon and two Barred Forest-Falcons. These incidents were too few to be analyzed statistically, and remain anecdotal evidence. Because my proximity to the prey species may have had a deterrent effect on predators, members of single-species flocks that foraged lower in the vegetation (Valburg, pers. observ.) may have benefitted relatively more than mixed-species flocks. It is interesting, however, that I did not observe a single instance of a predation attempt involving a single-species flock member, the most common social grouping seen in Common Bush-Tanagers.

DISCUSSION

Since Common Bush-Tanagers are primarily territorial, individuals associate with mixed-species flocks only as the flocks move through their territory (Powell 1977). Birds not participating in the mixed-species flock within their territory tended not to leave their territory and join other flocks, and instead remained solitary or in single-species groups comprised of other bush-tanagers who did not maintain territories. Previous studies of flock participants have focused on color-banded individuals while they were within the mixed-species groups (Morse 1970, Austin and Smith 1972, Hogstad 1978, Alatalo 1981). Although several studies have suggested that changes in behavior resulting from interspecific competition do occur when a mixed-species flock is joined, these studies compared individuals foraging solitarily to other individuals foraging in flocks (Morse 1970, Herrera 1985). Other studies have focused on flocks whose participants were too difficult to locate when not with the flock, or flocks whose participants flocked all the time (Hutto 1987). This study augments previous work by examining a single population of Common Bush-Tanagers in all types of social groupings, and by showing that foraging behavior and dietary composition change dramatically when individuals participate in mixed-species flocks.

The switch to insectivory observed in this study confirms the hypothesis that foraging behavior of mixed-species flock participants tends to converge (Buskirk 1976). Because the mixed-species flocks at Monteverde, like mixed-species flocks reported from other tropical and temperate regions, are composed largely of insectivores (Moynihan 1962, Morse 1970, Austin and Smith 1972, Powell 1979, Munn 1985), it follows that a convergence of behavior should result in a higher level of insectivory even for a mostly frugivorous tanager species.

The large overlap in the range of sizes of single and mixed-species groups made it possible to distinguish between the effects of group size and group composition. Some benefits of mixed-species flocking, such as increased vigilance, and the "selfish herd" effect, have been attributed to the anti-predator effect of the presence of many individuals (Buskirk et al. 1972, Willis 1972, Pulliam 1973, Powell 1974). If increased group size resulted in changes in foraging behavior due solely to decreased risk of predation, then there should not have been such a marked difference between single-species and mixed-species flock foraging where flock size was similar. Group composition, as well as group size, was responsible for a significant switch to insectivory.

This study supports the hypothesis that birds may join mixed-species groups in order to facilitate the consumption of arthropod prey. Common Bush-Tanagers had access to all insect and fruit prey in both solitary foraging and single-species group foraging modes, but selected more insect prey per unit time when in a mixed-species group. This switch to insectivory may relate to enhancement of foraging technique or copying of insectivorous mixed-species flock members, and may also suggest that mixed-species flocks provide greater protection from predators, allowing more continuous attention to insectivory. Because this study did not attempt to ascertain the relative benefits of predator avoidance and foraging enhancement through mixed-species flock participation, I can only assert that the increased insectivory seen when Common Bush-Tanagers join mixed-species groups would follow from either scenario.

Because Common Bush-Tanagers did not leave their territories to join mixed-species flocks, they could not benefit by finding new patches of food unless they used different microhabitats within their three-dimensional territories during mixed-species flocking. It does not necessarily follow that a mixed-species group would tend to flush more insects than a single-species one. Rather, in the company of insectivores, Common Bush-Tanagers were most likely to benefit from using behaviors consistent with the habits of the insectivorous birds that largely comprised the mixed-species flocks. No food facilitation hypothesis rules out the probability that mixed-species flock members benefit from predator avoidance. It remains to be demonstrated that mixed-species flocks are better than single-species ones at eluding predators, although anecdotal evidence has long suggested the many benefits of mutual vigilance among heterospecific feeding associations (Devore and Hall 1965). Although the ultimate costs and benefits of joining a mixed-species flock remain elusive, the increase in insectivory shown for Common Bush-Tanagers participating in mixed species flocks suggests that enhanced foraging for insects may be a proximate benefit of mixed-species flocking for this species.

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