

# COPYING OF FORAGING LOCATIONS IN MIXED-SPECIES FLOCKS OF TEMPERATE-DECIDUOUS WOODLAND BIRDS: AN EXPERIMENTAL STUDY<sup>1</sup>

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**Abstract.** We examined "copying" of foraging locations among the members of mixed-species foraging flocks of deciduous woodland birds. We used 10 captive flocks, each consisting of a male and a female Downy Woodpecker (*Picoides pubescens*), a male and a female White-breasted Nuthatch (*Sitta carolinensis*), three Tufted Titmice (*Parus bicolor*), and two Carolina Chickadees (*P. carolinensis*). Low-ranking individuals were less likely than dominants to take even a single mealworm (*Tenebrio* sp.) from a cryptic food supply, but when they did take at least one mealworm they tended to do so more quickly than dominants. Subordinates were quicker to follow a conspecific than a dominant heterospecific in extracting a mealworm from the cryptic supply. We examined how two types of learning, local enhancement and social facilitation, might enhance food finding among these four species. Compared to higher-ranking individuals, subordinates were more likely to generalize to a similar foraging site (social facilitation) than to go to the exact site of a food find (local enhancement). Our results also suggest that the intraspecifically subordinate chickadees and titmice may be at an advantage in mixed-species rather than single-species flocks because dominant heterospecifics may interfere with their foraging less than may dominant conspecifics.

**Key words:** Copying; foraging; local enhancement; mixed-species flock; *Parus bicolor*; *Parus carolinensis*; *Picoides pubescens*; *Sitta carolinensis*; social facilitation.

## INTRODUCTION

Two general bodies of hypotheses have been advanced to explain the adaptiveness of foraging in mixed-species groups. These hypotheses reason that individuals participating in mixed-species foraging groups accrue the benefits of enhanced predator avoidance and increased foraging efficiency (reviews in Moriarty 1976, Morse 1980, Krebs and Davies 1981, Powell 1985). Of the several mechanisms besides decreased vigilance time that could promote foraging efficiency of animals participating in mixed-species assemblages, namely copying, beating, and kleptoparasitism, only copying has theoretical promise of explaining the adaptiveness of foraging for low-ranking individuals of mixed-species flocks wintering in temperate deciduous woodlands. The beating effect cannot operate during temperate winter when low temperatures render poikilothermic prey dormant, and kleptoparasitic attacks occur asymmetrically with respect to dominance status and thus cannot explain flock membership for subordinate individuals. In con-

trast, the opportunities for imitative foraging within mixed-species woodland bird flocks may be considerable as the birds making up such flocks are generally all active arboreal foragers (Buskirk 1976) exhibiting roughly similar foraging behavior.

There is a modest amount of evidence from manipulative (Krebs et al. 1972, Baker et al. 1981) and mensurative (Waite 1981) studies that copying is a direct benefit of flock membership in monospecific flocks. However, although several authors have reported observations of copying by free-ranging birds in mixed-species flocks (e.g., Moynihan 1962, Morse 1980), with the exception of a few experimental studies, the evidence is largely anecdotal. Krebs (1973) clearly demonstrated that individual Black-capped (*Parus atricapillus*) and Chestnut-backed (*P. rufescens*) chickadees copied the foraging location of an individual of the other species which had just taken food. However, because the two species used are congeners with nearly identical morphology, show a great deal of foraging niche overlap (Smith 1967), and appear to avoid competition largely through habitat segregation, it remains unclear whether Krebs' results bear on the hypothesis that copying promotes mixed-species flocking among more

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disparate species that characteristically forage together in nature (but see Caldwell 1981).

Sasvari (1985) studied observational learning of foraging tasks in juveniles and adults of three parid species, Great Tit (*Parus major*), Blue Tit (*P. caeruleus*), and Marsh Tit (*P. palustris*), and in two thrush species, Eurasian Blackbird (*Turdus merula*) and Songthrush (*T. philomelos*). His results are difficult to interpret because since the teaching bird was always subordinate to the learning bird, learning could have occurred after the teacher had been supplanted from food rather than through observational learning per se.

The present study attempts to answer the question of whether copying of foraging locations by different members of a foraging guild has the potential to operate as a proximate mechanism promoting foraging efficiency. We tested whether and how copying actually might occur among the four most common species of the bark-foraging guild of central Ohio, Downy Woodpecker (*Picoides pubescens*), White-breasted Nuthatch (*Sitta carolinensis*), Tufted Titmouse (*Parus bicolor*), and Carolina Chickadee (*P. carolinensis*). We examined how two types of imitative learning, local enhancement and social facilitation, might promote the formation of foraging flocks during the nonbreeding season. Local enhancement we define after Thorpe (1963) as occurring when an individual, after observing either a heterospecific or a conspecific make a food find, goes to the exact site at which the food was found and engages in an apparent search for food. Social facilitation has been described as contagious behavior in which the actions of one individual release identical behaviors in other individuals present at the time of the performance (Thorpe 1963). In a narrower sense, we consider social facilitation as occurring when an individual, after observing a food find by either a heterospecific or a conspecific, searches for food in a similar, but not the same, microsite (see further explanation in Methods).

## METHODS

Individuals for five captive mixed-species flocks were captured between January and March 1984 and those for five additional flocks between November 1984 and March 1985. Each captive flock consisted of a male and a female Downy Woodpecker, a male and a female White-breasted Nuthatch, three Tufted Titmice, and two Carolina Chickadees. Hereafter, these species will some-

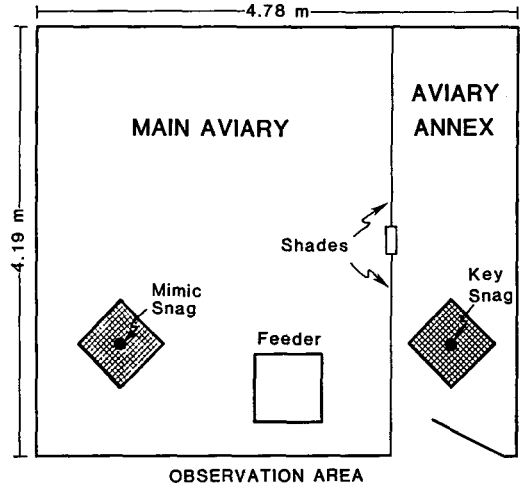


FIGURE 1. Plan of the aviary showing the locations of the mimic and key snags and the annex.

times be referred to as DW, WBN, TT, and CC, respectively. All birds were captured in rural woodlots in Morrow County, Ohio using either radio-controlled stove-pipe drop-door traps baited with sunflower seeds (*Helianthus* sp.) or "Graves tree traps" baited with beef suet (Pierce and Grubb 1981). To ensure that the birds of each captive mixed-species flock used in the experiment had had some familiarity with each other in the wild, we attempted to capture all nine birds for each captive flock at the same trapping station. This was possible for only six of the 10 flocks. However, we were able to ensure that each captive pair of nuthatches actually had been paired in nature by capturing a male and a female nuthatch that repeatedly had arrived together at a trapping station. Finally, we attempted to capture TT and CC that were using the feeders contemporaneously.

Between the times when they were captured and tested, all nine birds of a given flock were housed for at least 10 days in a large indoor aviary (Fig. 1) on the Ohio State University campus, Columbus, Ohio. Before each bird was released into the aviary, its cheek patches or breast were marked with a unique color using waterproof felt-tip marking pens. As the two species of parid used in the study were sexually monomorphic, it was difficult to sex them reliably on the basis of external features, and as the birds in this study were neither laparotomized nor sacrificed, only the woodpeckers and nuthatches were

sexed. The birds were kept on a natural photoperiod, and the aviary temperature was held at  $18.9 \pm 1.4^\circ\text{C}$  ( $\bar{x} \pm \text{SE}$ ) to minimize the effect of thermal factors (Grubb 1975, 1977, 1978). The birds were maintained on an ad libitum diet of sunflower seeds and mealworms (*Tenebrio* sp.) made available on a 0.6- × 0.6-m feeding tray placed 1.5 m above the aviary floor. Two water sources were also always available. After each replicate had been completed, the birds involved were released at the site of their capture.

#### DOMINANCE HIERARCHIES

After the birds in each flock had spent at least 3 days acclimating to the aviary environment, dominance hierarchies were determined periodically over at least 2 days. While scanning the aviary, we recorded all interactions in which one bird successfully used a "supplanting attack" (sensu Hinde 1952). Records taken during 20 15-min observation sessions were entered into a win-loss matrix (Waite 1986). We also recorded the following dominance-subordination interactions (modified after Smith 1976): (1) retention of position on perch and threat display when another bird approached to within 15 cm, (2) waiting within 0.5 m of the feeder until another bird (the winner) had moved at least 1 m away from the feeder before moving onto the feeder and taking a food item, and (3) chasing another individual either in flight or while hopping along the substrate.

#### DIET SELECTION

On the sixth and/or seventh day of each flock's captivity, we used focal animal sampling (Lehner 1979) to record the diets of all birds. Each time the focal bird took a food item from the feeder, from the floor or from a cache, we recorded: (1) whether the food item was a sunflower seed or mealworm, and (2) the elapsed time (min) since the beginning of the observation session. In flocks 1 to 5, each focal bird was observed in a single observation session until it had consumed at least 10 food items. In flocks 6 to 10, each focal animal was observed for at least four observation sessions in each of which it consumed at least five food items. We randomly selected 50 mealworms from each of two lots and determined their mass on an analytical balance. The mean mass of a single larva was  $0.063 \pm 0.021$  g ( $\bar{x} \pm \text{SD}$ ). We divided the sunflower seeds into two categories, small, black seeds and large, white-

and black-striped seeds, because CC virtually always took the small, black seeds, whereas DW, WBN, and TT invariably chose the large striped seeds. We then proceeded as with the mealworms except that all seeds of each type came from a single lot. We husked 200 seeds and rejected those that were insect-infested, as the birds appeared to do. The masses for large and small seeds were  $0.046 \pm 0.012$  g and  $0.027 \pm 0.010$  g ( $\bar{x} \pm \text{SD}$ ), respectively. The energy contents of mealworms and sunflower seeds from lots we used were 1.36 and 4.94 kcal g<sup>-1</sup>, respectively (Lancaster Laboratories, Lancaster, Pennsylvania). Thus, the mean energy contents of mealworms and large and small seeds were 0.086, 0.227, and 0.133 kcal per item, respectively. These values were used to calculate the energy intake rates of birds both before (assumed to be steady state) and during an experimental trial.

#### COPYING EXPERIMENT TEST PROCEDURE

Throughout the study, the aviary contained two small vertical tree trunks, the key snag and the mimic snag, in addition to tree branches arranged as perches. These snags were 2-m tall, 10-cm-diameter American elm (*Ulmus americana*) saplings (Fig. 2). Within the key snag we fashioned a hollow core 30 cm long by 4 cm in diameter. At the lower end of this hollow core was a semi-circular hole 1 cm in radius through which the birds had access to a supply of mealworms during an experimental trial. We killed the mealworms by freezing them so none would crawl out of the hole during the experiment. At the upper end of this hollow core on the opposite side of the sapling from the key hole, we drilled a hole 2 cm in diameter to serve as a loading port for the mealworms. During experimental trials this loading port was plugged with a black rubber cork. Three semicircular bracket fungi 12 cm in diameter were glued to the snag near the hole, one approximately 1 cm directly below the key hole. The mimic snag was arranged similarly except that it did not contain a hollow core; the semicircular hole in the mimic snag led to a dead end 5 cm into the snag. Finally, each snag was surrounded at the base by a plywood box 0.7 × 0.7 × 0.5 m high covered with 2.5-cm wire screening. This arrangement ensured that any mealworms dislodged from the key hole by a feeding bird would fall into the box below. Thus, during an experimental trial the aviary remained essentially de-

void of food except for the cryptic supply of mealworms accessible through the key hole.

On generally the eighth day of captivity for each flock, the control trial was conducted beginning at approximately 09:30. First, the feeding tray was removed and the aviary floor was swept to remove any spillage. However, the aviary was never completely devoid of food because WBN cached food quite extensively (Waite 1986) and it was not possible to remove completely all spilled food items without endangering the birds by our extended presence in the aviary. No food was available in the key snag during the control trial. In retrospect, we realize that our control would have been stronger had we somehow been able to arrange for the key snag to contain mealworms that the birds could potentially see, but not reach physically. Of course, employing such a procedure would have precluded using the birds as their own controls. After removing the food from the aviary, two observers watching through a one-way window recorded on cassette recorders for 30 min all landings on top, upper, shelf, lower, and box of both snags (Fig. 2). Additionally, all inspections of the key and mimic holes were recorded. An inspection of a hole was defined as a bird pausing and turning its head to peer directly into the hole and/or probing in the hole with its bill.

In the evening of the day when a control trial had been run, the dominant TT was captured and isolated overnight in the aviary annex (Fig. 1). Beginning at approximately 09:30 the following morning, the only food available to this model TT was the supply of mealworms in the key snag. After the model TT had located the cryptic food supply, defined as having taken and eaten six mealworms from the key hole, the partition-wall between the main aviary and the aviary annex was raised (Fig. 1) allowing all birds access to the entire aviary. Then, as in the control trial, the food was removed from the aviary. During the experimental trial, all landings on both snags, all inspections of the mimic hole and all mealworms taken from the key hole were recorded until 70 mealworms had been taken. Using these experimental procedures, we generated values of key and mimic snag use during the control trial, when the entire aviary was essentially devoid of food, that could be compared to values of snag use during the experimental trial after the first mealworm had been taken from the key snag in the presence of all birds. For analyses using two

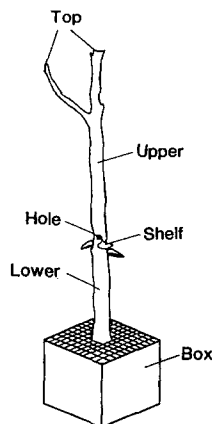


FIGURE 2. A snag (key or mimic) showing the names of its parts and the arrangement of the hole and the shelves.

measures of snag use, latency to land and number of landings, the control trials were considered to begin after 10 min had elapsed. This was a sufficient delay to allow all birds to resume activity following the behavioral freeze typically provoked by our presence in the aviary. This procedure also preserved a long enough time interval for each control trial (i.e., 20 min) to allow statistical comparisons of snag use between the control and experimental trials. Experimental trials were considered to begin when a bird took the first mealworm from the key snag. Unfortunately, we did not record how many minutes elapsed between the time when the model titmouse was released from the annex back into the main aviary and the subsequent time when the first mealworm was taken from the key snag. However, it is our impression that in every experimental trial this interval was at least as long as the 10-min latency period we used in control trials.

Finally, immediately after the 70th mealworm had been taken from the key hole, we removed all remaining mealworms from the key snag and then we recorded the use of both snags, including all landings and hole inspections, for an additional 30 min. This last procedure allowed us to assess whether and the extent to which these birds might look for food at similar microsites after a cryptic food supply had been depleted.

Unless otherwise noted, parametric and non-parametric statistical tests are from Snedecor and Cochran (1967) and Siegal (1956), respectively. Statistical significance was set at the 0.05 level.

TABLE 1. Dominance-subordination hierarchies.

Flock	Dominance rank								
	1	2	3	4	5	6	7	8	9
1	MDW	FDW	MWBN	<b><u>RTT</u></b>	FWBN	WTT	BTT	WCC	RCC
2	MDW	FDW	MWBN	<b><u>RTT</u></b>	FWBN	BTT	WTT	RCC	WCC
3	MDW	FDW	MWBN	<u>BTT</u>	FWBN	WTT	RTT	RCC	WCC
4	MDW	FDW	MWBN	<b><u>FWBN</u></b>	<u>RTT</u>	BTT	WTT	WCC	RCC
5	MDW	FDW	MWBN	<b><u>BTT</u></b>	FWBN	WTT	RTT	RCC	WCC
6	MDW	FDW	MWBN	<b><u>BTT</u></b>	FWBN	WTT	RTT	RCC	WCC
7	MDW	FDW	<b><u>BTT</u></b>	MWBN	FWBN	WTT	RTT	WCC	RCC
8	MDW	<b>FDW</b>	MWBN	FWBN	<u>BTT</u>	WTT	RTT	RCC	WCC
9	MDW	FDW	<u>WTT</u>	MWBN	FWBN	RTT	BTT	RCC	WCC
10	MDW	FDW	MWBN	FWBN	<u>RTT</u>	BTT	WTT	RCC	WCC

Boldface print indicates the first individual to take a mealworm from the key hole in each replicate. The model TT is underlined for each replicate. Bird identities are as follows: MDW = male Downy Woodpecker, FDW = female Downy Woodpecker, MWBN = male White-breasted Nuthatch, FWBN = female White-breasted Nuthatch, RTT = red Tufted Titmouse, BTT = blue Tufted Titmouse, WTT = white Tufted Titmouse, RCC = red Carolina Chickadee, and WCC = white Carolina Chickadee.

## RESULTS

Dominance relationships are given in Table 1. Each dominance hierarchy was linear and there were no changes in dominance within any of the dyads during the period of captivity. For all individuals adjacent in the hierarchy, the dominance relationship could be resolved by percent wins (viz., there were no ties). These hierarchies were used to determine whether dominance rank was related to various measures of copying.

The model TT was the first bird to take a mealworm from the key hole in five of the 10 replicates (Table 1). The replicates in which a bird other than the model TT was the first bird to take a mealworm were excluded from some of the analyses to be reported below.

For birds of each intraspecific dominance rank, we compared the mean time lag to land on each snag during the experimental trials to the mean lag during the control trials. Only female DW ( $0.4 \pm 0.5$  min vs.  $7.4 \pm 6.2$  min,  $t = 2.415$ ,  $P < 0.05$ ,  $df = 4$ , one-tailed) and female WBN ( $5.2 \pm 2.8$  min vs.  $12.8 \pm 7.4$  min,  $t = 2.361$ ,  $P < 0.05$ ,  $df = 4$ , one-tailed) landed on the key snag significantly sooner during the experimental than during the control trials.

That subordinate individuals were slower to copy is suggested by a significant positive correlation between dominance rank and the ratio of mean minutes to land on the upper, shelf, or lower parts of the key snag during the experimental trial to the mean minutes to land during the control trial ( $r_s = 0.67$ ,  $P < 0.05$ , one-tailed;

model TT excluded). Of course, this was a measure of snag use, not of copying per se.

A positive correlation also emerged between dominance rank and the proportion of replicates in which birds took at least a single mealworm from the key snag (Fig. 3). However, a significant negative correlation emerged between dominance rank and the latency to take a mealworm in terms of the number of visits by other birds to the key hole during which at least one mealworm was taken ( $r_s = -0.74$ ,  $P < 0.05$ , two-tailed). This suggests that although socially low-ranking individuals were less likely to take at least one mealworm, when they did they generally did so sooner than did dominants. Similar correlations between dominance rank and the latency to take a mealworm in mean minutes and mean number of mealworms taken from the key hole following the initial extraction of a mealworm were nonsignificant ( $r_s = 0.64$ ,  $P = 0.10$  and  $r_s = 0.57$ ,  $P > 0.10$ , respectively).

A further way of examining the apparent disadvantage of low-ranking individuals in procuring food by local enhancement was to compare across dominance ranks the relative energy acquisition rates during the copying experiment and during the preexperiment diet selection. We reasoned that if the propensity to copy were influenced by an individual's dominance status, then subordinates might experience a lower energy intake during the experimental trial than during the diet-selection sessions when the food was more spatially diffuse and thus more easily obtainable by subordinates. Whereas birds of all

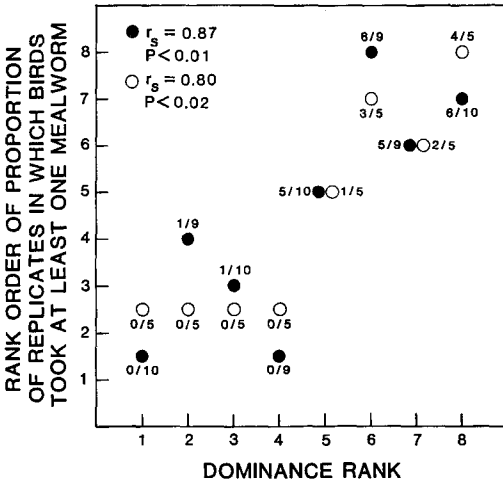


FIGURE 3. Relationship between dominance rank and the proportion of individuals that took at least one mealworm from the key hole after another bird had taken the first one. Spearman's rank correlation coefficient ( $r_s$ ) is for a one-tailed test. Two correlations are given. The solid circles represent the correlation for all 10 replicates. The open circles represent the correlation for only those replicates ( $n = 5$ ) in which the model TT was the first bird to take a mealworm. The numerals associated with the points represent the number of replicates in which copying did not occur divided by the number of replicates used in analysis. A positive correlation indicates that low-ranking individuals tended to copy in a smaller proportion of replicates than did dominants. Since the model TT was excluded from this analysis, the dominance ranks in every case correspond to: 1 = male DW, 2 = female DW, 3 = male WBN, 4 = female WBN, 5 = intermediate TT, 6 = subordinate TT, 7 = dominant CC, 8 = subordinate CC.

dominance ranks, except female nuthatches, had lower energy acquisition rates during the copying experiment than during the preexperiment diet-selection period ( $P_s < 0.05$ , two-tailed paired  $t$ -tests), no significant negative correlation emerged between dominance rank and the ratio of the rate of energy acquisition during copying to the rate during diet selection ( $r_s = -0.357$ ,  $P > 0.05$ ). Thus, while the proportion of low-ranking individuals that took even a single mealworm was low, even when data for cases in which a bird did not take at least one mealworm were included in the analysis, we could not demonstrate statistically that subordinates ingested relatively less energy than dominants during the copying experiment. However, lumping dominants and subordinates of each species yielded a significant across-species heterogeneity ( $F_{3,36} =$

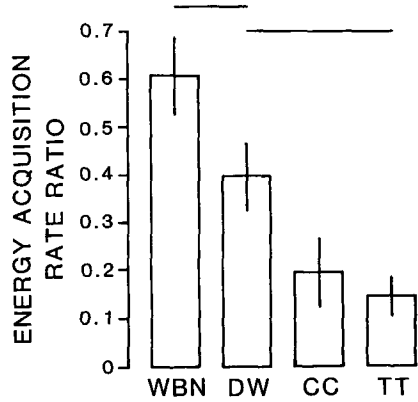


FIGURE 4. The ratio, for each species, of the rate of energy acquisition during copying to the rate during diet selection (assumed to be steady state). The analysis included all 10 replicates and did not eliminate any cases in which a certain individual failed to take even a single mealworm during copying. The bars represent the means, and the vertical lines indicate  $\pm$  SE. Means not differing at the 0.05 alpha level, as determined using Tukey's studentized range test, are connected by a horizontal line.

9.63,  $P < 0.0001$ ) and two significant between-species contrasts; the ratio for WBN was greater than that for both TT and CC (Fig. 4).

Dominants tended to begin using the mimic snag after we had depleted the mealworms in the key snag (Fig. 5). It appears that because high-ranking birds had freer access to the point source at the key hole, they tended not to generalize to a similar microsite (i.e., the mimic hole) until after the food source had been exhausted. Conversely, subordinates tended to generalize to the mimic hole more often before the depletion, apparently because they had restricted access to the key hole.

We reasoned that the latency to copy conspecifics relative to the latency to copy heterospecifics should decrease with decreased interspecific dominance status as individuals of more subordinate species presumably would have fewer opportunities to engage in local enhancement. The results in Figure 6 support this surmise by showing that the latency to copy conspecifics relative to heterospecifics was related inversely to interspecific dominance status.

Finally, subordinate CC lost more dominance-subordinate interactions per hour (see Methods) to dominant CC than they lost to dominant heterospecifics on a per capita basis (2.44 vs. 0.82,  $t = 3.286$ ,  $df = 9$ ,  $P < 0.01$ , two-tailed

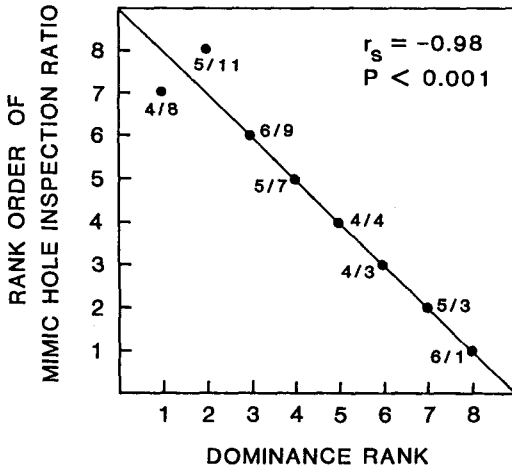


FIGURE 5. The relationship between dominance rank and the ratio of the mean number of mimic hole inspections during the 30 min after the first mealworm was taken to the mean number of mimic hole inspections during the 30 min after we depleted the mealworms in the key hole. The values associated with the points represent the ratio of total mimic hole inspections ( $n = 10$ ) after the first mealworm was taken to the number of inspections after the simulated depletion. Spearman's rank correlation coefficient ( $r_s$ ) is for a one-tailed test. The diagonal line represents a correlation of  $-1$ . The observed negative correlation indicates that dominant individuals tended to increase their rate of generalization to the mimic hole after depletion, whereas subordinates tended to devote relatively more attention to the mimic hole before depletion. This analysis was based on the aggregate ranks for all 10 replicates, including the five replicates in which the model TT was not the first bird to take a mealworm. The mean dominance rank of birds other than the model TT which took the first mealworm was 5.0 (see Table 1); hence the inclusion of these five replicates should not have introduced a bias.

paired  $t$ -test). Subordinate TT showed a similar, albeit nonsignificant, tendency to lose more dominance-subordination interactions per hour to dominant TT than to dominant heterospecifics on a per capita basis (1.80 vs. 0.63,  $t = 2.005$ ,  $df = 9$ ,  $P = 0.08$ , two-tailed paired  $t$ -test).

## DISCUSSION

The results of this study suggest that copying in the form of local enhancement may not be an important benefit, especially for the subordinate members (i.e., chickadees and titmice) of mixed-species flocks of temperate-deciduous woodland birds. Only female DW and female WBN took significantly less time to land on the key snag

during experimental trials compared to the control trials. Thus, the extraction of single mealworms from the cryptic supply did not cause a shift to where birds, especially the interspecifically subordinate TT and CC, searched for food.

In general, food finding proceeded slowly, at least during the first 20 min after the first mealworm had been taken, and TT and CC were less likely to take food from the cryptic supply than were their dominant heterospecific flockmates. The relatively small number of replicates, the sometimes insufficiently long control trials, and the individual variability in the behavior of a given species, especially the low-ranking TT and CC, could have contributed to our difficulty in detecting statistical differences between the experimental and control trials in these measures of copying. Also, the propensities of TT and CC to copy the foraging locations of dominants might have been inhibited because, in the aviary, they were forced to remain within some maximum distance of dominants and thus could not fly from them to avoid kleptoparasitic attacks.

Our results suggest that low-ranking individuals, owing to their restricted access to the key hole, tended to generalize to the mimic hole while the key hole still contained food (Fig. 5). Thus, although local enhancement may be a common benefit to socially high-ranking birds that have access to point food sources, social facilitation may be a more prevalent form of copying among subordinates. When we compared the tendencies of the various species to copy, we found that low-ranking individuals also copied conspecifics sooner than they copied dominant heterospecifics (Fig. 6), further suggesting that local enhancement is not an important proximate mechanism promoting mixed-species rather than single-species flocking in interspecifically subordinate species, such as CC.

Although socially low-ranking individuals tended to be slower than dominants to use the key snag and were less likely than dominants to take even a single mealworm from the key hole (Fig. 3), when subordinates did take a mealworm they tended to do so before the dominants. This mixed strategy of copying relatively soon after the first mealworm was taken or not copying at all may explain in part the lack of striking central tendencies for TT and CC in the attention they paid to the snags after the initial food find. Taken together, these results suggest that TT and CC were so constrained by their social inferiority

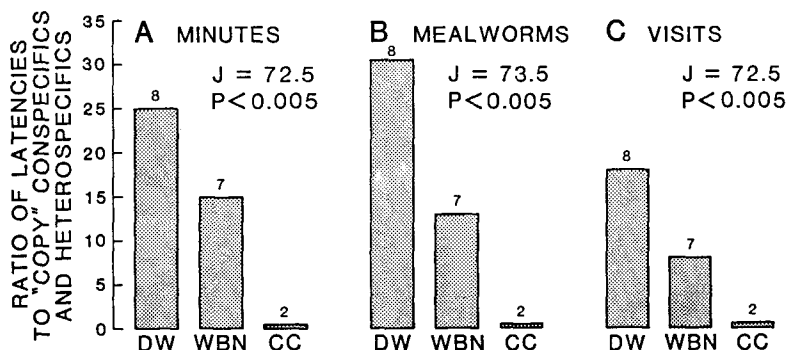


FIGURE 6. The ratio, for each species except TT, of the latency to copy conspecifics and the latency to copy heterospecifics. This ratio is given for (A) mean number of minutes that elapsed, (B) mean number of mealworms taken, and (C) mean number of visits to the key hole during which at least one mealworm was taken. Lower values for this ratio indicate a stronger tendency to copy conspecifics. The Jonckheere ordered alternatives test ( $J$ ) was one-tailed because we reasoned that the ratio should increase with increased interspecific dominance status. The bars represent the medians. The numerals above the bars indicate the number of trials in which both individuals of a given species took at least one mealworm, but neither was the first bird of that flock to do so.

that they were unlikely to copy at all after dominant heterospecifics had begun to monopolize the point food source.

Although the ability to feed on clumped food sources certainly appears biased in favor of socially superior flock members, subordinates are not completely precluded from using defendable food resources. Sullivan (1984a) reported 13 instances in which a Black-capped Chickadee (*Parus atricapillus*) displaced a Downy Woodpecker from an excavation site from which it then extracted food. In one captive flock in the present study, we observed a female DW supplant a female WBN that was husking a sunflower seed. The DW searched for the seed for approximately 2 sec before flying from the branch. Within 1 sec of the woodpecker's departure, a CC flew from several meters to the exact site and proceeded to find and eat the seed. In another instance, the dominant TT of a captive flock descended on a vertical trunk to within 0.3 m of a male DW that was handling a sunflower seed. After apparently using an alarm call to cause the DW to fly off, the titmouse removed the seed from a bark crevice. Thus, even in the aviary where a superabundant, rather diffusely arranged food supply was always available, we observed instances of apparent local enhancement and food piracy against a dominant flockmate by a CC and a TT, respectively. The energy gains of these apparently rare events, however, probably do not rep-

resent a substantive proportion of a titmouse's or a chickadee's total energy demands.

Because TT and CC may usually be prevented from feeding in close proximity to dominant heterospecifics, and because the food items found by dominant flock members probably are typically sufficiently small that an entire item would be consumed immediately, TT and CC may benefit less from local enhancement per se than from pilfering caches recently made by WBN. We have watched free-ranging TT steal WBN caches by flying to the exact cache site a few seconds after the nuthatch has departed, and extracting the food item.

Some of the benefits accruing to DW and WBN from foraging in mixed-species flocks seem obvious: (1) as this study shows, they copy the foraging locations of TT and CC; (2) they kleptoparasitize TT and CC for food (Waite and Grubb, unpubl.); and (3) both DW (Sullivan 1984a, 1984b) and WBN (Waite and Grubb, unpubl.) exploit the alarm-call system of the two parid species. Moreover, the costs to DW and WBN of foraging with TT and CC, such as rare occurrences of food piracy, appear to be minimal.

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