

ADAPTIVE ADVANTAGES OF MIXED-SPECIES FEEDING FLOCKS AMONG SEED-EATING FINCHES IN COSTA RICA

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There have been many explanations offered for the adaptive features of mixed-species flocks of foraging birds. Studies by Morse (1970) and Austin & Smith (1972) suggested that certain species within mixed-species assemblages reduce competition by feeding in different sites. Although such shifts in foraging behaviour support the general ecological principle that partial niche differentiation alleviates competition, another (Buskirk 1972) found the converse: within mixed-species flocks of tropical insectivores, feeding overlap among species increased. Moreover Krebs (1973), by demonstrating in aviary studies that members of one species increase their feeding efficiency when observing the foraging pattern of neighbouring species, supplied support for the hypothesis that observational learning occurs in mixed flocks and brings about the increase in dietary overlap noted in some cases. The purpose of our study was to examine in the field the extent to which mixed-species flocks utilize social cues to increase feeding efficiency, and the bearing of this on differentiation of the feeding niche.

METHODS

Observations were made on mixed-species flocks of fringillids in the vicinity of Turrialba, Costa Rica (approx. 83.5° W, 10° N, 600 m alt.) during the first half of January 1973. Previously vegetated by humid forest, this area now chiefly consists of fields of agricultural use or origin. The climate is rather uniform throughout the year (Budowski & Schrender, MS). Mean temperatures range seasonally from a low of 21 °C in January to a high of 24 °C in May. The dry season is of short duration and never very severe, lasting only a few months, being driest in March. Our observations therefore coincided with the beginning of the dry season.

Three species of finches predominated the flocks we studied: the Yellow-faced Grassquit *Tiaris olivacea*, the Black (Variable) Seedeater *Sporophila aurita corvina* and the White-collared Seedeater *Sporophila torquella*. These three species are similar in size and appearance, with the White-collared Seedeater being slightly smaller and having a bill of slightly different proportions (Table 1). Several other species of finches, occasionally

TABLE 1

Measurements of the subject species (in mm); data from Ridgway (1901)

Species	Origin	Number and sex	Wing length	Average exposed culmen	Average depth of bill
Yellow-faced Grassquit	Costa Rica	6 ♂	53.3	9.7	7.1
		3 ♀	50.3	9.4	—
Black Seedeater	Costa Rica and Nicaragua	9 ♂	54.1	9.4	8.4
		8 ♀	52.8	9.4	8.4
White-collared Seedeater	Costa Rica	6 ♂	52.3	8.6	7.6
		1 ♀	50.8	8.9	8.1

seen in these flocks, included the Blue-Black Grassquit *Volatinia jacarina*, the Thick-billed Seed Finch *Oryzoborus funercus*, and the Rufous-collared Sparrow *Zonotrichia capensis*. The breeding season for the Yellow-faced Grassquit, the Black Seedeater and the White-collared Seedeater in eastern Costa Rica begins around April and continues well into September (Skutch 1954). During our study there was no indication of breeding behaviour.

Feeding behaviour was analysed with respect to the food consumed, and the manner in which it was consumed. At each study site a few birds of each species were collected. The grass seeds were removed from the foregut, identified and counted, and the length of the longest axis measured. The vegetation was collected by clipping two 0.5 m² quadrats from areas where large numbers of birds were feeding at each study site, and the relative abundance of the seeds determined. Although in the more complex fields this method of sampling was insensitive to the patchiness of the environment, the data were used to compare the abundances of food items consumed and those potentially available for consumption. To calculate degree of dietetic specialization, we used the determination of electivity developed by Ivlev (1961): $E = (r_i - p_i)/(r_i + p_i)$, where E is the electivity value, r_i is the relative percentage of the i th food item in the ration, and p_i is the relative percentage of the i th food item in the environment. Large positive values indicate specialization, i.e., preference for a particular food item, while negative values indicate avoidance. Values close to zero indicate that the consumer is eating food items in the same proportion as they occur in the environment.

Energetic values for each grass-seed species were measured using a Phillipson micro bomb calorimeter. Observation of the actual feeding movements were also recorded. It immediately became apparent that the feeding episodes of these birds were frequently punctuated by perching episodes. Birds often abruptly terminated a feeding bout by flying to nearby trees or fences. After a period of singing, preening, scratching or just resting, they would return to the ground and renew their feeding activities. Therefore two foraging variables were studied, i.e., the durations of feeding and of perching bouts. Since observations on individual birds sometimes encompassed many feeding and perching bouts, the average bout-length per bird was used in the analysis.

There are three major factors that can influence feeding movements of these types. First, certain species-characteristic traits or preferences may shape the manner in which a bird forages. For instance, a bird may prefer one species or size of grass seed. Having located such a patch, the length of the bird's feeding bout may be considerably longer than if it were still moving about hunting for such an area. In addition, species may show characteristic differences in vertical foraging position or amount of hopping about. Second, feeding patterns may be influenced by both the type and abundance of neighbouring birds. Agonistic interactions, for example, could interrupt a feeding episode. Conversely, birds could be stimulated to feed for longer intervals in the presence of neighbours. Third, environmental factors can influence the pattern of feeding. With respect to spatial (habitat) considerations, fields of different structural complexity are likely to affect the availability of both the number of microhabitats and the number of vertical foraging positions. Temporal influences may be equally important, since the optimal manner of feeding may change throughout the day.

We thus propose a heuristic model $(x, y) = S_c + N_1 + E_1$, stating that the variations in the duration of both feeding and perching bouts (x and y , respectively) are potentially influenced by species-characteristic behaviour (S_c), interactions with neighbours (N_1), and interactions with the environment (E_1).

Two persons worked as a team, one observing and the other recording. After locating a bird in a study field, an attempt was made to follow it for as long as possible. The team timed the duration of all feeding and perching episodes and recorded foraging height, hopping rate, pecking rate, distance covered, as well as the identity, proximity and number of nearest neighbours. Records of vertical foraging height were assigned to one of three categories: feeding from perches (elevated objects such as twigs, fence wires or grass stems), from the ground, or alternating from ground to perch. It should be noted that even while on the ground, these birds always plucked seeds off grass stems, and not from the ground. Similarly, the amount of hopping by birds feeding on the ground was

assigned to one of three groups: no hopping, hopping intermittently (less than 5 hops/minute), or hopping frequently (more than 5 hops/minute).

Because no agonistic interactions were observed in these mixed-species flocks, the neighbour-interaction factor simply reflects the species composition of the birds surrounding the subject. Since the average inter-bird distance was less than 1 m, those birds with no neighbours within 20 m were considered solitary. For those in groups, those whose nearest neighbours (within 5 m) consisted solely of conspecifics were considered members of homospecific subgroups, while those whose nearest neighbours included other species were considered members of heterospecific groups.

Both spatial and temporal environmental factors were considered. Three study sites were selected. First, a lawn on the landscaped grounds of the Instituto Inter-Americano de Ciencias Agrícolas (IICA). This lawn was mowed frequently and consisted almost entirely of two species of grasses. Second, (Pod Site), an overgrown field near the village of La Suiza, where the ground cover was much denser, consisting of grasses several feet tall, with scattered small bushes and a few trees. Third, (Bridge Site), the most complex, consisted of an old coffee plantation on the banks of the Rio Revantazon; the coffee bushes were planted in regular rows $1\frac{1}{2}$ m apart, between which grew a dense and tall grass cover interspersed with broken coffee branches. The day was partitioned into four periods: dawn (06.00–08.00 hrs), mid-morning (08.00–11.00 hrs), noon (11.00–13.00 hrs) and afternoon (13.00–17.00 hrs). Only three periods were subsequently used in the analysis because the general inactivity around noontime precluded gathering sufficient data.

These grouping procedures, although sacrificing some information, enabled us to test the model using standard analysis of variance techniques. Thus we can analyse how the various factors influence the behavioural variables of feeding- and perching-bout length. Inspection of the data revealed that both feeding and perching bout lengths were exponentially distributed (i.e., most birds fed and perched in bouts of short duration). In order to use variance analysis the distribution of values was normalized by using a logarithmic transformation.

RESULTS

In the first set of analyses of variance, the three main effects—species, time of day at which the feeding bout was recorded, and species composition of the neighbouring birds (if any)—all significantly affected the duration of both feeding and perching bouts. A graph of the results is presented in Figure 1 with associated *F* statistics and levels of significance recorded in Table 2.

There were significant differences in the duration of feeding bouts between some of the species. Those of the White-collared Seedeater were significantly longer than those of either other species, while those of the Yellow-faced Grassquit were not significantly longer than those of the Black Seedeater. Time of day also significantly affected the duration of a feeding episode. Birds feeding between 08.00 and 11.00 hrs had the longest feeding bouts. In addition, feeding bouts occurring in the early morning were even shorter than those occurring in the afternoon. Although this time effect appears to be more important than the species effect (Table 2), neither seems as important as the effect of the species composition of neighbouring birds. Solitary birds displayed shorter feeding bouts than those in homospecific groups. The bout length of both, however, was shorter than that of birds which had both conspecifics and other species as neighbours.

The lack of significant statistical interactions between the main effects in this analysis implies that changes in the time of day affected each species in a similar fashion, that each neighbour arrangement was affected similarly by temporal variation, and that the neighbour arrangement affected each species in a similar fashion.

With respect to the duration of perching bouts, again the three species exhibited significant differences. The Black Seedeater's perching episodes were longer than those of the Yellow-faced Grassquit, and both had longer perching bouts than the White-collared

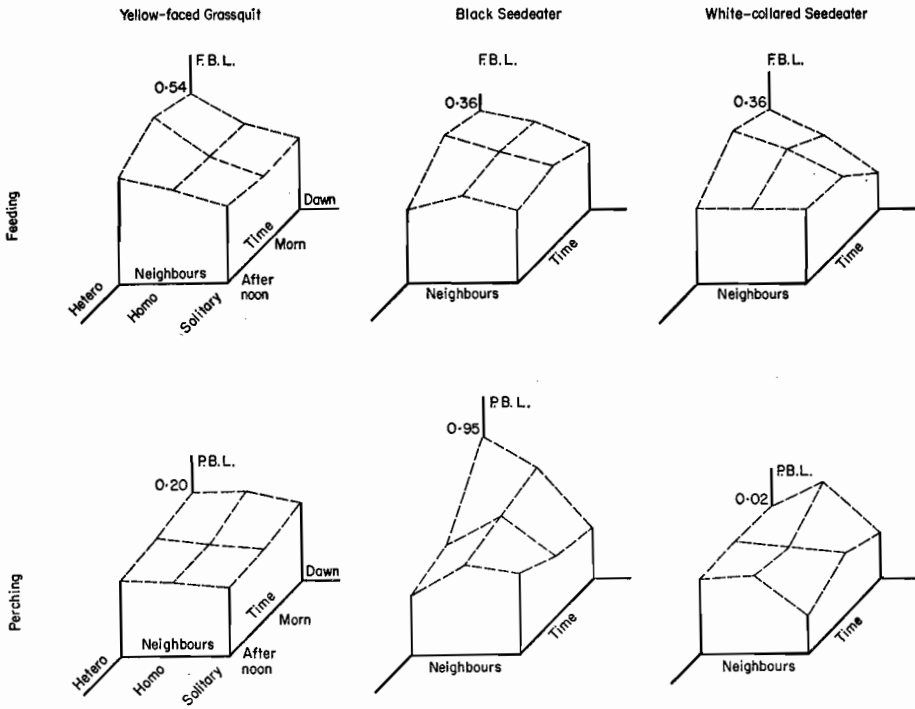


FIGURE 1. Duration of feeding and perching bout response surfaces for each species. The vertical axes represent the bout length whereas the horizontal axes represent either the time of day when the observation was recorded or the species of the neighbouring birds. Smooth surfaces represent the absence of interactions between the main effects.

TABLE 2

Analysis of variance: Duration of the feeding and perching bout length with respect to species, time of day, and species of neighbours

Source	df	ms	Feeding <i>F</i>	<i>P</i>	ms	Perching <i>F</i>	<i>P</i>
Species differences	2	0.48	3.5	< 0.05	0.35	3.3	< 0.05
Time differences	2	0.75	5.4	< 0.005	0.41	3.95	< 0.05
Neighbour differences	2	2.08	14.9	< 0.0001	1.77	17.0	< 0.0001
Sp. × time	4	0.14	1.04		0.08	0.79	
Sp. × neighbours	4	0.08	0.66		0.38	3.6	< 0.01
Time × neighbours	4	0.20	1.44		0.30	2.87	< 0.05
Sp. × time × neighbours	8	0.06	0.46		0.21	2.09	< 0.05
Error	441	0.139			0.105		

Seed eater. Time of day also significantly affected the duration of the perching bout. Perching bouts during the early morning were longer than those later in the morning or in the afternoon. Perching episodes were influenced significantly by the species composition of neighbours, much as were the feeding episodes. There are two statistically significant two-way interactions (neighbour by species, and neighbour by time), both involving the main behavioural effect. The implication is that, with respect to perching, the three species were affected differently by the composition of their neighbours, and

that different periods of day affected the grouping of neighbours in a different manner. The presence of a significant three-way interaction implies that although the main effects exerted a considerable influence on the duration of a perching bout, most of the important biological relationships were complex. This seems reasonable, since many diverse motivations are involved in initiating and prolonging a perching episode. Whereas a bird feeds to acquire nutrients, a bird may perch to preen, scratch, sing, observe, hide or rest.

In the second set of analyses, the model's micro-habitat is defined spatially instead of temporally; the main effects are now species, field in which the feeding or perching bout was recorded, and species composition of the neighbouring birds (if any). Only one main effect, that of the identity of neighbouring birds, significantly influences the duration of the feeding bout (Table 3). As before, the longest bouts were displayed by birds surrounded by heterospecific assemblages, while the shortest were exhibited by solitary birds. In this analysis only the Yellow-faced Grassquit and Black Seedeater are compared, because insufficient data on the White-collared Seedeater were collected in one study area. Since in the first set of analyses these two species rarely differed, it is not surprising that there are no significant differences between them in this set of analyses. It is interesting to note that, although not significant, the three study sites may have influenced to varying degrees the duration of the feeding bout for these two species (see Fig. 2).

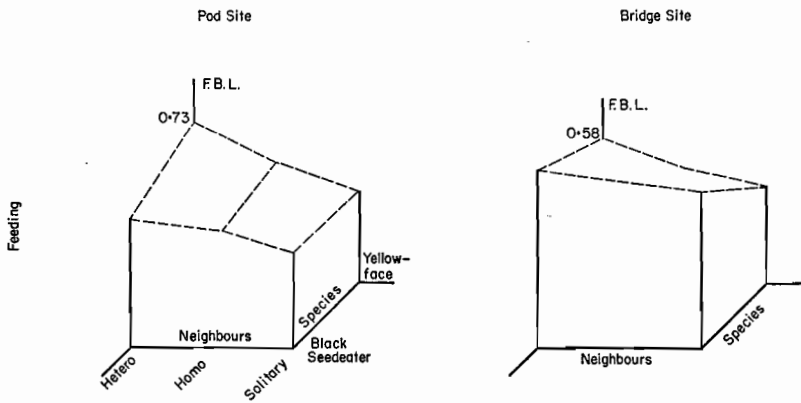


FIGURE 2. Duration of feeding and perching bout response surfaces for two fields. The vertical axes represent the bout length whereas the horizontal axes represent either the species of bird or the species of the neighbouring birds. Smooth surfaces indicate the absence of interactions between the main effects.

TABLE 3

Analysis of variance: duration of the feeding and perching bout length with respect to species, field structural differences, and species of neighbours

Source	df	Feeding			Perching		
		ms	F	P	ms	F	P
Species	1	0.0004	0.00		0.16	1.14	
Field	1	0.01	0.11		0.14	0.03	
Neighbours	2	2.70	22.2	< 0.0001	1.56	11.46	< 0.0001
Sp. × field	1	0.34	2.82	< 0.1	0.07	0.53	
Sp. × neighbours	2	0.20	1.70		0.80	5.8	< 0.005
Field × neighbours	2	0.24	1.95		0.20	1.44	
Sp. × field × neighbours	2	0.33	2.70		0.17	1.2	
Error	243	0.12			0.14		

Again the species composition of the neighbouring birds was highly significant in influencing the length of a perching bout. However, the significant two-way interaction (species by neighbour) indicates that this neighbour effect had a different influence on each of the two species.

Another factor which significantly influenced the duration of feeding bouts was vertical feeding height. Although a two-way analysis of variance (Table 4) of vertical feeding height versus bird species shows no significant species differences, it does show that differences in feeding bout length were significantly influenced by feeding position. Generally, feeding bouts during which the bird alternated between a perch and the ground were longer than those performed solely from a perch. It is interesting to note, however, that although all the species preferred to feed from the ground (by approximately 3 : 1), the number of Yellow-faced Grassquits alternating between a perch and the ground while feeding is significantly greater ($P < 0.005$, $\chi^2 = 24.8$) than the number of either species of seedeater. Contrasted with this apparent species difference is the fact that bill-length and wing-length of the three species are not significantly different (Table 1). Since similar morphological characteristics may indicate that all three species are adapted to eat the same seeds efficiently, these behavioural differences in vertical feeding position may permit them to forage together.

TABLE 4

Analysis of variance: duration of feeding bout with respect to species and feeding height

Source	df	ms	F	P
Species	2	0.25	1.3	
Heights	2	1.53	8.1	< 0.001
Sp. × heights	4	0.12	0.6	
Error	337	0.19		

Another behavioural measure of feeding differences, that of horizontal distance covered during a feeding bout, was influenced by the composition of neighbouring birds (Table 5). For all three species, most of the solitary individuals had feeding bouts which lacked any horizontal hopping movement. Those individuals, regardless of species, which were surrounded only by conspecifics showed a slight tendency to move about while feeding, though few to any great extent. For birds surrounded by conspecifics and other species, the situation was different. In these flocks, both seedeaters appeared to prefer to feed without moving, whereas the grassquit usually moved a great deal.

The species of the neighbour is only one of the species interactions which had an important influence in determining the duration of a feeding bout. Two other factors, the distance between neighbours and density of surrounding birds, were also important. Regardless of species of neighbour, the duration of the average feeding bout increased as the number of neighbours increased. However, no simple trend exists for the relationship between the species of the neighbour and the average distance between the subject individual and its neighbours. In the case of the Yellow-faced Grassquit, as the between-bird distance increases, the length of the feeding bout decreases, regardless of the species of the neighbour. For the Black Seedeater, in conspecific assemblages, as the inter-bird distances increase the bout length also increases; whereas in mixed species assemblages as the inter-bird distances increase, the bout length decreases. Only enough data were collected for conspecific assemblages of the White-collared Seedeater, and they manifest increases in length of feeding bout with increases in inter-bird distances.

TABLE 5

Horizontal distance covered (hopping) during a feeding bout as related to species differences and species of neighbours

A. With conspecific and heterospecific neighbours			
Degree of hopping	Species of birds ¹		
	Y	B	WC
None	7	43	6
Intermittent	52	20	4
Frequent	14	1	2
			$\chi^2 = 51.7$ $P < 0.001$
B. With conspecific neighbours only			
Degree of hopping			
	Y	B	WC
None	38	7	7
Intermittent	51	7	10
Frequent	6	1	1
			$\chi^2 = 1.25$ n.s.
C. With no neighbours			
Degree of hopping			
	Y	B	WC
None	28	10	11
Intermittent	8	1	2
Frequent	3	0	1
			$\chi^2 = 4.8$ n.s.

Note: ¹ Y = Yellow-faced Grassquit, B = Black Seedeater, WC = White-collared Seedeater.

Information gathered on diet is summarized in the Appendix, Tables 7-9. On the simplest field (IICA), none of the birds specialized on the most abundant seed species, *Axonopus compressus*, although this had the highest value energetically both by quadrat and by weight (Table 6). Nonetheless, almost all the birds collected, regardless of species, had eaten more of this species of grass than any other. Furthermore, only one grassquit and one White-collared Seedeater showed an electivity to the next most abundant seed, *Fimbristylus dichotoma*. All the other birds were specializing, although the overall quantities were low, on rare seeds which we did not collect in the quadrat samples, and were possibly gathered by the birds before arriving at the study fields where they were collected.

In the field of intermediate complexity (Pod Site), no species seemed to elect for the most abundant seed species, *Paspalum conjugatum*, which was again energetically the

TABLE 6

Energetic value of grass seeds

Species	Cal./mg of seed	Cal./quadrat	Site
<i>Axonopus compressus</i>	4.36 ± 0.02	3335	IICA
<i>Fimbristylis dichotoma</i>	3.91 ± 0.01	602	IICA
<i>Paspalum conjugatum</i>	4.23 ± 0.01	13147	Pod
<i>Digitaria adscendens</i>	3.80 ± 0.03	3922	Pod
<i>Oplismenus burmannii</i>	3.57 ± 0.11	521	Pod
<i>Eleusine indica</i>	4.01 ± 0.04	2262	Bridge
<i>Paspalum conjugatum</i>	4.26 ± 0.01	2113	Bridge
<i>Digitaria adscendens</i>	4.10	439	Bridge

richest seed by both quadrat and weight. The grassquit, however, exhibited a high electivity for the next most abundant and energetically rich seed, *Digitaria adscendens*, while the Black Seedeater also showed some preference for this seed species. Nevertheless all three species showed positive electivities for rare *Panicum* spp.

At the most complex site (Bridge), again neither the grassquit nor the Black Seedeater showed a preference for the most energetically rich (by quadrat) and abundant seed, *Eleusine indica*. However both species (the White-collared Seedeater was not present) seemed to demonstrate strong preferences for the next most abundant and energetically valuable (by weight) seed, *Paspalum conjugatum*. However, while the Black Seedeater we collected had eaten only *Paspalum*, the grassquits varied their diets, showing a positive electivity for the rare *Eragrostis* spp.

DISCUSSION

Earlier we proposed a model stating that the duration of both feeding and perching episodes is influenced by (a) species specific behaviour, (b) interactions with neighbours and (c) interactions with the environment. Such a model appears to provide a better appraisal of the feeding response than the perching response, since the perching bout analysis has revealed that there are significant higher order interactions that must be accounted for before the details of perching behaviour can be fully understood.

Most studies in the area of feeding ecology have concentrated on only two factors of our model: species-specific characteristics and adaptations to habitat characteristics (MacArthur 1958, Gibb 1956, 1960, Newton 1967, Cody 1968). We found these two factors to be less important in determining the duration of a feeding episode than the effects of behavioural interactions with neighbours. The results indicate that these three species do not manifest significant differences in feeding bout length. However, differences in the duration of feeding episodes can largely be explained by the presence or absence of neighbours, the species of those neighbours, and the abundance of those neighbours. The analysis showed that feeding with neighbours, especially if some are of other species, significantly increased the duration of the feeding episode.

In addition, other results support the contention that the differences between species are minimal. First, all species clearly preferred to feed from the ground, although the Yellow-faced Grassquit showed a propensity to vary its vertical foraging position. Second, it appeared that the degree of hopping was more influenced by the type of neighbour than by species considerations. Third, each finch species appeared not to specialize on its own species of grass(es). Furthermore their similar bill sizes would argue against differentiation by seed size. It also seemed doubtful that the finches were differentiating between seed species on the basis of size; mean size of seeds found in the crops for all three species are not significantly different (IICA $F_{2,89} = 2.86$, n.s.; Pod $F_{2,57} = 1.08$, n.s.; Bridge $t_{24} = 1.32$, n.s.). Nonetheless the birds were not feeding as generalists. The comparison between gut content and field abundances indicates that they were specializing on the rarer seeds, presumably since these seeds are highly energetic or easy to get at. Thus it appears that these three finches were not partitioning fields in the classical sense.

Lack (1971) found a similar situation among the finches of English farmland which, he noted, 'is not merely an artificial habitat but has repeatedly changed as one type of agricultural practice has succeeded another, so that there could hardly have been time for the birds to evolve ecological isolation in farmland'. The fields which constituted our study areas in Costa Rica are also of relatively recent origin. Thus, the bird species associated with them have had, as with English finches, relatively little time to evolve ecological isolation along specific lines. They have, rather, altered their feeding patterns in a facultative manner, responding to social cues involving the species type, density and distances of neighbouring birds.

From a behavioural perspective, hunger and perception of an area's profitability are

the important factors responsible for initiating a feeding bout. Feeding will continue until (a) satiation, (b) the food supply is no longer suitable, (c) a predator is perceived or (d) a disturbance is created by a neighbour. If termination occurs because of (b) or (d) competition may be occurring. Clearly the data indicate that no interference competition (d) is occurring. However, a more diffuse type of competition (exploitative) where one bird 'out eats' another may be occurring.

Although there appeared to be sufficient grass remaining on each site at the beginning of the study, three factors suggest that these fields serve as optimal habitats only for short periods. First, the habitat itself is transitory. At the end of the study the grass was cut at two sites (IICA and Bridge). Since the birds do not eat seeds from the ground, such actions force them to locate new foraging habitats. Second, a 0.02 ha plot (Pod Site) can not indefinitely support the approximately 350 birds we estimated to be present. Since large numbers of birds increase the foraging pressure, the fields will be totally harvested rather quickly. Third, even if not denuded completely, heavy foraging will continuously alter the pattern of resource availability. Thus the changing abundances of the various seed species will necessitate new foraging strategies.

If each bird relied only on past experience and trial and error learning to locate new fields and perfect optimal foraging strategies appropriate to the conditions of the new field (inter-field differences were profound), then such a process could prove energetically prohibitive. However, the energetic cost of this process could be cut considerably and feeding efficiency increased if birds used other aggregations of finches as indicators of good fields, and also copied the foraging patterns employed by these birds (Krebs 1973). Such forms of social learning could only evolve if all birds involved alternatively served as 'finder' and 'copier'.

If procurement of seeds proceeded at a slower rate in the presence of neighbouring birds of other species, then the longer uninterrupted feeding episodes would not necessarily result in increased feeding efficiency (i.e., more seeds consumed per unit time). Some evidence, although not enough for statistical significance, suggests that for the Yellow-faced Grassquit the pecking rate for seeds (a good measure of seed procurement rate) was not affected by the presence or absence of neighbouring birds. From a sample of 10 birds, those feeding alone averaged 32 pecks/minute, whereas those in conspecific subgroups averaged 36 pecks/minute; those in hetero-specific groups averaged 34 pecks/minute. Thus it does not appear that the presence of neighbours affects peck rate, and we conclude that longer feeding bouts do imply greater feeding efficiency. More casual observations indicated the situation was no different for the other two species of seedeaters.

In any given field the diet of the three species of finches was similar. This might be expected if the birds were feeding as generalists. However, each species was specializing, thus suggesting that some social learning process existed among the species so as to synchronize their feeding pattern, especially since they all seemed to prefer rare seeds.

Thus we have shown that not only is feeding efficiency increased in these mixed assemblages, but that there is much overlap in diet. As a result we believe that the social learning hypothesis espoused by Krebs (1973) supplies the best mechanism to explain the data. Since these birds must periodically explore new fields to locate the best patches of food, it is advantageous to join with other conspecifics, thus increasing the scope of the search. By joining with other species the diversity of searching patterns can also be increased. Such subtle differences as in propensity to hop (horizontal movement), and to alternate between perch and ground while feeding, manifest this type of diversity in our mixed flocks. Therefore those birds which normally would not forage in a particular place or manner may be induced to do so by inter-specific neighbours. As long as some patches of food are better than others and there is food for many birds (at least temporarily) feeding in mixed flocks will be profitable. In addition continued monitoring of neighbours

will be necessary since the pattern of resources will change and the best food items will become difficult to locate.

There is however, no assurance that the explanation we propose necessarily applies uniformly throughout the year. Moreover, it does not necessarily supply the sole reason for the existence of mixed flocks. As noted by Pulliam (1973), mutual predator defence would reduce the number of alerting movements performed by individual birds in a group. Thus without sacrificing safety feeding episodes could be lengthened. With respect to our mixed assemblage, however, Pulliam's argument is incomplete, since it does not account for the observed dietary similarity. Nevertheless this does not suggest that arguments other than ours are not valid in other mixed flocks. The fact that mixed assemblages occur in many different feeding guilds and habitats makes it hazardous to search for a single explanation of mixed-species flocking.

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SUMMARY

The feeding ecology of three Costa Rican finches occurring in mixed flocks, *Tiaris olivacea*, *Sporophila aurita corvina* and *Sporophila torquella*, was investigated by measuring both behavioural and ecological variables. Observations on foraging height, rate of hopping and pecking rate, as well as the identity, proximity and number of nearest neighbours were recorded. In addition the duration of all feeding and perching episodes were timed. Comparisons were also made between the abundances of food items (grass seeds) consumed and those potentially available for consumption.

The analysis of variance of the feeding behaviour revealed that the presence or absence of neighbouring birds, whether of the same or different species, influenced the duration of feeding bouts more significantly than did either differences in habitat or species-characteristic behaviour. In addition the dietary comparisons revealed overlap in both species and size of seed consumed. Such similarities suggest that these species are not partitioning fields in the classical sense.

We propose that the increase in the duration of the feeding bout associated with the presence of mixed species aggregations leads to increased feeding efficiency and is the result of intra- and inter-specific social learning. Certainly flocking is often advantageous, since searching in a group facilitates finding clumped resources; mixed species flocking, by increasing exposure to a diversity of foraging places and patterns, can further augment feeding efficiency.

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APPENDIX

Food available and food consumed by subject species

TABLE 7

IICA site. Grasses in quadrat: Axonopus compressus 84%, Fimbristylis dichotoma 16%

Species and sex	Species of grass	Contents of crop		Electivity index
		No. of seeds	% of total	
Yellow-faced Grassquit ♀	<i>Axonopus compressus</i>	10	53	+0.23
	<i>Fimbristylis dichotoma</i>	1	5	-0.53
	<i>Panicum</i> sp.	4	20	+
	No. 5	1	5	
	Unidentified	3	17	+
Yellow-faced Grassquit ♂	<i>Axonopus compressus</i>	9	47	-0.28
	<i>Fimbristylis dichotoma</i>	6	32	+0.32
	<i>Paspalum conjugatum</i>	2	11	+
	<i>Panicum</i> sp.	1	5	
	No. 10	1	5	
Yellow-faced Grassquit ♀	<i>Axonopus compressus</i>	20	48	-0.27
	<i>Fimbristylis dichotoma</i>	0	0	-1.00
	<i>Eragrostis</i> sp.	3	7	+
	<i>Panicum</i> sp.	14	33	+
	Unidentified	5	12	+
Yellow-faced Grassquit ♂	<i>Axonopus compressus</i>	0	0	-1.00
	<i>Fimbristylis dichotoma</i>	1	10	-0.23
	<i>Paspalum conjugatum</i>	2	20	+
	<i>Eragrostis</i> sp.	5	50	+
	<i>Panicum</i> sp.	1	10	+
	Unidentified	1	10	+
White-collared Seedeater ♀	<i>Axonopus compressus</i>	15	38	-0.38
	<i>Fimbristylis dichotoma</i>	16	40	+0.43
	<i>Paspalum conjugatum</i>	1	2	
	<i>Panicum</i> sp.	8	20	+
Black Seedeater ♂	<i>Axonopus compressus</i>	18	36	-0.40
	<i>Fimbristylis dichotoma</i>	0	0	-1.00
	<i>Paspalum conjugatum</i>	4	10	+
	<i>Eleusine indica</i>	16	32	+
	<i>Panicum</i> sp.	8	16	+
	No. 11	3	6	

TABLE 8

Pod Site, Grasses in quadrat: Paspalum conjugatum 60%, Digitaria adscendens 19%, Oplismenus burmanii 4%, Non-grass Unknown 17%.

Species and sex	Species of grass	Contents of crop		Electivity index
		No. of seeds	% of total	
Yellow-faced Grassquit ♂	<i>Paspalum conjugatum</i>	4	11	-0.69
	<i>Digitaria adscendens</i>	18	50	+0.44
	<i>Oplismenus burmanii</i>	0	0	-1.00
	<i>Panicum</i> sp.	12	33	+
	Unidentified	2	6	
Black Seedeater ♂	<i>Paspalum conjugatum</i>	3	30	-0.34
	<i>Digitaria adscendens</i>	2	20	+0.01
	<i>Oplismenus burmanii</i>	0	0	-1.00
	<i>Panicum</i> sp.	4	40	+
	Unidentified	1	10	+
White-collared Seedeater ♀	<i>Paspalum conjugatum</i>	5	14	-0.62
	<i>Digitaria adscendens</i>	0	0	-1.00
	<i>Oplismenus burmanii</i>	0	0	-1.00
	<i>Panicum</i> sp.	17	46	+
	<i>Panicum</i> sp.	13	22	+
	No. 8 Unidentified	1 1	9 9	
White-collared Seedeater ♀	<i>Paspalum conjugatum</i>	5	100	+0.25
	<i>Digitaria adscendens</i>	0	0	-1.00
	<i>Oplismenus burmanii</i>	0	0	-1.00

TABLE 9

Bridge Site. Grasses in quadrat: Eleusine indica 48%, Paspalum conjugatum 43%, Digitaria adscendens 9%

Species and sex	Species of grass	Contents of crop		Electivity index
		No. of seeds	% of total	
Yellow-faced Grassquit ♂	<i>Eleusine indica</i>	0	0	-1.00
	<i>Paspalum conjugatum</i>	49	82	+0.31
	<i>Digitaria adscendens</i>	9	15	+0.23
	<i>Eragrostis</i> sp.	1	2	
	Unidentified	1	1	
Yellow-faced Grassquit ♀	<i>Eleusine indica</i>	0	0	-1.00
	<i>Paspalum conjugatum</i>	37	36	-0.09
	<i>Digitaria adscendens</i>	13	12	+0.12
	<i>Eleocharis caribea</i>	1	1	
	<i>Oplismenus burmanii</i>	8	8	
	<i>Eragrostis</i> sp.	25	24	+
	No. 2	8	8	
	<i>Panicum</i> sp. Unidentified	7 4	7 4	
Black Seedeater ♂	<i>Eleusine indica</i>	0	0	-1.00
	<i>Paspalum conjugatum</i>	115	100	+0.40
	<i>Digitaria adscendens</i>	0	0	-1.00