

MIXED-SPECIES FLOCKS OF BIRDS IN HILL FOREST IN CEYLON

LINDA PARTRIDGE
AND
RUTH ASHCROFT

The aim of this study was to obtain a description of the composition and behavior of mixed-species flocks of birds in the forest of Horton Plains, Ceylon, with a view to discovering the selective advantage to the birds of flocking behavior.

Most hypotheses advanced to explain the selective advantage of flocking for birds involve either reduced predation or increased food intake by the birds. Miller (1922), Lack (1968) and Goss-Custard (1970) suggested that the chance of sighting approaching predators increases with the number of potential prey individuals present in a flock. The alarm calls of the first to see the predator give all the members of the flock a cue to take evasive action such as mobbing or hiding. Lazarus (1972) pointed out that there are mathematical models in search theory which suggest that clumping reduces the probability of detection or capture of any individual by a predator. However, the constant calling characteristic of bird flocks must make these birds detectable to predators at a greater distance than solitary individuals.

For mixed insectivorous flocks, Willis (1972) suggested that species that forage in a way or in a part of the environment which would hamper their ability to detect approaching predators tend to be associated with those whose foraging behavior makes them more likely to observe approaching predators. Different species may tend to detect different predators from one another and associate for this reason. Moynihan (1962) viewed mixed-species flocks as a means of having larger numbers of individuals in a flock to increase its efficiency as an anti-predator device, without increasing intraspecific competition.

Possible functions of mixed-species flocking also concern feeding. Swynnerton (1915), Rand (1954), and Brosset (1969) suggested that the species in the flock, as a result of their movement through the forest, flush insects which are eaten by the other members of the flock. Murton (1971a, b) and Krebs et al. (1972) indicated that association with other birds may help an individual to locate food, either in the sense of learning the type and location of potential food from other members of

the group, or by individuals joining others seen feeding as an efficient method of locating areas of high prey density. Morse (1970), Slud (1960), and Short (1961) suggested that the formation of mixed-species flocks may in some way enable all the species involved to exploit the available food in a maximally efficient way. This is, they suggest, because it would lessen the chance of a bird foraging in an area previously searched by other individuals.

METHODS

Horton Plains is an area of natural deciduous forest interspersed with grassland at an altitude of 2000 m in the central hill region of Ceylon. The forest is approximately 10 m from the ground to the top of the canopy, and there are three main vegetation layers. The lowest layer consists of a dense undergrowth of herbs and shrubs, the middle of small trees, and the top of the canopies of larger trees.

We studied the mixed-species flocks in the forest by direct observation in the months of August and September during the wet season of 1970. Breeding occurs mainly early in the year, from December to early March.

It was obvious when a given bird was in a flock. The flocks were noisy and cohesive. We could not follow them for any distance because the vegetation was dense, but the birds moved slowly and we could approach to within a few meters of them.

In many cases we were able to record the species composition of the flock, the relative abundance of the species present, the vertical and horizontal distribution of each species, feeding sites, feeding methods, obvious interactions between the birds in the flock or between them and any other birds including potential predators.

RESULTS

We saw 96 flocks, but for only 38 were we fairly sure that we had not missed most of the flock. Only the latter were used for the analysis of flock composition. The flocks contained between 10 and 80 birds of up to 10 species, and a species of squirrel was also present in some flocks. The minimum number of species in one flock was three. The species and the number of flocks in which each was present are shown in Table 1. Nomenclature follows Henry (1971).

No flock contained all species, and no species was present in all flocks, but every flock contained either Ceylon Hill White-eyes or Ceylon Grey-headed Flycatchers. The data

TABLE 1. The number of flocks (out of 38) in which each species was present.

Species	Number of flocks
Yellow-eared Bulbul (<i>Pycnonotus penicillatus</i>)	31
Ceylon Grey Tit (<i>Parus major</i>)	28
Ceylon Hill White-eye (<i>Zosterops ceylonensis</i>)	27
Black-fronted Babbler (<i>Alcippe atriceps</i>)	21
Ceylon Grey-headed Flycatcher (<i>Culicicapa ceylonensis</i>)	17
Ceylon Scimitar Babbler (<i>Pomatorhinus horsfieldii</i>)	15
Dusky Striped Jungle Squirrel (<i>Tamias</i> sp.)	14
Velvet-fronted Blue Nuthatch (<i>Sitta frontalis</i>)	10
Ceylon Pied Shrike (<i>Hemipus picatus</i>)	2
Rufous Babbler (<i>Turdoides rufescens</i>)	1

did not show any tendency for particular pairs of species to appear in a flock together or to avoid each other.

Squirrels appeared to keep up with the birds as they moved through the forest. We never saw them join or leave a flock.

One species, the Ceylon Warbler (*Bradypterus palliseri*), other than those listed in Table 1, was occasionally seen with the flocks. These birds were observed in pairs and were territorial. Apparently, they joined a flock for a short time while it was passing through their territory. Other birds in the forest did not appear to associate with the flocks at any time. These species included the Ceylon Blackbird (*Turdus simillimus*), the Ceylon Scaly Thrush (*Oreocincla dauma*) and the Crimson-backed Woodpecker (*Chrysocolaptes guttaeristatus*). We saw the Ceylon Trogon (*Harpactes fasciatus*) once, and it was in the vicinity of a flock, but we were not sure whether it was actually moving with the group.

It was impossible to count the individual birds since it was difficult to be sure that all the birds had been seen and also because many flew back and forth in the flock. White-eyes and flycatchers usually made up half the flock (20 to 30 birds). There were usually 2 to 10 each of Yellow-eared Bulbuls, Ceylon Grey Tits and Black-fronted Babblers; and 1 to 4 Velvet-fronted Blue Nuthatches, Ceylon Scimitar Babblers and Dusky Striped Jungle Squirrels. The numbers may be partly a feature of the absolute numbers of a species in the area, since the species which were more numerous in the flocks tend to be present in a higher proportion of the flocks.

Several of the species listed as occurring in mixed flocks were also seen in small single-

species groups in the forest, but all were most frequently seen in the mixed-species flocks. Ceylon Hill White-eyes, Yellow-eared Bulbuls, and Ceylon Grey Tits were also seen outside the forest, foraging in bushes in the surrounding grassland. We never saw a single-species group encounter a mixed flock, nor did we see an encounter between two mixed flocks.

It was not possible to tell whether individual flocks were constant in composition nor do we know whether the flocks disbanded at night. We did not see members of flocks resting together at any time of day. There were not obvious peaks of bird activity in the early morning or at dusk, and we saw flocks on the move at all times of the day, including immediately after dawn. We never saw a flock form in the morning. The only information on composition came from color-banding the birds. Success in catching birds was low, and we did not see any of the color-banded birds in flocks subsequently. However, four Black-fronted Babblers originally caught together were retrapped together 11 days later in the place where they were originally banded. The same was true for two Ceylon Hill White-eyes. This suggests some degree of social cohesion and site attachment in these two species.

We did not discover whether each flock had a group home range. It was our impression that the flocks followed a fixed route for a few days at a time because we often saw flocks of similar composition in the same place at the same time for up to five consecutive days. H. E. McClure (pers. comm.) has suggested that since it is usually impossible to see or be sure one has seen the flock as a whole, we miss the fact that individuals are constantly joining the flock and then remaining in their territory or returning to it as the flock moves on. The fact that we did not see our banded birds in a flock, but caught them in the same place at a later date is consistent with McClure's idea, although it does not positively support it.

The bird species in the flocks were mainly insectivorous, with the exception of Ceylon Hill White-eyes and Yellow-eared Bulbuls which also ate fruit. It was rarely possible to record the feeding activities of all the individuals in the flocks, but usually we could record the total range of feeding sites for each species and the relative numbers of different individuals feeding in different parts of this range.

Each species appeared to have characteristic ranges of feeding sites (Table 2), although there was extensive overlap between some pairs of species. In these cases the two species

TABLE 2. The feeding positions of the birds expressed as the percentage of individual birds of each species seen feeding in each position.^a

Species	Trunk	Main branches	Outer branches	Canopy	Shrub tops	Ground and undergrowth
Rufous Babbler ^b	P	P	P			
Ceylon Hill White-eye			×	×××	×	
Yellow-eared Bulbul			×	×××	×	
Ceylon Grey-headed Flycatcher			××	×××	×	
Ceylon Pied Shrike		×	××			
Ceylon Grey Tit	×××	××	××	×	×	
Velvet-fronted Blue Nuthatch	×××	×	××			
Ceylon Scimitar Babbler						×××
Black-fronted Babbler						×××
Dusky Striped Jungle Squirrel	×××	×××	×			×

^a × = 1–20%; ×× = 30–69%; ××× = 70–100%; P = Present.

^b Only one observation of this species.

appeared to take different foods, since they were using different feeding techniques. Thus, Ceylon Hill White-eyes, Yellow-eared Bulbuls, and flycatchers all fed in the canopy, but the flycatchers took insects on the wing, the white-eyes searched the surfaces of the leaves minutely for insects, and the bulbuls appeared to feed on larger items which they took from both twigs and leaves. It was not clear how much the bulbul and white-eye differed in the fruits taken, since at the time of our study fruit was confined to small bushes on the periphery of the forest, where both species fed on it.

The Ceylon Pied Shrike was dissimilar from the other birds in that it took large insects on the wing and from branch surfaces. The Velvet-fronted Blue Nuthatch searched for insects in the bark of the tree, spiralling down the main branches and trunk. The Ceylon Grey Tit fed in a similar manner, but appeared to be a more assiduous searcher, probing minutely in the bark, and it also had a greater range of feeding sites than the nuthatch. Squirrels searched on the trunk and main branches. They searched particularly in bunches of dead leaves and moss, and unlike any of the birds tore off pieces of bark and searched underneath. Ceylon Scimitar Babbler and Ceylon Black-fronted Babbler both searched in the undergrowth. The latter searched on the ground and in the vegetation up to about 1 m in height while the Ceylon Scimitar Babbler searched between 1 m and 3 m. Rufous Babbler were seen only once, although in very large numbers, and were on main and peripheral branches. Records (Henry 1971) of the gut contents of the species listed above indicate that they take different foods.

The only observations of food-stealing were intraspecific, involving Ceylon Grey Tits or

Yellow-eared Bulbuls. No interspecific encounters of this type, or other aggressive interactions between birds were observed.

The horizontal distribution of the species in the flock was consistent and is shown in figure 1. This was determined by standing at a fixed point, and recording the order in which each species appeared and disappeared as the flock went past the observation point. Thus the range in the flock for each species was found by knowing the relative time of appearance of the first individual and the last individual of that species. The range shown for each species in figure 1 is the maximum overlap with other species recorded in any flock. The diagram shows that the birds at the top of the vertical range (white-eyes, flycatchers and bulbuls) usually led the flocks, while those at the bottom (babbler and squirrel) followed last, the other species appearing in an intermediate position.

The birds called frequently; a flock could be heard some distance away. The birds at the rear of the flock probably used the calls of the front members to enable them to locate the rest of the flock, since we observed on several occasions that when the babbler were trailing behind the front birds, they would move in the direction of the calls even though the other birds were out of sight because of dense foliage. Since the flocks did not follow a straight path, this frequently meant that the birds at the rear of the flocks took a different route through the forest from the front members.

We do not know what predators, if any, took these birds. We never saw an interaction between a flock and a bird of prey, and could guess the reaction of the birds to predators only by their reaction to us. This reaction did not appear to be very strong. All species, including the squirrel, gave loud calls, and the birds then either quickly resumed feeding, or

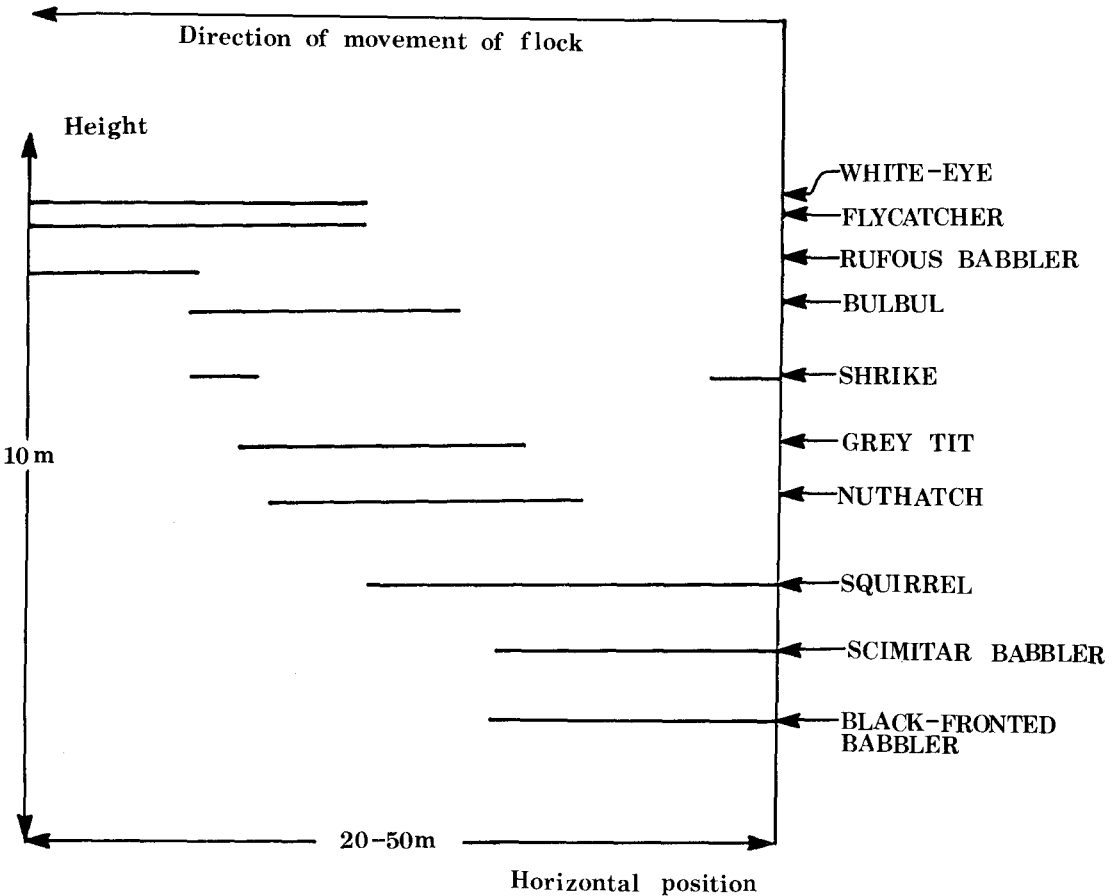


FIGURE 1. The spatial distribution of species within flocks. Lines are drawn at the average horizontal and vertical position of each species.

became silent and moved quietly away. There was no mobbing response.

DISCUSSION

The survival values of flocking to these birds are not obvious. However, even from the limited information available it is possible to discard some hypotheses for the species which we studied.

It seems unlikely that the birds benefit from the flushing of insects by other species in the flock. The birds spanned such a large horizontal distance that the rear birds, especially the babblers, frequently did not follow the same path as the front birds. This must mean that they did not encounter or see any of the insects disturbed by the front birds. The very stereotyped feeding techniques of the birds also suggest that this effect may not be important. It may be significant for members of the same species.

Social learning may be important for members of single-species groups within mixed

flocks. Learning of the type and location of potential prey could occur. This seems unlikely to be a major benefit of mixed-species flocking since the different species in these flocks take largely different foods and from different parts of the vegetation. Particularly in view of the fact that socially subordinate flock species are probably forced out of suitable feeding sites by dominant species (Morse 1970), it seems unlikely to be a reason for flocking. There could be a mixed-species benefit in food-finding if insects in the forest were patchily distributed so that high densities of food at one level in the vegetation were correlated with high densities above and below. This might be the case for different life stages of one insect and its associated predators and parasites. If so, the flock could be a means of locating the patches efficiently. However, it is hard to explain the consistent horizontal order of the species on this basis. Nor is there evidence for the occurrence of high density patches of woodland insects in phase at all levels above the ground.

We doubt that, as a result of being in flock, birds avoid researching areas that had been previously occupied by other individuals. The birds flew back and forth a great deal, and also frequently fed out of sight of one another; it seems highly likely that areas were researched. Thus, we do not see that members of mixed flocks of this kind derive any substantial advantage in feeding as a result of the presence of other species which take different foods.

The consistent horizontal order of species in these flocks, with the species high in the canopy leading, has not been described in other flocks, although McClure (1967) noticed the reverse order. In the flocks which he observed in Malayan forest, the canopy birds were left behind due to their slower foraging speeds; they frequently stopped feeding and caught up with the rest of the flock. In the Ceylon flocks we watched, the babblers also got left behind at times and would subsequently stop foraging and catch up with the other birds. The possibility that different species in flocks have different optimum speeds of movement through the forest when foraging suggests that there must be strong positive advantages in flocking that compensate for loss in efficiency as a result of adapting their foraging speed to that of the rest of the flock, as well as the loss in time and energy involved in maintaining contact with the other flock members. Willis (pers. comm.) has suggested that the staggering of species could possibly result from a cascade of insects downwards from the top birds being used by the lower species that follow. However, as we have pointed out, the different species in the flocks took very different routes through the forest so that this effect is unlikely to have been important.

Willis (1972) has also suggested that low-level foragers with restricted vision may benefit from travelling with canopy species which can see further and, therefore, presumably detect approaching aerial predators sooner. The followers could help to warn of predators approaching from the rear and below. Possibly, the canopy species act as "leader" species, and the others as "followers" when the flock moves. This explanation might involve no advantage or disadvantage to the leader species from their presence in the mixed flocks.

The species most often seen out of mixed-species flocks, either singly or in single-species groups, were the Ceylon Hill White-eye, Yellow-eared Bulbul, Ceylon Grey Tit and Rufous

Babbler with the Ceylon Grey-headed Flycatcher and Ceylon Pied Shrike the next most frequent. The Velvet-fronted Blue Nuthatch, Ceylon Scimitar Babbler and Black-fronted Babblers were never seen out of mixed-species flocks. This would be predicted if these latter three species (i.e., the low level foragers) benefit most by association with the other species.

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Department of Zoology, University of Edinburgh, Edinburgh, United Kingdom. Address of second author: Department of Zoology, South Parks Road, Oxford, England. Accepted for publication 26 June 1975.