Mixed flocks of different species of birds are common in many parts of the world, perhaps especially in the tropics. Some of them have been discussed at length and in detail (see references in Moynihan, 1962 and 1978, and Powell, in press). Their principles of organization are well known. It is still possible, however, to discover new groups, relations, details, and peculiarities. Thus, for instance, an association observed in western Sénégal in 1977, in the course of a comparative survey of Coraciiformes, was noteworthy in several respects.

The behavior of the members of the association looked dull and ordinary at first glance, but it was found to be remarkably sophisticated on analysis. The interspecific social reactions were simple in form. They were not stimulated or reinforced by special morphological features as in some other kinds of interspecific associations in other biotopes and continents. This does not mean that they were either casual or primitive. There is reason to believe that the simplicity of appearance could only be permitted by complex changes in responsiveness to incoming information. Such changes would seem to be at least as specialized as most morphological adaptations to facilitate group cohesion. The peculiarities of this Senegalese association may be related to the habitat, a fertile patch in a generally arid but varied and variable region.

Most of the observations (approximately 90 hrs) were made at the Centre de Géophysique of the Office de la Recherche Scientifique et Technique Outremer near the town of M Bour on the “petite côte” south of Cap Vert between January 22 and February 26, 1977.

This region of Sénégal has a seasonal climate. January and February are always dry. In 1977, there was virtually no rain at all at M Bour during these months. The soil of the region is
sandy. The natural vegetation should be low forest and scrub, probably dominated in most areas by acacias, especially *Acacia seyal*. This has been, or is being, replaced in many areas. The grounds of the Centre de Géophysique are certainly modified. They include an area of irrigated or watered garden, with recently introduced exotic plants such as casuarinas, bougainvilleas, frangipani, and hibiscus, plus some African species, a baobab (*Adansonia digitata*) and the "kad" (*Acacia albida*), which may well have been sown or transplanted at an earlier period (Pélissier, 1966). The garden area is a strip, approximately 600-700 m long and 100-500 m wide, stretching along a beach. It is bordered inland and at both ends by an expanse of more than a km² of scrubby second growth. Still further inland, the whole park is bordered by a highway and crop fields, practically bare in January and February.

1. — THE PRINCIPAL SPECIES

Three of the most conspicuous species of birds in the area are the Redbilled Hornbill (*Tockus erythrorhynchus*), the Longtailed Glossy Starling (*Lamprotornis caudatus*), and the Sénégal Coucal (*Centropus senegalensis*). (The scientific names used here follow Serle *et al.*, 1977.)

Some individuals of all three species probably are resident in the area. There would appear to be an influx of additional individuals, at least starlings and hornbills, in the dry season. All three species were abundant in January and February of 1977. There may have been something like 50 Longtailed Glossy Starlings and 30 Redbilled Hornbills in and around the park. The number of coucals seemed to be of the same order of magnitude.

None of the birds was breeding at this season.

The three species are not closely related to one another phylogenetically. They obviously have different habits, adaptive strategies and tactics. They are nonetheless broadly overlapping. It is not surprising that they interact socially in certain circumstances.

2. — DAILY RHYTHMS

It may be useful to summarize the activities of the birds in rather broad terms, not only to follow their social interactions but also to place their various encounters in perspective, in their proper setting.

2.1. EARLY MORNING

The local Longtailed Glossy Starlings roosted in groups, of their own species alone, in trees. I found one roost of 20-25 individuals in a clump of casuarinas. This roost was occupied for
several nights in succession and then abandoned for no very obvious reason. Groups of the species may well change roosts “normally” and more or less frequently. Possibly the composition of roosting groups also changes from night to night. In any case, all the individuals at M Bour become active at dawn. They usually scattered immediately. Small groups on the order of 3-9 individuals, and occasionally single birds, dispersed in all available directions. Some of them went far. As might have been expected, given the local topography, some of them moved out of the park into the adjacent fields. The ones that scattered within the park, and that I was able to follow, fed actively and semi-continuously for the first hour or several hours.

Almost all feeding was terrestrial. Standing or walking about slowly, the birds pecked down at the ground again and again. The soil was bare in some places, partly or completely covered by a thin layer of dry leaves or short grass in other places. As far as I could tell, these starlings did not usually, at this season, probe into the ground to any great extent or depth. Nor did they turn over or flick aside leaves frequently or vigorously. It was evident that they were picking up and swallowing something(s). Unfortunately, most of the items picked up were too small for me to identify them by sight. I think that many of them must have been small invertebrates, perhaps flies or ants (both abundant in the area).

Activity gradually changed, became more varied, as the morning wore on. The starlings continued to feed off and on, in irregular bouts, but they also began to rest, to preen, and to perform other comfort patterns. Most of their preening and resting was done in bushes and trees. At the same time, they tended to come together in larger groups, still of their own species alone, and to reconcentrate or congregate in the irrigated part of the park.

The groups of Longtailed Glossy Starlings seemed to be unstructured. I could not detect consistent subgroups, pairs or families, within them. The small feeding parties were fluctuating in composition.

The Redbilled Hornbills had a similar rhythm. Like most of their relatives, they probably roosted in trees in groups, perhaps large groups. I did not find a (or the) roost at M Bour. It may have been in the second growth. The hornbills were seen to disperse at dawn. They did so as promptly as the starlings, but they moved over smaller distances on the average. All or most of them remained in the park even after scattering. They also fed actively and rapidly on the ground during the first part of the morning. They flicked aside leaves, with conspicuous side-to-side movements of the head and bill, more frequently than did the Longtailed Glossy Starlings, but otherwise fed in much the same
ways. Presumably they also were taking invertebrate prey. Whatever they were taking was very small. (In my experience, the species is almost exclusively insectivorous. But other individuals in other parts of Sénégal at other seasons often take larger insects such as big hairy caterpillars. The behavior of the Redbilled Hornbills at M Bour in January and February suggested that they did not have a great choice of foods. Such larger prey as may have been theoretically available at the same time and place probably were being taken by other species — see below.)

The scattering of the hornbills was more revealing than that of the starlings in one respect. The hornbills did expose particular social bonds. They usually divided into pairs. Every pair that I saw closely was composed of a male and a female. There were also a few trios, perhaps families, and some apparently single individuals, perhaps separated from their mates only temporarily. These were exceptions, not the rule.

Like the starlings, the hornbills slowed down as the morning wore on. They began to rest and to preen, again usually in trees and bushes, and to congregate or assemble among themselves in the garden area.

The hornbills and starlings at M Bour seldom reacted to one another in any definitive or purposive manner during the early morning period of intensive feeding (although other individuals of the same species of starling visited Redbilled Hornbills at dawn on Cap Vert itself in August and September of 1976 — personal observation). The starlings also appeared to be of little interest to individuals of other species at M Bour during the early morning period.

The local Redbilled Hornbills, by contrast, were obviously attractive to some other species from the moment they became active at dawn.

One of the attracted forms was the Sénégal Coucal. Individuals of this species were much less gregarious among themselves than were either the starlings or the hornbills. They were also more sedentary. Most of them were in pairs in January and February. As in the case of the Redbilled Hornbills, there may also have been a few trios and single birds. Each pair of coucals had its own home range, essentially a territory. The dimensions of many territories were on the order of 50 m by 50 m. Trespassing was rare (except in one set of circumstances — see below). The coucals often joined and followed any hornbills that happened to show up in their territories at any time of the day. They also were ground feeders; but they appeared to be taking small prey from the surface in much the same ways as the Longtailed Glossy Starlings.

A second species attracted to the Redbilled Hornbills was the Hoopoe, *Upupa epops*. The individuals of this species at M Bour
in January and February appeared to belong to the nominate European subspecies; i.e., they were migrants in winter quarters. They obviously were in nonreproductive mood. They seemed to be both nonterritorial and effectively "solitary" (but see also Skead, 1950, on South African Hoopoes). Whatever their other social proclivities, the Hoopoes at M Bour definitely reacted positively to the Redbilled Hornbills. They may have joined and followed the hornbills even more frequently and readily than did the coucals. They were ground feeders of a more specialized kind than some of their competitors and associates. They often probed well down into the soil.

A third species apparently attracted to the Redbilled Hornbills was the Longtailed Shrike, *Corvinella corvina*. These shrikes can be highly and closely gregarious among themselves, forming rather large unspecific flocks. At M Bour in January and February, however, there were only three individuals, presumably a family, present most of the time. Two other individuals, perhaps a separate pair, came in occasionally. The feeding habits of the shrikes were even more distinctive, in the context, than those of the Hoopoes. The shrikes usually found their food on but not from the ground. They were "pouncers". They would perch in trees and bushes, usually 1-2 m up, fly down to the ground, pick up some prey item, and immediately fly up to a perch again. The prey that they captured may have been larger, on the average, than the prey taken by their associates. Large items are preferred by other, nonassociated, species of pouncers (see below). But the organisms taken by the Longtailed Shrikes were still small in actual size; and, as usual, I was not able to identify them.

The relations between the hornbills and their companions during the first hours of the morning seemed to be relaxed. Individuals of other species simply turned up, fed in more or less close proximity (1-10m) to the hornbills, sometimes drifted after or along with the hornbills moving from place to place, and then went off on their own again, usually to return, more often sooner than later. The contacts might, in fact, have appeared to be accidental if they had not been so frequent and repeated, accompanied by other changes in behavior, and confined to a very partial selection of the birds present in the area. See discussion.

2.2. Second phase

At some point between 8:30 A.M. and 10:30 A.M., the Redbilled Hornbills and the Longtailed Glossy Starlings, in their own groups, usually homogeneous in one case, often heterogeneous (with associates) in the other case, came together and merged with one another to form a larger mixed flock. The initiation of the merger was difficult to analyze. I often missed the crucial
steps at crucial moments. Subsequent behavior later in the day suggested that the Redbilled Hornbills may have been the active agents in bringing the whole enlarged assemblage together in the first place; but I was never able to make quite sure of this. Whatever the initial stimulus, the merger usually was swift, more like a precipitation than an accretion.

It was often accompanied by an increase in the relative number and frequency of obvious, visually conspicuous, interspecific reactions, including close following and joining. The increase was remarkable because the birds were beginning to rest and to perform maintenance activities by this stage. They were moving only intermittently, but they were more strongly social than before when they did move.

The majority of the new social responses were by the Redbilled Hornbills to the Longtailed Glossy Starlings. The hornbills were strongly attracted to the starlings. There was also some reverse attraction, but the hornbills joined and followed the starlings much more frequently than they were joined and followed by the starlings. The species previously associated with the hornbills, i.e., the coucals, Hoopoes, and Longtailed Shrikes, seldom joined or followed the starlings directly — although such responses did occur occasionally — but they maintained their relationships with the hornbills and thus tended to join and follow the starlings indirectly at one remove.

Inevitably, the starlings were the usual leaders of the group. They also were an “energizing” influence. They did not, at this stage, roam over great distances. When they were active, however, they made many minor movements from site to nearby site. They were rather more active than the hornbills, or coucals, might have been expected to be in their absence. The greater restlessness of the starlings often seemed to set off a chain reaction, inducing the other members of the group to move on, sometimes without any apparent enthusiasm or feeding purpose. A Pied Piper effect.

Another species was seen to join the enlarged mixed flock from time to time. There was a party, presumably a family or extended family, of seven Sénégal Woodhoopoes, Phoeniculus purpureus, in the garden part of the park. This party visited the hornbill-starling group at very irregular intervals. Woodhoopoes are insectivores, probers and gleaners. The local birds at M Bour in January and February usually fed by probing the bark of trees, especially casuarinas, frequently only a few cm above the ground. This is low for the species. The M Bour woodhoopoes also fed on the ground itself, usually (not always) near the bases of plants or between spreading exposed roots of trees. When they did so, they picked up small prey like the other ground feeders of the neighborhood.
They were not, on the whole, closely integrated into the larger mixed group. Their visits were brief as well as intermittent. They were not often followed or joined by individuals of other species. Nor did they themselves do much close following or joining of other species (after their first arrivals).

There was some variation in the size and composition of associations from day to day, but it was not very great during the limited period of my observations. When interspecific gregariousness was fully developed, most of the relevant birds were sufficiently attracted to one another to have formed what was essentially only a single large mixed flock in the park, or at least the garden area, of M Bour. At its largest, by the end of the morning on most days, the flock seemed to include all the local Longtailed Shrikes and Hoopoes, all or almost all the Redbilled Hornbills, and a substantial percentage of the population of Longtailed Glossy Starlings. All the local woodhoopoes were also present on occasion, as were a few adventitious representatives of other species mentioned below. The large flock always included two and sometimes four coucals. (Usually two pairs, each in its own territory at opposite ends of the flock. But this was also the situation in which one pair of coucals, swept along by the flock, sometimes passed into the territory of another.) The total number of individuals in the flock could be 75 or slightly more. This is considerable by any standards, although some mixed flocks, including some of the same species, are known to reach even larger sizes in other areas and at other times. Again see below.

The mixed flock was usually maintained through the middle of the day. The birds tended to feed less frequently, and to rest and preen for longer intervals, as the heat increased, but they continued to stay more or less closely together, even in the trees and bushes.

2.3. AFTERNOON

Interspecific cohesion gradually diminished and was eventually lost in the course of the afternoon. Small subgroups drifted off and disappeared from (my) view. Probably they scattered to feed in other areas again. The hornbills disappeared before the last of the starlings. There were always a few starlings left and still active between sunset and complete nightfall, sometimes feeding in new ways, e.g., flycatching for emerging winged ants or termites.
3. — DISCUSSION

Several aspects of the behavior of the birds of the M Bour association deserve to be considered separately.

3.1. ROLES

Different species played different roles in the association. The classificatory terms suggested by Moynihan (1962), in an analysis of neotropical flocks, can also be applied to these Senegal birds. At M Bour in January and February, the Longtailed Glossy Starlings were “nuclear” (important to the formation and maintenance of mixed groups), and “passive” (more joined and followed than joining and following), at least for the Redbilled Hornbills; the Sénégal Coucals and the Hoopoes were either regular attendants or “active” (more joining and following than joined and followed) if nuclear; the Longtailed Shrikes were probably only attendants but certainly regular; and the woodhoopoes probably should be considered to have been only occasional attendants. The Redbilled Hornbills had more complicated relations. They were highly nuclear but in different ways in different circumstances, to or with different partners. They were active nuclear vis à vis the Longtailed Glossy Starlings, but passive nuclear in relation to all or most other members of the association.

This is a wide spread of roles for a few species.

3.2. BEHAVIOR WITHIN GROUPS

The maintenance of mixed flocks did not depend solely upon following and joining.

The association at M Bour was remarkably peaceful in one sense. Individuals of the same species sometimes quarreled and fought among themselves. The Redbilled Hornbills were the most ill-tempered. They had many violent (nonterritorial) disputes among themselves, pecking and grappling on the ground and in the air. But I saw almost no signs of hostility among individuals of different species; only a few mild “supplants”, and even some of these were rather dubious (not certainly or unmistakably hostile). There were fewer conflicts between species in the M Bour association than in any other mixed groups that I have ever watched. It is rare indeed to find any social relations among any animals, that are at the same time so close or personal and yet apparently so little ambivalent.

Another reflection of the same temperament was a nearly complete indifference to the disputes of others. None of the starlings, hoopoes, coucals, etc., paid more than the slightest attention to the spectacular fights of the hornbills. They merely
moved away a few cm when and if it looked as if they might get trampled in the mêlée. Thus even these disputes had almost no disruptive effects upon the larger group as a whole.

The association was also remarkably quiet. Most birds are noisy in flocks, of their own or of several species, uttering many “call” or “contact” notes. Some of the members of the M Baur association were noisy when they were in unmixed groups. Thus, for instance, the Longtailed Glossy Starlings indulged in a great deal of rather parrot-like “conversational chatter” when they were in groups of their own species alone, and the woodhoopoes uttered many loud rattles in similar circumstances. They all, however, tended to shut up as soon as they became involved in a mixed flock. Most of them, in fact, were quite silent most of the time. A partial exception, a particular vocalization of the starlings, will be discussed below. So will the possible advantage of being quiet.

The friendly nature of the social relations among different species was emphasized by details of spacing. Sometimes pairs and families of some of the forms were easily recognizable within the mixed flocks. In which case, the members of such subgroups tended to stay closer to one another than to individuals of other species. At other times, for many minutes on end, internal segregation seemed to break down entirely, and the various individuals were all jumbled together apparently without regard to specific identity. This, again, is not very common in other mixed flocks.

3.3. Social limits

The friendliness of the birds of the M Baur association was not promiscuous. Many overlapping species were not member of the association. Among the nonmembers, at this place and time, were several weavers (*Ploceus cucullatus*, *Bubalornis albirostris*), sparrows (*Passer griseus*), babblers (*Turdoides plebejus* and *T. reinwardii*), the West African Thrush (*Turdus pelios*), various shrikes (*Laniarius barbarus*, *Malaconotus sulfureopectus*, *Tchagra senega*, *Lanius senator*), drongos (*Dicrurus adsimilis*), the magpie-like Piapiac (*Ptilostomus afer*), the Abyssinian Roller (*Coracias abyssinicus*), several bee-eaters (*Merops* spp.), the dryland Striped Kingfisher (*Halcyon chelicuti*), as well as plantain-eaters (*Crinifer piscator*), francolins (*Francolinus bicalcaratus*), various pigeons (mostly *Streptopelia* spp.), and small parrots (*Poicephalus senegalus*). Some of these species were extremely common in the area.

Members and nonmembers of the association often approached and passed by one another, but their movements were very seldom or never coordinated for any appreciable length of time. Most of the observed encounters between the two classes did seem to
be "accidental" or "coincidental", unlike the other meetings cited above.

The nonmembers were exceedingly heterogeneous. Perhaps their only common feature in the M Bour context, apart from their interspecific behavior, was equally negative. Few or none of them fed in the same general ways as the regular or frequent members. Some forms such as the pigeons and finches fed on the ground but probably took mostly vegetable matter. The roller and the kingfisher were pouncers but took relatively large prey. The nonmember shrikes certainly took insects, but usually in trees and bushes above ground.

The park at M Bour was visited by strays from other areas and habitats. Three of the strays were closely related, phylogenetically, to members of the large mixed flock. Their behavior was somewhat anomalous. Groups of the starling *Spreo pulcher* showed up in the garden on several occasions during the first days of my observations. They tended to feed on the ground during their visits, sometimes alone, at other times in apparent but brief association with the Longtailed Glossy Starlings. A very few individuals, single birds and pairs, of a third species of starling, a short-tailed form of *Lamprotornis* (probably *purpureus*), showed up on other days toward the end of my observations. They also fed on the ground, sometimes alone, at other times with the mixed flock. As far as I could tell, they usually associated more closely with Redbilled Hornbills than with their relatives. Perhaps prudently. Once I saw a long-tailed starling swoop at a short-tailed individual in an apparently aggressive manner. Gray Hornbills, *Tockus nasutus*, may have been more frequent visitors. Twice I saw a single individual, and once a trio, with the mixed flock in the garden area, and I heard the characteristic calls of the species not far away on other days. When the Gray Hornbills were with the mixed group, they tended to remain on the outskirts in trees a few meters away from the Redbills. They did not seem to be feeding on the ground at this season.

Gray Hornbills generally prefer more open or drier sites than do Redbills. They also migrate. Almost certainly, they are never common in the M Bour park itself. They were less abundant in the surrounding countryside in January and February than at some other times of the year. The rather loose contacts between the two species of hornbills at M Bour in January and February were in striking contrast to their association a few km to the south, at the edge of the forest of Nianing along the road to Joal, only a few months earlier in mid-October of 1976. There the two species were joined in an enormous and cohesive flock that included more than 50 (perhaps nearly 100) Gray Hornbills, 7+ Redbills, and a relatively minor assemblage of Longtailed Glossy Starlings, (an)other *Lamprotornis*, Hoopoes, and other
birds. At Nianing, the social integration of the two hornbills was very close, nearly perfect. They repeatedly followed and joined one another. There was almost no overt hostility between them. This in spite of the fact that the Gray Hornbills were very aggressive toward birds of other species, violently attacking Abyssinian Rollers and even such unlikely targets as lapwings, *Vanellus spinosus*.

It may be mentioned that both kinds of hornbills were feeding both on the ground and in the trees at Nianing.

3.4. Proximate Functions

The functions and rewards of the habit of associating in mixed flocks, *i.e.*, the reasons why the habit has been selected for in evolution or ontogeny, are usually difficult to determine. Presumably they are various. Any single species may derive several different benefits, at the same or different times, and different species may derive different mixes of benefits. There is some evidence, from other studies of other flocks, that two series of potential advantages relate to food and to protection. Several obvious possibilities come to mind. Cooperating members of a mixed group may, in effect if not intention, help one another to discover food sources, actually flush prey for one another, and/or stimulate one another to feed more continuously and actively. Groups may have better chances of discovering predators than would any single individual alone. Members of a group may alert one another by alarm calls. They may cooperate in mobbing or active defense, attack, against predators in appropriate circumstances.

Some of the possibilities may apply to the association at M Bour.

It can hardly be coincidental that the regular members of the group were ground feeders, probably largely insectivorous, at the time of their association. Yet they did not seem to be providing or discovering food for one another to any considerable extent. I never saw a typical ground feeder catch an insect obviously flushed by a companion (although the pouncing *Corvinella* may have done so). The very small prey usually taken from the ground in January and February appeared to be widely and rather evenly distributed. The sandy soil seemed to be much the same everywhere. During the mid-morning period, the birds tended to move gradually through the area, feeding semi-continuously as they went, instead of shifting abruptly from one obviously favored site to another. The association continued when the birds were resting and preening. Even the influence of the restless Longtailed Glossy Starlings did not always induce feeding by companions. Whatever the importance of the food factor to the formation and
maintenance of the association, the effect probably was indirect for this particular flock at this particular time and place.

The significance of protection is also problematical. Most of the members of the association were wary. It might be supposed that birds that feed on or probe into the ground would be exposed and vulnerable. They must necessarily spend much of their time looking downward, rather than in other directions from which predators are likely to come. Both terrestrial and flying predators are common in Sénégal. Many of the birds at M Bour were seen to perform communal antipredator patterns in response to a special stimulus. The Longtailed Glossy Starlings have a distinctive alarm call, a loud rasp. This is the one vocalization that they are not reluctant to use in mixed groups. Other species react to it instantaneously and vigorously. On one occasion, for example, a single Longtailed Glossy Starling which flew up from the ground to a low perch in a casuarina tree, uttering rasps in flight, was immediately joined by five other individuals of the same species, six Redbilled Hornbills, two coucals, and several woodhoopoes. All the birds flitted about noisily and excitedly, forgetting their usual rule of silence in mixed groups. The reaction seemed to be incipient mobbing. The releasing object was a small snake in the grass.

It may be doubted, nevertheless, that the M Bour association is primarily a combination against predators. There are surprising discrepancies within and without the association. The rare alarm vocalizations of Redbilled Hornbills were usually ignored by both members and nonmembers of other species. Some nonmembers, e.g., weaverbirds, tended to react to the rasps of Longtailed Glossy Starlings like members. Other ground-feeding birds, e.g., thrushes, pigeons, and francolins, did not form mixed flocks even though they should also have been vulnerable. Obviously protection cannot explain everything.

Some of the species of the M Bour association also occur in other and different mixed flocks elsewhere. The habit of associating must be an adaptation to a range of conditions, not just a particular setting. The benefits derived from the habit must vary with locality as well as the other factors. Thus, for instance, flocking may be more likely to facilitate discovery of food in areas in which prey is both large and patchily distributed than it was at M Bour in January and February when other conditions prevailed. There is no reason to suppose that all the possible or potential advantages of interspecific gregariousness should be enjoyed continuously.

Perhaps only one general advantage is frequently recurrent. It has been suggested (Moynihan, 1978) that members of mixed groups may benefit from association simply because they can observe, follow, and “monitor” their companions. They may have
to share resources with their associated competitors. At the same time, however, they are probably, in many cases, ensuring that their competitors do not get a free and undisturbed head start, discover a new resource or invent a new trick to exploit an old resource, without allowing participation or imitation by companions. (Note that the principle should apply to almost all resources of any kind, not only those that relate to feeding or protection.) The insurance provided by monitoring must be expensive but it may be worthwhile. The benefits could be as great for the M Bour flock as for any other.

3.5. Ethological implications

That flocking really is advantageous, somehow, somewhere, for the members of the M Bour association is demonstrated by their overt behavior. It is also indicated by analysis of the mechanisms involved.

Many regular members of other kinds of mixed flocks, perhaps most of the nuclear types, have evolved overt signals and structures to encourage interspecific gregariousness. These adaptations may take several forms. They include "neutral" color (and vocal) patterns, designed to give the least possible offense to potential companions, and "social mimicry", convergent resemblances designed to attract, mislead, and/or soothe particular classes of companions. The members of the M Bour association would seem to be remarkable because they have not developed such characters.

They are diverse in appearance, color, color pattern, and shape (see Figure 1). It is true that they are generally brown, black, or pied; but many of the specific arrangements of colors are too distinctive to be neutral and much too dissimilar to be plausibly ascribed to mimicry. More conclusively, the few local species that do resemble one another closely do not have the same, or even very similar, interspecific social relations. Thus, the Longtailed Glossy Starling, the Sénégal Woodhoopoe, and the Piapiac are all black and long tailed; but the first is highly nuclear in the association, the second is barely nuclear, if at all, and the third usually keeps quite apart from the others and from their companions.

Of course, the blackness of these three forms, and of the other starlings and the Buffalo Weaver *Bubalornis*, must be useful to them. Probably in several ways. As Hamilton (1973) has stressed, it must affect insulation and thermoregulation. It must have social effects as well. Moynihan (1960) noted that black (and white) coloration is common among gregarious species. The sheer conspicuousness of these colors can be a rallying signal. (Hamilton seems to have misunderstood these remarks. Black
Figure 1. — Birds of the M Bour association. Top left: two Longtailed Glossy Starlings. Center left: a Sénégal Woodhoopoe. Bottom left: a Hoopoe. Bottom right: a Redbilled Hornbill. Top left: a Longtailed Shrike. Just below the shrike is a Sénégal Coucal. (Note: The birds are not drawn to correct scale. The larger species are shown relatively small, while the smaller species are shown relatively large. Other differences in appearance between the species are minimized or obscured by the restrictions of the black and white technique.)

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and white can be adaptations to gregariousness among other things. The gregariousness does not have to be interspecific. Nor is mimicry necessarily implied. It may or may not be manifest or pertinent in particular instances. The black species at M. Bour would seem, in fact, to be good examples of nonmimicry. Their blackness may be supposed to be largely or exclusively intraspecific in functions. They all, whatever their interspecific relations, tend to be gregarious among themselves. This is as characteristic of Piapiacs and Buffalo Weavers as of all the other forms of similar plumage.)

Since species that do not look alike do associate with one another, and species that do look alike do not associate, and differences in appearance between some of the associates and nonassociates are rather subtle, the birds that habitually come together at M Bour must recognize one another, as potential companions, by many and probably complex clues. They cannot be reacting to only a few special sign stimuli of limited variety. They must, instead, be responding to different configurations of stimuli, perhaps with many of the qualities of Gestalts. Recognition and interpretation of such configurations probably is more difficult, and would be expected to take more time on the average, than reactions to fewer and simpler sign stimuli in otherwise identical circumstances. Presumably (given the usual need for clarity and speed of decision) birds would not use a more complex system if simpler alternatives were not, for some reasons, inappropriate or nonfeasible.

It is interesting that special acoustic sign stimuli have not taken the place of visual ones. Yet the usual quietness of the birds of the M Bour association, while they are together, may subserve some of the same functions as the neutral patterns of other species of other flocks. The M Bour birds are as varied in voice as in visual appearances. By not vocalizing while they are together, they must at least keep one kind of diversity to a minimum. They must avoid adding acoustic confusion to the prevailing visual complexity.

3.6. OTHER ASSOCIATIONS IN OTHER AREAS

The members of the M Bour association may have to use many clues, subtle distinctions, and configurations because their interspecific relations are unusually variable and opportunistic.

Despite the artificiality of the garden habitat, the flock studied at M Bour in January and February of 1977 probably was not entirely atypical of the immediate region and period. Mixed groups of Redbilled Hornbills and Longtailed Glossy Starlings were also seen, in early February, in the more natural acacia forest of reserve of Bandia, 20 km to the north of M Bour, and in
the fields and scrub along the highway to Kaolack 10-20 km to the east. This does not mean that associations were uniform everywhere. Even at Badia, the starlings also seemed to be attractive to other smaller birds such as *Ploceus cucullatus* and the common bulbul *Pycnonotus barbatus*. Many of the species seen at M Bour were also found to be equally or more abundant in the drier region of Cap Vert, near Yeumbeul between Rufisque and Dakar, during the same period. At this time and place, they showed few traces of interspecific gregariousness. The local Hoopoes were solitary, while the Longtailed Glossy Starlings, Redbilled Hornbills, and Sénégal Woodhoopoes usually occurred in flocks of their own species alone, even in the late mornings. The nearest thing to a real mixed flock seen at Yeumbeul was a feeding group of Longtailed Glossy Starlings and Buffalo Weavers. This may have been semicasual, but it seemed to be more significant, more nearly truly social, than the incidental encounters between the same two species at M Bour. The large mixed flock seen at the edge of the forest of Nianing along the road to Joal in October of 1976 has already been mentioned. Gray Hornbills were not only predominant in this group but also highly nuclear, quite unlike their conspecifics in either M Bour or Yeumbeul.

Thus the evidence suggests that several of these species show considerable flexibility in the selection of partners and roles. The flexibility is expressed in shorter periods of time and over smaller distances than are most of the corresponding variations of other species previously studied from this point of view, such as the mixed associations of finches, tanagers, honeycreepers, warblers, and other birds of the high and cold humid zones of the Andes (Moynihan, 1978). In the Andes, different populations of a single species may show different behavior in different regions; but the various populations are more or less resident, stable, and geographically isolated, at least partly separated from one another. Their distinctive features probably are based upon conservative local traditions or perhaps even genetic evolution. In Sénégal, on the other hand, geographic barriers are minimal and many birds are nomadic or migratory. Such differences in behavior as distinguish different populations and groups in Sénégal are more likely to be the results of individual choices and decisions, made in direct response to prevailing conditions in any given area at any given moment of time, than are the superficially similar variations of the birds of the cold humid zone of the Andes. Senegalese birds must also have traditions, but they probably often are traditions of rapid (and reversible) change.

### 3.7. Ecological correlates

The peculiar features of these Senegalese birds, their movements and flexibility of social behavior, would seem to be adaptations to a difficult and frequently changing environment. The
species and subspecies that occur in the M Bour association are characteristic of the Sahel. This zone is rigorous and fluctuating (ranging from very dry to less dry according to year and season). It is also varied insofar as it is marked by irregularly scattered patches of greater humidity, groundwater or water courses, temporary or permanent swamps, ponds, streams, and rivers in limited edaphic and topographical situations. Doubtless the expansion of human populations and shifts in agricultural practices have added to the variety in recent centuries. The behavior of the birds associated with one another at M Bour and sometimes elsewhere may help them to combine, separate, and recombine to seize the most fugitive opportunities.

3.8. COMMENT

The absence of special visual sign stimuli and the partial suppression of acoustic signals in the M Bour association could be considered “negative” features. But anything more positive in the way of attractive stimuli, e.g., coincidence of colors or mimicry, might simply close off options. A feature attractive to one companion might well be repellent to another potential partner. The chances of incompatibility must increase with both diversity of partners and frequency of changes of relationships.

It is remarkable that negative characters can contribute so much to friendly responses of such strength and magnitude as those of some of the birds at M Bour. Extra “added” inducements to bring animals together are obviously useful in many circumstances, but they are not always possible to arrange. An ability to disregard differences in appearance, real social barriers for most animals, apparently can be an effective substitute for positives invitations or incitement. The development of this capacity to disregard must entail at least a new classification of input and perhaps a reordering of output. Any individual selecting different companions of different other species in different circumstances must assess them without prejudice. It must try to estimate their possible advantages and disadvantages as partners irrespective of their resemblances to other individuals of the same species or previous companions of other species.

The fact that the birds of the M Bour association can do so successfully may be one of their greatest assets in the struggle for survival. It is also, almost certainly, an extreme specialization. Most other birds and mammals are less flexible at an individual level. Like some other rare characters, e.g., intelligence, social opportunism may evolve only when it is the only solution.
SUMMARY

An association of several different species of birds was observed at M Bour in western Sénégal in early 1977. The two species of greatest social weight were the Longtailed Glossy Starling (*Lamprotornis caudatus*) and the Redbilled Hornbill (*Tockus erythrorhynchus*). Individuals of both species were gregarious among themselves. The Redbilled Hornbills also were attractive to coucals (*Centropus senegalensis*), Hoopoes (*Upupa epops*), and Longtailed Shrikes (*Corvinella corvina*). They were themselves attracted to the starlings. The net result of the interactions among these species was the daily formation of large mixed flocks. The flocks were sometimes visited by birds such as *Phoeniculus purpureus* and *Tockus nasutus*, but they were ignored by many other species in the neighborhood.

The benefits derived from the habit of associating in mixed flocks were obviously varied. Mutual help in finding or flushing food seemed to be less important, in the local circumstances, than protection against predators or the regulation of competition by monitoring of rivals.

Some aspects of the behavior involved in the formation and maintenance of the mixed flocks were distinctive. They may be adaptations to facilitate social flexibility in the short term and over small distances. Opportunism would be expected in the rigorous and fluctuating environment of most of Sénégal. The species that associated with one another at M Bour are known to show other kinds of interspecific behavior in other areas and/or at other seasons, not far away in either space or time. Some of the variation may be due to individual choice. Among the apparent consequences or correlates of this opportunism are the absence of certain kinds of visual signals, the partial suppression of acoustic signals, and a reliance upon many and probably complex clues for recognition of potential companions. The mechanisms of such interactions probably are highly specialized.

RESUME

Au début de 1977 l’auteur a observé dans la région de M Bour, Ouest du Sénégal, l’association de plusieurs espèces d’oiseaux. Parmi ces dernières, deux avaient une importance particulière, le Merle métallique à longue queue (*Lamprotornis caudatus*) et le Petit Calao à bec rouge (*Tockus erythrorhynchus*). Un grégarisme intra-spécifique caractérise ces deux espèces. Les calaos attiraient également les coucals du Sénégal (*Centropus senegalensis*), les huppes (*Upupa epops*) et les corvinelles (*Cornivella corvina*). Les calaos étaient aussi attirés par les merles métalliques. La consé-
quence de toutes ces interactions était la formation chaque jour de grandes bandes pluri-spécifiques. Ces dernières recevaient quelquefois la visite de *Phoeniculus purpureus* et de *Tockus nasutus* mais étaient ignorées par bien d'autres espèces d'oiseaux vivant dans le même milieu.

Les bénéfices que les participants pouvaient tirer de cette association en bande mixte étaient de toute évidence divers. L'aide réciproque qu'ils pouvaient s'apporter pour la découverte de la nourriture semblait moins importante dans ce cas que la protection contre les prédateurs et la réduction de la compétition interspécifique par observation continue du comportement des compétiteurs.

Quelques aspects des comportements impliqués dans la formation et le maintien des bandes mixtes sont caractéristiques. Ils peuvent constituer des adaptations destinées à faciliter la « souplesse sociale » à court terme et sur de petites distances. Dans l'environnement rigoureux et saisonnier qui caractérise cette partie du Sénégal, on s'attendrait à plus d'opportunisme. Les espèces associées à M Bour sont bien connues pour faire preuve d'autres comportements interspécifiques dans d'autres régions et/ou à d'autres saisons. Quelques-unes des différences constatées peuvent être dues à des choix individuels. Parmi les conséquences apparentes ou les corollaires de cet opportunisme, on peut citer l'absence de certains types de signaux optiques, la disparition partielle des signaux acoustiques et le fait que les oiseaux se basent sur des indices nombreux probablement complexes pour reconnaître leurs associés potentiels. Les mécanismes de telles interactions sont probablement hautement spécialisés.

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