Social, Sexual, and Pseudosexual Behavior of the Blue-bellied Roller, *Coracias cyanogaster:* The Consequences of Crowding or Concentration

MARTIN MOYNIHAN

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ABSTRACT

Moynihan, Martin. Social, Sexual, and Pseudosexual Behavior of the Blue-bellied Roller, *Coracias cyanogaster:* The Consequences of Crowding or Concentration. *Smithsonian Contributions to Zoology,* number 491, 23 pages, 15 figures, 3 tables, 1990.—Blue-bellied Rollers (*Coracias cyanogaster*) occur in West Africa. They are typical of *Coracias* species in being sit-and-wait predators. They pounce upon relatively large prey (arthropods and vertebrates) in low, sparse vegetation or on bare ground. They differ from their closest relatives, other species of the same genus, in preferring humid or semi-humid habitats. In West Africa, such habitats are naturally forested. Blue-bellied Rollers often perch high in trees. Still, they prefer to pounce low. This means, in effect, that they are dependent upon clearings to some appreciable and significant extent. Patches of bare earth and sparse vegetation probably were few and scattered before the spread of agriculture. In these earlier circumstances, Blue-bellied Rollers must have had to concentrate upon whatever open spaces were available. They may have been more crowded on a restricted local level than other species of rollers.

All *Coracias* are large, powerful, and aggressive. Concentration and crowding must have been difficult to manage or to support. The ancestors of modern Blue-bellied Rollers would seem to have evolved several behavioral mechanisms to cope with their problem. They may have become more tolerant of conspecifics than their relatives. In the Basse Casamance region of Sénégal and perhaps other areas, they have also developed the habit, unique among rollers, of performing pseudocopulations, reverse mountings, sometimes with apparent cloacal contacts, sometimes repeatedly. Sexually-derived patterns are potentially capable of being used to control agonistic encounters irrespective of actual sex. They seem to do so in two ways. They can function as threat. They also canalize aggression to minimize the risks of contact fighting with neighbors and intruders.

Adaptations to forested conditions have survived, even though much of the land has been largely cleared for centuries or perhaps thousands of years.

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Contents

Social, Sexual, and Pseudosexual Behavior of the Blue-bellied Roller, *Coracias cyanogaster*: The Consequences of Crowding or Concentration

Martin Moynihan

Introduction

Birds of the traditional order Coraciiformes are diverse, conspicuous, abundant, and ecologically important in the tropics, most notably in Africa. They include kingfishers, bee-eaters, (probably) hornbills, and other forms, as well as rollers of the genera *Coracias* and *Eurystomus*. This paper is concerned with the Blue-bellied Roller, *Coracias cyanogaster*.

The species occurs in West Africa (Serle and Morel, 1977). Something is known of its status or position in the wild. Thiollay (1985) describes the feeding habits of the species in the Ivory Coast. Moynihan (1988) compares it with the Abyssinian Roller, *Coracias abyssinica*. None of the published accounts gives the details or "mechanisms" of social interactions within the species. Yet some of the details are very remarkable indeed.

I observed the species in Sénégal, mostly in the southwest of the country, in the Basse Casamance, at intervals between 14 August and 9 December, 1976, between 22 January and 12 March, 1977, during the brief period of 15–21 June, 1981, and from 1 October to 2 December, 1985. The birds were watched, followed, photographed, and their vocalizations were recorded. They were not trapped, marked, or ringed. The time spent actually observing in the field was on the order of 700–725 hours. This was divided, extremely variably, between observations of Blue-bellied Rollers and of other species in the same areas. Precise figures cannot be given; but the time devoted to the Blue-bellied Rollers was approximately 150 hours. Most observations were made in the mornings and late afternoons. The number of Blue-bellies seen was 200+. Of these, 20–25 individuals were studied fairly intensively; in some cases on consecutive days, in other cases at approximately weekly intervals for a month or more. Sites of observation extended along several hundred kilometers of roads and trails.

The appearance of the species is shown in the illustrations (Figure 1). The general *gestalt*, when the birds are at rest, is chunky and powerful. The bill is rather heavy and slightly hooked. Most of the plumage of the front part of the body, the head, neck, throat, and breast, is pinkish tan. Most of the rest of the plumage is black or sapphire blue. There is a patch of turquoise in the wings, also blue-green in the tail. The outer feathers of the tail are elongated to form short "streamers." Blue and blue-green are characteristic of many rollers and other coraciiform birds such as kingfishers of the genera *Halcyon* and *Alcedo*. The arrangement of colors in *C. cyanogaster* is, however, rather distinctive. On plumage alone, it would be supposed that *C. cyanogaster* is less closely related, phylogenetically, to other species of *Coracias* than the latter are to one another. This is not insignificant in view of the fact that *C. cyanogaster* also has distinctive behavioral traits.

There is little sexual dimorphism; none in plumage color; but males of the species in the Ivory Coast average slightly heavier than females of some areas (Thiollay, 1985). They may also tend to have longer (less abbreviated) streamers. A slight difference in apparent size and shape between the members of any pair or couple was detectable wherever and whenever I was able to observe closely. One may suppose that this reflected a distinction of sexes.

ACKNOWLEDGMENTS.—I am grateful to the Ministère de la Recherche Scientifique et Technique of the Republic of Sénégal for much assistance. Olga F. Linares provided the photographs and sound recordings. Eugene S. Morton and Kimberley Young made the Sonagrams. Maria-Luz Jimenez prepared the text and the tables. Many of my colleagues at the Smithsonian Tropical Research Institute were helpful in a

Martin Moynihan, Smithsonian Tropical Research Institute, Apdo. 2072, Balboa, Panama.

FIGURE 1.—Three postures of Blue-bellied Rollers. *Top:* An individual scanning the neighborhood for prey. The neck feathers are slightly fluffed. The carpal joints are held away from the body. *Center:* A forward leaning pre-flight posture. *Bottom:* Looking downward before pecking at the substrate. The neck feathers are slightly Ruffled.

variety of ways. Ms. Claudine Sierra provided a draft of the French summary. Olga F. Linares and Maria-Luz Jimenez assisted with the Spanish summary.

Data

HABITAT

As Blue-bellied Rollers are not generally familiar to ethologists, it may be useful to say something about the present and presumed past habitus or natural history of the species.

The Basse Casamance lies in a transition zone between the arid Sahel and the full Guinean rain forest. The region is coastal, low-lying, intersected by a network of tidal creeks. The relief is gentle. There are large expanses of land that are called "plateaux" by the local people; but they are never more than a few tens of meters above sea level. The climate is seasonal, more or less humid for part of the year. Rainfall records for 20 years, taken at Ziguinchor, the capital of the Basse Casamance, a central location, are shown in Table 1. (Like much of West Africa, Sénégal has suffered from intermittent drought; but the years 1976, 1981, and 1985 were not extremely dry).

With this sort of climatic regime, the natural vegetation of the Basse Casamance and/or adjacent areas a few thousands of years ago, before the expansion of human activities (Porterès, 1950; Linares, 1971), must have consisted primarily of light forest verging on forested savanna with mangrove swamps along the creeks and only occasional clearings (Figure 2).

The situation has changed. Patches of forest survive (or have regenerated); but most of the land is occupied by cropfields, peanuts, millet, sorghum, irrigated rice, pastures, and degraded scrub. There also are scattered trees such as Oil Palms, acacias, Baobabs, Silk-cotton trees, etc. Numerous patches of bare earth are found along roads and highways on the outskirts of villages and in certain cropfields, especially peanuts (these fields have relatively few weeds). The environments of the (nearly) present day Basse Casamance are described by Aubréville (1948), Adam (1961, 1962), and Pélissier (1966) (Figure 3).

Blue-bellied Rollers use many features of their environment for one purpose or another. They do not take advantage of all features. They tend to avoid the telephone, telegraph, and electrical lines and pylons that have spread almost throughout Sénégal in recent years and that are used by several other coraciiforms, e.g., *Coracias abyssinica* and *Halcyon senegalensis*.

There are other variations of usage. One point should be stressed before proceeding further. Senegalese Blue-bellied Rollers seem to do best, to be most abundant, when they have access to both bare earth or low, sparse vegetation and to tall trees, which they use as observation posts and resting places. Trees also provide nesting holes, a vital resource (Short, 1973, 1979). Combinations of tall trees and bare ground in close juxtaposition are now common in the Basse Casamance. They may have been less abundant (the bare areas less numerous and more scattered) a few thousands of years ago. This probably is relevant to the evolution of the social behavior of the species.

Other populations of Blue-bellied Rollers may have similar ecological preferences. Thiollay (1985) says that individuals of *C. cyanogaster* near Lamto in the Ivory Coast inhabit wooded savannas.

TABLE 1.—Rainfall data of Ziguinchor (measurements in mm).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1965	-	-	-	traces	0.8	140.9	447.0	674.2	384.4	95.1	14.2	-	1756.6
1966	-	-	-	-	traces	92.3	173.0	467.8	573.7	285.4	11.6	-	1603.8
1967	traces	traces	-	-	traces	135.7	479.4	718.4	460.5	212.5	-	-	2006.5
1968	-	2.7	-	-	traces	30.7	265.9	159.9	288.7	134.6	-	-	882.5
1969	-	-	-	0.1	traces	124.7	332.3	433.0	350.6	219.9	0.1	-	1460.6
1970	-	-	traces	-	14.3	64.4	392.3	565.8	300.9	60.6	traces	-	1398.3
1971	-	-	-	traces	traces	71.5	260.1	345.5	329.6	92.9	-	-	1099.6
1972	traces	-	-	traces	0.5	84.4	213.3	378.6	226.4	48.6	-	-	951.8
1973	-	-	-	-	traces	89.0	308.5	588.4	255.1	48.4	-	-	1289.4
1974	-	-	-	-	1.1	29.7	374.2	546.5	258.0	30.9	traces	-	1240.4
1975	-	-	-	-	traces	33.3	364.3	497.5	471.3	50.8	traces	traces	1417.2
1976	traces	traces	-	-	27.2	49.5	292.1	513.7	213.7	162.8	23.8	13.9	1296.0
1977	-	-	-	-	-	69.5	156.7	237.0	219.2	108.0	traces	traces	790.4
1978	-	-	-	-	2.2	189.2	406.6	454.3	241.4	162.9	55.2	1.6	1513.4
1979	6.0	-	traces	traces	traces	230.1	274.5	419.5	181.2	76.8	5.2	0.8	1194.1
1980	-	4.6	-	-	traces	43.1	167.5	159.8	315.8	7.1	traces	0.6	698.5
1981	-	-	traces	-	27.2	49.7	417.1	319.3	294.4	112.7	1.1	-	1221.5
1982	0.1	-	-	-	17.6	31.0	193.4	324.0	207.5	124.3	-	traces	897.8
1983	-	-	-	-	7.6	108.2	212.1	135.1	320.5	22.9	-	-	806.4
1984	-	-	-	-	traces	266.5	393.6	227.2	302.0	45.3	4.4	-	1239.0

FIGURE 2.—A more or less natural forest in the Parc National de la Basse Casamance.

FEEDING

Blue-bellied Rollers are predatory. Their usual method of hunting is stereotyped and typical of many coraciiforms. They sit and wait on perches, high or low, and then *pounce down* upon their prey in sparse vegetation or, more frequently, on the ground. (They have, in effect, become commensals of man in some areas of peanut cultivation). The prey items taken by the usual hunting method tend to be large (Figure 4). They include beetles and orthopterans; occasional frogs, snakes, and lizards; and probably other animals, such as spiders and caterpillars. Prey is seized in the bill; one of the reasons why the bill is powerful. After capture, the prey is taken to a perch, where it may be battered before being swallowed.

Pounces are not frequent. Blue-bellied Rollers can be endlessly patient. The species follows a low energy expenditure strategy in most circumstances.

A few other hunting techniques can be used. Some prey are taken from leaves and fronds of tall trees. I saw instances of apparent "fly catching" of insects high in the air. Individuals may also rather awkwardly hop along mud flats, beaches, and strandlines, poking at or even probing into the substrates, presumably in search of crustaceans, "worms," and other marine creatures. These alternative methods of feeding may be valuable in times of emergency. They are, however, exceptional. Pouncing in restricted areas on dry ground is still the preferred method.

Large prey are uncommon and often scattered; thus, each item is valuable. Single items cannot be shared easily. Blue-bellied Rollers, even in groups (see "Intraspecific Relations/Structures"), never cooperate to hunt or to flush prey communally. They are in strong competition with one another and with other species for food and other resources (Packer and Ruttan, 1988).

INTERSPECIFIC RELATIONS

The fauna of Sénégal is rich. There are many opportunities for encounters between individuals of different species.

FIGURE 3.—A modern scene of rice fields, a dirt road, and scattered trees.

Encounters can take various forms, from predator-prey interactions to purely social responses.

Blue-bellied Rollers are bold and often aggressive. They do not seem to worry overmuch about the possibility of predation upon themselves. In the open, they are large, powerful, and agile enough to hope to escape or to defend themselves successfully. They must be more vulnerable to mammalian carnivores and rodents, certain hawks, snakes, and perhaps monitor lizards in their nest holes. Still, I never saw them react strongly to potential predators upon themselves. They do, however, react to other animals; always in a hostile rather than a friendly way. I saw them threaten, supplant, attack, or pursue other birds, Abyssinian Rollers (*Coracias abyssinica*), Broad-billed Rollers (*Eurystomus glaucurus*), a Gray Hornbill (*Tockus nasutus*), a Black-and-White-Tailed Hornbill (*T. fasciatus*), Gray Kestrels (*Falco ardesiaceus*), a Black Kite (*Milvus migrans*), a Lizard Buzzard (*Kaupifalco monogrammicus*), a Palm Nut Vulture (*Gypohierax angolensis*), Hammerkops (*Scopus umbretta*), Brown Babblers (*Turdoides plebejus*), doves (*Streptopelia* spp.), and Gray-headed Sparrows (*Passer griseus*). (The names used here follow Serle and Morel, 1977.)

Some of the birds toward which aggression is shown, e.g., Abyssinian Rollers, Gray Kestrels, and the hornbills, seem to be competitors for food and/or nest holes. Others, e.g., doves and sparrows, are entirely harmless to the rollers; they take different foods and nest at other sites. Attacks upon them may be redirection, deflections from more serious disputes. Aggressive as they are, Blue-bellied Rollers do not launch redirected attacks as frequently as do Abyssinian Rollers.

The Blue-bellied Rollers of the Basse Casamance win all or most of the hostile interspecific encounters in which they become engaged. They are dominant. Their presence in any given area must have effects upon the distribution and behavior of other species.

The dominance may be most extreme when it is least instantly visible. Three species of *Halcyon* kingfishers (*senegalensis, malimbica,* and *chelicuti*) are common in the Basse

FIGURE 4.—A small group of Blue-bellied Rollers. The two individuals on the left are preparing to swallow prey.

Casamance. Although smaller than rollers in body size, but with larger bills, they also are sit-and-wait pouncers upon arthropods and small vertebrates. (They are *martin-chasseurs* in the French sense.) The three common Senegalese species of *Halcyon* have overlapping habitat preferences. Individuals of any two species use the same perches, perhaps even the same nest holes, and hunt some of the same kinds of prey, but never simultaneously. They keep apart from one another at any given moment by a sophisticated system of spatial and acoustic avoidance (Moynihan, 1987a). Blue-bellied Rollers participate in the same avoidance system. They overlap the *Halcyon* species, but never (in my experience) encounter them face to face. This cannot be accidental. Probably the most significant relation is between *C. cyanogaster*, the dominant roller, and *H. senegalensis*, the middleman among the kingfishers. Given the size differences, one might suppose that the kingfishers keep away from the rollers more often than the rollers keep away from the kingfishers.

Blue-bellied Rollers do not show as much overt aggression toward other species as do some of their relatives. Perhaps they do not have to do so because their social dominance is so widely recognized.

INTRASPECIFIC RELATIONS

STRUCTURES.—There is geographic variation in the social behavior of Blue-bellied Rollers. Relations among the birds of the Basse Casamance were not the same as those described by

Thiollay (1985) for the birds of the Ivory Coast. Population densities are different in the two regions. They should be considered separately. For convenience, I will begin with the Basse Casamance.

In this region, the species is fairly abundant. It is essentially resident. A few individuals may wander locally, for distances unknown, during the non-breeding season (I noticed this particularly at the beginning of my work in 1985), but there are no conspicuous, massive inflows or outflows of large numbers of individuals with the beginning or end of the heavy rains. Of course, I did not observe during all months of the year; but the species is not supposed to be migratory anywhere (Curry-Lindahl, 1981).

In the Basse Casamance, Blue-bellied Rollers are usually found singly or in small groups of two, three, or four individuals. Apparently single individuals are problematic. They may be strays and/or only temporarily isolated. Small groups (Table 2) are relatively stable. Groups of two seem to be pairs of one male and one female. A size difference is evident. Probably the members of most pairs have long been mated to one another. I never saw anything like pair-formation. Perhaps males and females mate for life, barring accidents. Possibly groups of three or four are composed of one old pair, plus one or two younger individuals, or one young with an attracted companion. Unfortunately, I also failed to see the initial coming together of small groups. There is nothing very distinctive about the juvenal plumage of the species at a distance. It is, however, suggestive that the small groups are of nuclear family size.

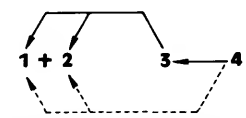
On the evidence of physical appearance, size, shape, and streamers, the Blue-bellied Rollers of the Basse Casamance have an approximately balanced sex ratio. There are no indications of a preponderance of males as in some populations of the related Pied Kingfisher, *Ceryle rudis* (Douthwaite 1973, 1978; Reyer, 1980, 1984; pers. obs.).

The social and sexual relations within groups of three or four individual Blue-bellied Rollers are complicated. Typically, two individuals, perhaps members of the old(er) and longer established pair, are more or less "at ease" with one another.

TABLE 2.—Groups in the Basse Casamance during years of study (total number of groups counted: 58; total number of individuals counted in groups: 180; average number of individuals per group: 3.1).

Number of individuals per group	Number of groups counted
2	28
3	15
4	9
5	2
6	2
9	1
12	1

Whenever they come together, they do so with little or no hesitation or hostile ("greeting") display. A third individual may appear to be less confident. A fourth individual often appears to be distinctly uneasy. It approaches its associates less frequently and/or less closely than the associates do one another. It may show alarm patterns. A common arrangement is a group with two individuals strictly (repeatedly and predictably) bound to one another (here I am talking about social bonding, not closeness in space), a third individual more loosely bound to the first two, and a fourth individual also bound, even more loosely, to the first two or, perhaps more often or visibly, to the third individual. A graphic representation of a full nexus would be



When the first and second individuals are bound together with one another, and the fourth individual is bound to the third, one might perhaps speak of two pairs, one well established and the other incipient. But all four individuals rejoin one another repeatedly.

The difficulty of analysis is compounded by several features. One is the fact that the highest intensity hostile (agonistic) and sexual (copulatory) performances of the species are remarkably similar in physical forms. This similarity is a main subject of this paper, and is described and discussed at some length below.

Spatial relations can be confusing. Blue-bellied Rollers are so aggressive, in correlation with their hunting habits, that the members of pairs and groups are often far (hundreds of meters) apart from one another. They rejoin only on occasion. Among the occasions are reproductive activities and disputes with neighbors and intruders. Disputes can be misleading to a human observer. There usually are two parties. Often each party has its own champion (the senior males?). The two champions tend to follow one another about very closely, sometimes displaying vigorously, at other times sitting side by side for minutes on end. The other members of the two parties may simply watch from a distance. A human observer must be aware that two individuals close together in space may be opponents, while other individuals farther away may be "friends" of different opponents. Only after a dispute has been resolved can the real social bonds be identified.

The number of statements already made about relations among individuals gives rise to the question, how was identification achieved in the absence of ringing: more or less easily in the short run, over periods of hours; with more difficulty and less confidence in the long run, over periods of days. In the short run, a human observer can keep an eye on different individuals even when they are separated by dozens or hundreds of meters. In the long run, it may be fairly safe for an observer to assume that pairs and groups in the same places,

FIGURE 5.—Part of a large group assembled in the early morning.

showing the same behavior, with the same size and shape differences, are in some sense continuous.

Pairs and small groups have home ranges. These areas usually are defended; they are territories. In the Basse Casamance, they are diverse in size, but most of them are large. They can be irregular in shape. I saw territories as large as 1 hectare and as long as 400 m. There are overlaps of neighboring territories. In a few cases, overlaps are both very wide and very frequent. This may be a temporary or transitional phase during the gradual break-up of a nuclear family.

Blue-bellied Rollers can also occur in large groups. They do so rarely in the Basse Casamance. I saw one group of up to 9 individuals and another group of up to 12 individuals in late 1985 (Figure 5, Table 2). The birds did not appear to be breeding. Large groups were seen only in the early morning, during the period from first daylight to a half hour after sunrise, and in the late afternoon or evening, from a half hour before sunset to nightfall, before or after moving to or from communal sleeping roosts (in tall Silk-cotton trees). During the day, the birds scattered in pairs, trios, and quartets to occupy and defend territories of the usual types in the usual ways. Scattering is evidence that the large groups were compound, composed of smaller social units which still maintained their own internal cohesion(s).

Communal roosts and assemblies are not always necessary or inevitable. Even in 1985, many of the local Blue-bellies continued to roost in pairs and small groups in separate territories.

Large groups in the Basse Casamance seem to be fairly or relatively peaceful. Members do not usually show hostile

displays to one another. Nor are they congregating to seize singular opportunities. Adventitious flocks of Abyssinian and Broad-billed Rollers come together in response to sudden flushes of prey, swarms of insects, alive or dead (Moynihan, 1988; pers. obs.). This is not true of Blue-bellied Rollers. They do not feed in large groups; certainly not at dawn. Most rollers and *Halcyon* spp. have to wait for their ectothermic prey to warm up and become active as the morning progresses.

The Blue-bellied Rollers of the Basse Casamance are rather like some Gray Hornbills and Red-billed Hornbills (*Tockus erythrorhynchus*) that, in other parts of Sénégal, at other times of the year, also roost communally, assemble at dawn and dusk, and disperse during the day. One gets the impression that the members of assemblies are simply "checking in" to find out who has died, who has moved, who has survived and remained, who has arrived, who is in good or poor health, who has reached what stage in the annual cycle, etc. Communal roosts, and the movements to and from them, could be information-transferral centers or conduits.

A qualification should be inserted here. The assembly and dispersal system of Red-billed Hornbills cited in the preceding paragraph is not characteristic of the species always and everywhere. It did occur on Cap Vert in Sénégal in the early Autumn of 1976. It did not occur at M'Bour on the Petite Côte of Sénégal in January–February of 1977. At that time and in that place, there was a different regime of assembly and dispersal (Moynihan, 1978). Flexibility and opportunism can be shown in different ways.

Thiollay (1985) observed Blue-bellied Rollers at Lamto in the Ivory Coast at various intervals, most intensively in May–June, 1983. The birds were very abundant, more numerous than anywhere in the Basse Casamance during my periods of observation. Thiollay (1985) seems to say, to imply, that young of the year (or the most recent brood) were associating with adults. The number of young was not, however, very great. It is interesting, therefore, that most of the Lamto birds could be divided, by Thiollay's criteria, into groups of 3 to 13 individuals (plus a few singles, possibly strays). An appreciable number of groups included 7 or more individuals in relatively small areas.

The figures are shown in Table 3. They are in sharp contrast with the figures from the Basse Casamance shown in Table 2. How to interpret the difference is problematical. There is no point in applying conventional methods of statistical analysis. There are too many variables. Still, the difference, on the face of it, does seem to be real.

The members of particular groups at Lamto roosted together at night and dispersed (in pairs and small parties?) during the day; not usually going very far.

Possibly, Blue-bellied Rollers can be divided into nuclear and extended families or clans everywhere. The lines of division, the frequencies of joining and leaving, seem to be different in the Basse Casamance and in the Ivory Coast.

REPRODUCTION.—Morel and Morel (1982), surveying the Sénégambian region as a whole, say that Blue-bellied Rollers have been found to breed in April, June, and July. Thiollay (1985) says that the birds of Lamto breed *"a la fin de la saison sèche"* (February?). I found it impossible to define the breeding season in the Basse Casamance, simply because (as noted above and discussed below) some copulations and/or series of copulatory movements have nothing to do with reproduction directly. Still, there was a fairly dramatic increase of interest in potential nest holes in March of 1977.

TABLE 3.—Groups at Lamto, May–June, 1983 (total number of groups counted: 39; total number of individuals counted in groups: 255; average number of individuals per group: 6.5). (Taken from Thiollay, 1985, fig. 1.)

Number of individuals per group	Number of groups counted
3	2
4	5
5	8
6	5
7	8
8	6
9	1
10	1
11	1
12	1
13	1

HOSTILITY.—Blue-bellied Rollers dispute among themselves between periods of repose. Some disputes are low key in appearance. They are modulated by hints and suggestions. An observer can infer that an interaction is, or was, unfriendly only indirectly. The forms of the hints may be suggestive per se and one or more of the individuals involved eventually leave(s) the scene. Other disputes are energetic for a time. They may include chases and Swoops with loud vocalizations. Even the most violent, however, seldom lead to physical fights, striking, grappling, or the pecking of one bird by another. Presumably the bills of the species are too dangerous and/or too valuable to risk in combat without extreme provocation. Thus, the aggressive system is largely dependent upon signals.

SIMPLE INDICATIONS AND INTENTION MOVEMENTS.—Blue-bellied Rollers have both visual and acoustic signals. Thiollay (1985) does not discuss this aspect of behavior; so the following account is based upon my observations in the Basse Casamance.

The birds of this region have many postures and movements that encode social information. Some patterns are hostile, agonistic. They are diverse in forms. They include slight movements and intention movements of attack (advance), escape (withdrawal or retreat), and combinations of the two. Many patterns are slightly ritualized; they have become stereotyped and/or exaggerated. They can be said to be displays. Some examples of hostile displays are listed below. (The terms are descriptive. Following an old convention, the

initial letters of the names of certainly or probably ritualized patterns are capitalized.)

Individuals may stretch their necks upward to assume alert-looking Erect Postures, while the head and bill are kept horizontal, pointed downward, or (very occasionally) slightly raised. The feathers of the neck may be kept flat and smooth or, alternatively, raised, Fluffed, or Ruffled in Erect and other postures. Ruffling, sometimes extending to the crown and/or to the upper back, seems to be an indication that the tendency to attack is stronger than the tendency to escape. It often precedes advances. Birds in Erect Postures may turn their heads and bills toward or away from the individuals with which they are interacting. Looking toward, Staring, seems to be intimidating. It often induces retreat or escape by a partner or opponent. Turning away may be a single movement or repeated Head-flagging. This seems to express alarm and to function as "cut off" or even appeasement. Sometimes opponents or partners Tilt their heads laterally, away from one another, without turning or Flagging. Individuals may also lower their heads to look fixedly downward or peck vigorously at the substrate. Some or all of this pecking may be redirected attack. Several patterns could be intention movements of flying. Among them are Tail-spreading, Tail-wagging (up and down or backward and forward), and Carpal-raising (holding the carpal joints away from the body) (Figures 1, 6).

None of the patterns listed above is very distinctive morphologically. The same descriptive names could be applied to visual signals of many other birds, from gulls to finches. Other rollers show homologous patterns. The originality of Blue-bellied Rollers lies elsewhere.

The Erect Postures and associated patterns are not conspicuous at a distance. They are designed to be seen close up. Some performances are evidently of low intensity, almost casual. Others crackle with excitement. Even so, they tend to be slow. Opponents can sit, nearly immobile, for minutes on end. Then they may intermittently explode in a frenzy of very intense activity. Blue-bellied Rollers can appear to be stolid, but there are occasional conspicuous exceptions.

VOCALIZATIONS.—The common calls of the species seem to be at least partly hostile. They can be practically or roughly divided, as a first step, into Rasps and Rattles.

Rasps are harsh, buzzy, nasal, often twanging. To human ears, a single Rasp sounds like a single note. The basic version might be transcribed by something like "Arnh." The length of the apparent notes varies. Most Rasps are short; others can be very long, often conspicuously fluctuating in pitch. Loudness also varies. Some notes are soft. Long versions are loud and screaming. Rasps sometimes are uttered as "single" notes. More often they occur in sequences, either in series of essentially similar patterns or variants thereof, or in medleys with Rattles.

The Rattles themselves are mechanical in sound. The basic version might be transcribed as "r-r-r-r-r-r-r. . .". Like Rasps, there are variations in length and loudness and the sounds can be repeated in series and in medleys.

These summaries are simplifications of complex acoustic phenomena. Each "Arnh" is a rapid series of pulses of sounds. The audible components of typical Rattles are less rapid pulses. There are series within series. There is intergradation between Rasps and Rattles. Intergradation may proceed by various routes. Many Rattles, perhaps most, seem to be produced by a slowing down of, an increase of intervals between, the pulses that would otherwise form single Rasps at a faster rate in different arrangements. Other Rattles may, conceivably, be accelerated, (multiple) series of abbreviated Rasps (Figures 7–15).

All these sounds are similar to vocalizations of other rollers of Africa and southern Asia, species of *Eurystomus* as well as *Coracias*. Many rollers share the harsh, rasping, buzzy, nasal tone. Other types in Madagascar may tend to whistle instead (Milon et al., 1973; L. Wilmé, O. Langrand, pers. comm.).

The Rasps and Rattles of the Blue-bellied Rollers of the Basse Casamance are uttered in many social situations. They are characteristic of disputes among neighbors and intruders, both intra- and interspecific. They are occasionally uttered as "greetings" or "landing calls" when one member of a pair or small (nuclear family) group rejoins its companion(s). Rasps and Rattles, usually one or the other, can also occur during copulations and pseudocopulations. The latter performances are extremely hostile in some sense or in some directions (see "Copulation and Pseudocopulation in the Basse Casamance"). Both sexes, at least the two members of apparent pairs, utter both Rasps and Rattles with some considerable (if not necessarily absolutely equal) frequencies.

The wide overlaps of circumstances in which Rasps and Rattles are uttered and the frequency of medleys, indicate that the relative strengths of the attack and escape tendencies cannot be very different in the two patterns. Both Rasps and Rattles appear to be low intensity, brief expressions of irritation during mild disturbances. Longer and louder versions of them during pseudocopulations and aerial displays must be of higher intensity. In my experience in the Basse Casamance, Rattles are slightly more common than Rasps during relatively low intensity encounters, while screaming Rasps are characteristic of aerial displays.

The arrangements of Rasps and Rattles in series and medleys are variable. There is little stereotypy of phrases. One possible exception is a Rattle–"Slur" or Rattle–"Creak," a conventional Rattle of short to medium length followed immediately by a descending sound, an expiring Rasp and/or a faint echo or extension of a (the) Rattle. Examples are shown in Figures 13–15. Sometimes patterns of this type appear to be used as advertisements without "partners" nearby at the moment. When and if so, they could be functional equivalents of "Song," not pretty or melodious, but still serving to attract individuals of the opposite sex and to repel other individuals of the same sex.

Song-like patterns are poorly developed in rollers of Africa and Asia. They are unlike passerine birds and some alcedinine

FIGURE 6.—More postures. *Top:* Bill-up or Stretch Postures of Abyssinian (left) and Indian (right) Rollers. These patterns are typical of most *Coracias* rollers. As it happens, they are very rare or absent from the signal repertories of Blue-bellied Rollers. *Bottom right:* An extremely aggressive Erect Posture of a male Blue-belly. *Bottom left:* A relaxed posture of a female Blue-belly.

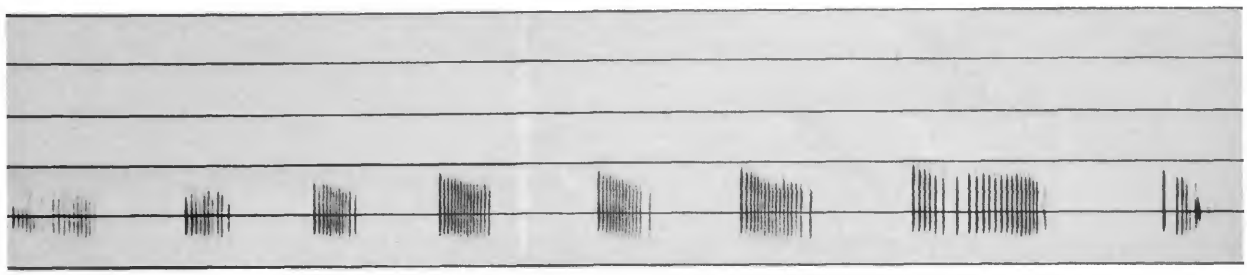


FIGURE 7.—Sonagram of a series of short, almost "conversational" Rasps. Time: ~2.5 seconds. In this and all the following sonagrams, the upper limit of the sounds shown is 8 kiloherz.

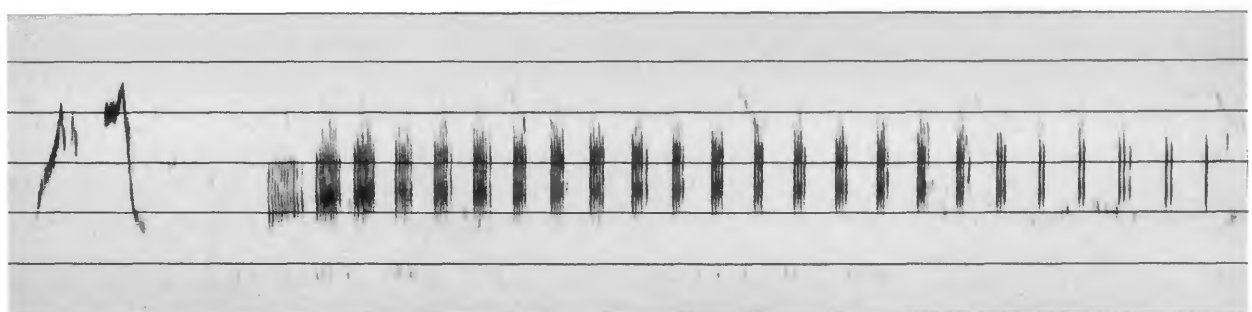


FIGURE 8.—Another series of short Rasps. Time: ~2.5 seconds.

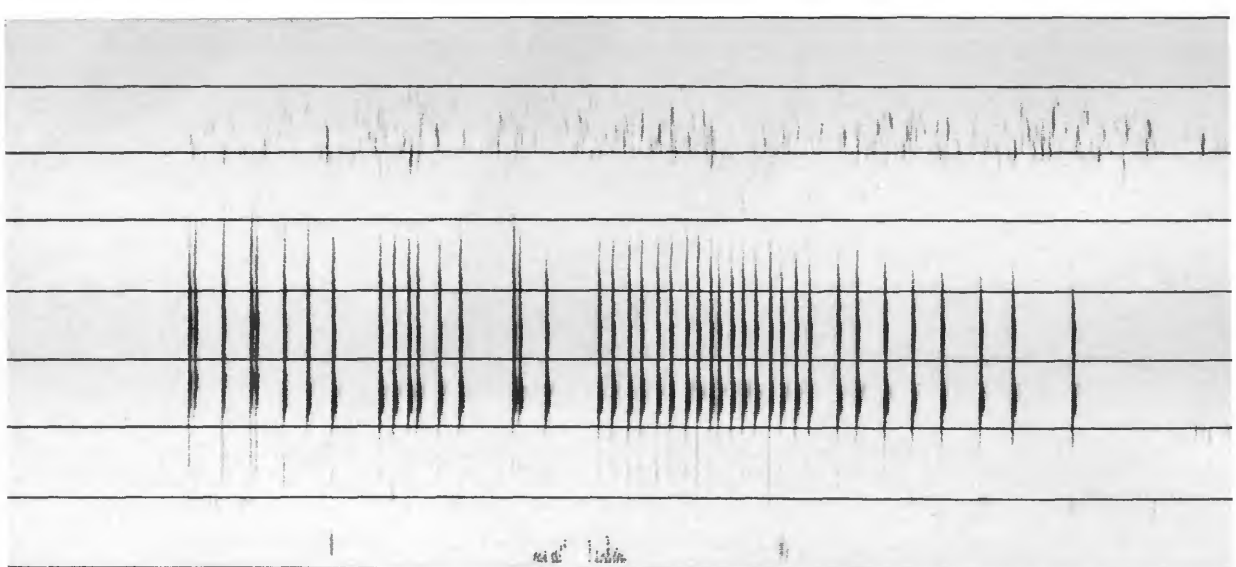


FIGURE 9.—A single (to human ear) long Rasp. Time: ~1.8 seconds.

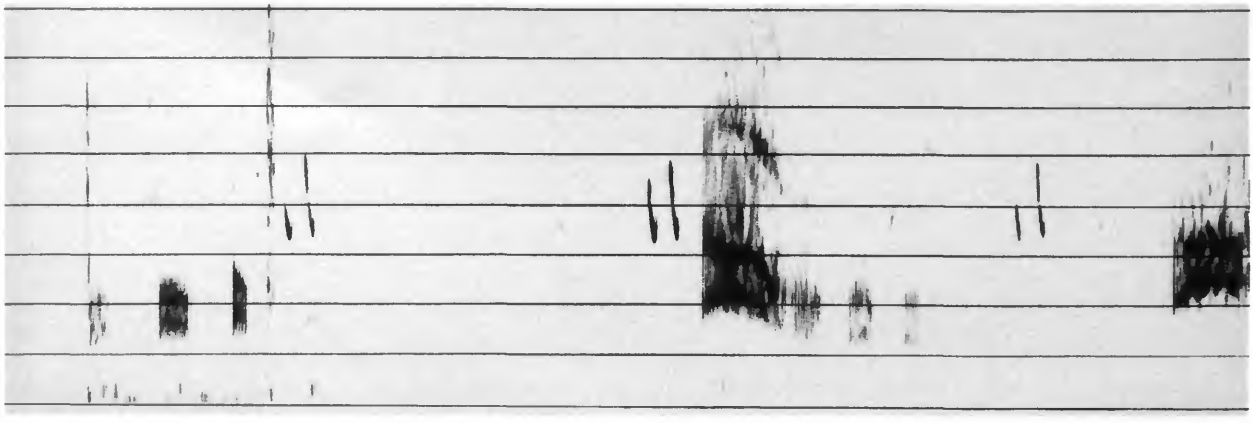


FIGURE 10.—Burst of short Rasps. These are the sorts of patterns which have been called "Chatters" in the cases of other species. Time: ~2.5 seconds.

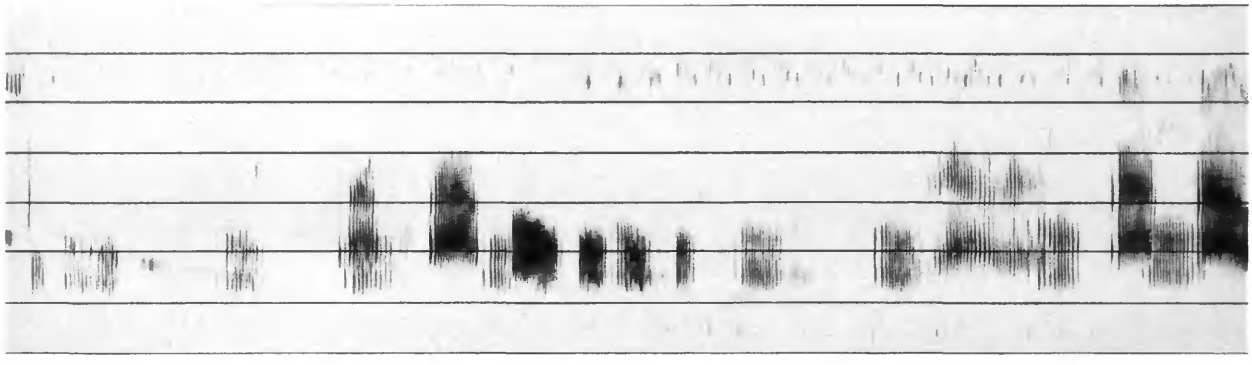


FIGURE 11.—Fluctuating "Chatters." Time: ~2.5 seconds.

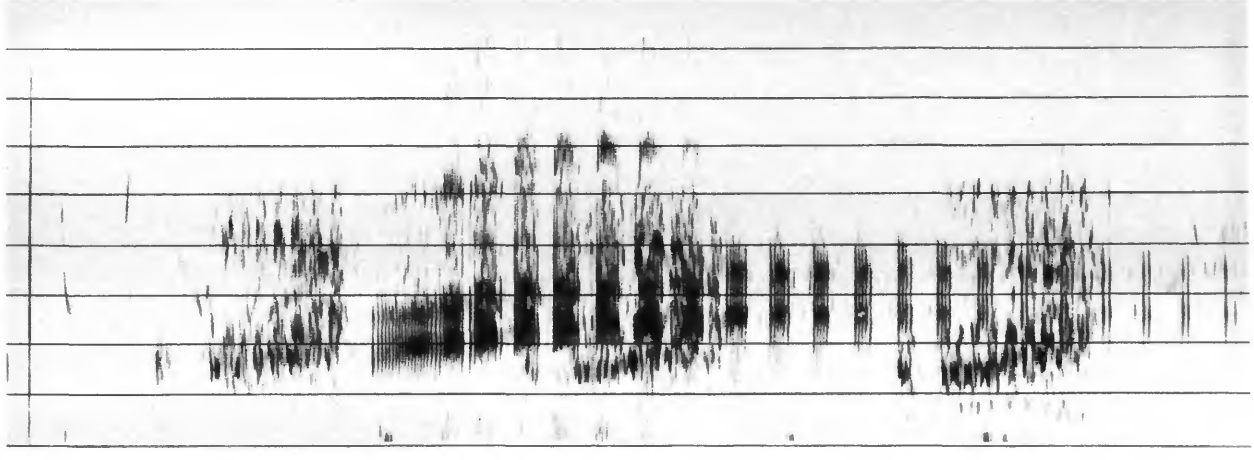


FIGURE 12.—Rattle. Time: ~2.5 seconds.

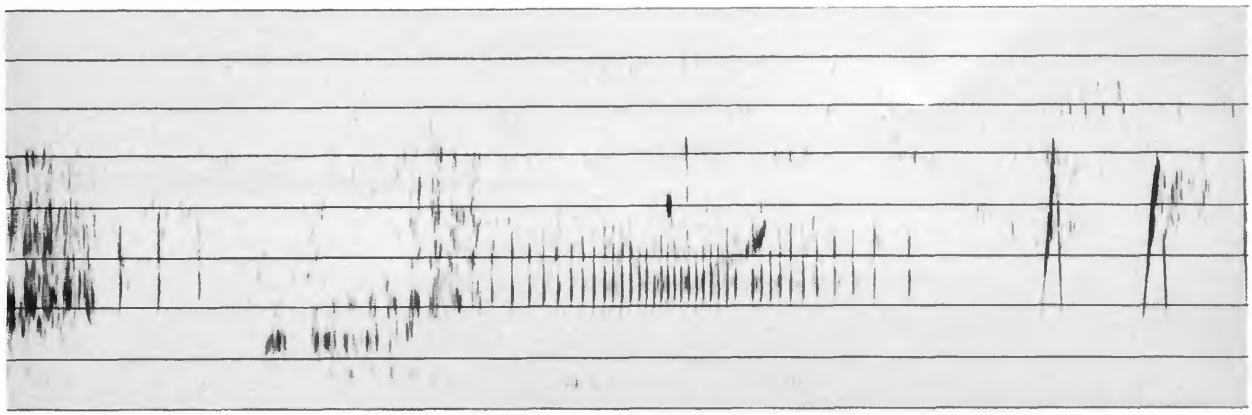


FIGURE 13.—End of Rattle shown in Figure 12, followed by Slur. Some passerine notes in background. Time: ~2.5 seconds.

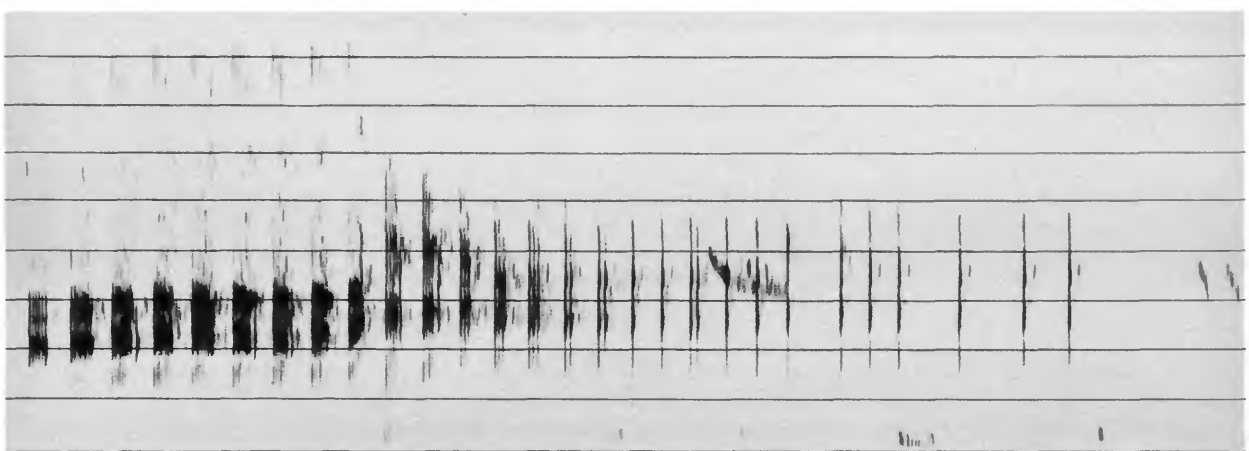


FIGURE 14.—A Rattle-"Creak." Again passerine notes in background. Time: ~2.5 seconds.

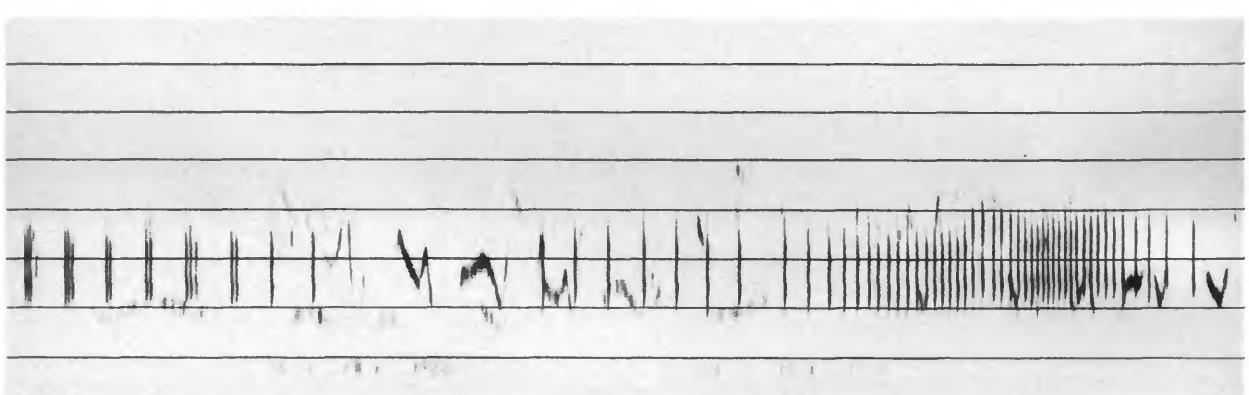


FIGURE 15.—Series of short Rasps, followed by a Slur. Time: ~2.5 seconds.

kingfishers in this respect. Besides the Blue-bellied Roller, I have observed the Abyssinian and Broad-billed Rollers and the Indian Roller (*Coracias benghalensis*) at length, and the Rufous-crowned Roller (*C. naevia*), the Blue-throated Roller (*Eurystomus gularis*), and the Dollar Bird (*E. orientalis*) for briefer periods. None of these species was noted to have as sequentially stereotyped, suggestively Song-like combinations as the Rattle-"Slur"s of the Blue-belly. Perhaps *C. cyanogaster* is developing a new arrangement of old elements expressly for the purpose of Song.

The elements certainly are old. The crude morphological difference between Rasps and Rattles, and the division of all or most of the vocal repertory between two formally distinct classes of patterns, with various temporal arrangements, has many parallels, not only in other rollers but also in other coraciiforms. The Giant Kingfisher of Africa (*Megaceryle maxima*) can be cited. The common vocalizations of the species are Yelps and Rattles (Moynihan, 1987b). Although the two sounds have different tonal qualities, different speeds and harmonics, an inspection of sonagrams would suggest that they may be strictly homologous with one another, variations on a single theme. They do not, however, intergrade with one another as frequently as do the Rasps and Rattles of Blue-bellied Rollers.

Perhaps the widespread distinction between Rattles and the "rest," i.e., apparently longer or more continuous notes, is a "primitive" feature in coraciiform birds, only being modified (probably slowly) in special cases (Davis, 1985).

This brings up a point of some general interest, a problem for students of animal communication. It would be nice if every signal had its own set of encoded messages without any fuzzy borders. Yet it is well known that signals change over time; they can grow or decay (Moynihan, 1970). At any given moment, something or other must be in transition. No system is ever entirely neat in the course of evolution (references in Moynihan, 1982:11, 12).

The vocalizations of Blue-bellied Rollers, simple as their basic elements may be, are flexible enough to permit modifications of the information encoded. Both Rasps and Rattles can be combined with many different postures and movements, in flight as well as when perched. Presumably each combination encodes slightly different information. The signal repertory of the species is not depauperate, even considering only the simple patterns. But there also are more elaborate performances.

AERIAL DISPLAYS.—These are pursuits and inhibited attacks with rises and falls, Soars and Swoops. A bird suddenly flies, either silently, Screaming, or Rattling. It chases or dashes at another individual. Before contact, the "attacker" Soars up, usually with set (dihedral) wings. In some cases, this seems to be another form of cut-off; the attacker simply turns away at the end of the Soar. In other cases, the attacker continues with a downward Swoop. Some Swoops are dramatic; the attacker plunges or plummets down with partly folded wings, only, again, breaking off and swerving away at the last moment. Some pursuits include repeated Soars and Swoops.

The aerial displays of Blue-bellied Rollers are less frequent and, even at their most dramatic, less spectacular than are those the lighter and more agile *C. abyssinica*.

I might add that none of the rollers that I watched was ever seen to perform an actual roll, a somersault, or complete turnover.

COPULATION AND PSEUDOCOPULATION IN THE BASSE CASAMANCE.—The copulatory movements of Blue-bellied Rollers are conventional in some aspects of form. One individual mounts onto the back of another. The upper bird may beat or wave its wings, apparently for balance. It may also lower its head and bill to seize the nape or crown feathers of the lower individual, probably to secure an even firmer balance. The lower individual usually raises its tail, between drooping wing-tips, and the upper bird lowers its tail. Sometimes, the cloacas of the two individuals are brought into contact and there is an opportunity for the sperm of one individual to be transferred to its partner. At other times, the raising and/or lowering movements are weak, incomplete, or interrupted.

Some copulatory patterns probably are effectively and immediately concerned with fertilization. I may have seen examples during the later part of my observations in 1977. Other performances of similar appearance almost certainly do not facilitate reproduction in the same way. They may be ancillary, auxiliary, or secondary. They probably are not directly concerned with fertilization. They may be instruments of competition among actual or potential rivals (of course not irrelevant to reproductive success or failure, but not exactly immediate at any given moment).

Counts and details should be useful. I saw, quite clearly, 73 instances of single or repeated "mountings" among members of at least 9 social units of Blue-bellied Rollers, including pairs and small-to-medium size groups. They were seen in many different areas of the Basse Casamance, one or more in every month of my field work in 1976, 1977, and 1985. All these mountings appeared to be copulations or attempted copulations. All conformed to the general schema outlined above; but appearances can be deceptive.

Of these apparently sexual interactions, 19 were simple in form. One individual mounted another, more often than not with the conventional wing and tail movements and seizure of nape feathers. Then the upper individual slid off; and there was nothing overtly sexual immediately (within 5 minutes) afterward.

The remaining 54 interactions were complex in form. They included "reversals." One individual mounted another, with or without wing and tail movements or seizure of nape feathers. Again, the upper individual slid off. But, in these cases, the originally mounted individual immediately mounted the originally mounting individual in turn. The reversal might or might not be accompanied by the usual accessory movements. Again, there was a (following) dismount: first A on B; then B on A. In

these cases, both the individuals involved played both male and female roles in rapid succession. I saw reversals in at least 7 social units, pairs, and small groups. The number of reversals per "bout" was varied. At one extreme, I noted 24–28 mounts with 12–14 reversals. At the other extreme, I saw several cases of only two mounts with one reversal.

These reversals indicate that at least one sex can play the role of the other. As it happens, in all the cases that I could see clearly, the two individuals involved in reversals appeared to be one male and one female. Again a size difference was visible.

Possibly some or all the reversals did not result in fertilization. I do not know if the sperm can move upward if a male is below a female. (Sperm do seem to move sideways in some woodpeckers—references in Short, 1982).

The important fact is that reversals occur during all or most of the year, while actual reproduction, the laying of eggs, and the rearing of young, is seasonal (Morel and Morel, 1982; Thiollay, 1985). Thus some of the sexually derived patterns seen outside the breeding season must be, in some sense, false, "fake," or "pseudo."

It should be stressed, however, that the actual movements of supposedly sexual copulatory patterns and presumably less immediately (or differently) effective pseudosexual reversal patterns can be identical in form. Tails and cloacas can go up or down in either circumstances, although not necessarily equally frequently (the recorded counts are too small to be conclusive).

The individuals observed to perform either simple and/or reversed copulations in the Basse Casamance seemed to do so with only one partner. Of course, there may have been occasional switches and exchanges which I missed; but I do not think that they could have been many or frequent.

The pseudosexual performances of the Blue-bellied Rollers of the Basse Casamance are evidently hostile. They are preceded and followed by all sorts of hostile displays, both visual and acoustic. They are particularly associated with aerial chases, Soars and Swoops, and screaming vocalizations.

One aspect of spatial and temporal arrangements is particularly suggestive. Although any given bout of reversals is performed by only two individuals, such behavior was never seen to occur when the performers were alone with one another. Bouts were always given in the vicinity of one or more other birds, not members of the performing pair. Apparently, it is the presence of the other(s) that stimulates the performance. Perhaps reversals are partly designed to influence the behavior of the other(s). Given the fact that the effect seems to be repellent rather than attractive, the complex of patterns could be said to function as threat. There may be other functions.

"SEXUAL" BEHAVIOR AT LAMTO IN THE IVORY COAST.—The Blue-bellied Rollers of Lamto, if not promiscuous, are at least accommodating and adventurous in their apparently sexual behavior. Thiollay (1985) says that up to three males may copulate successively, even two or three times, with the same female *"sans aucun comportement aggressif entre eux,"* and also that one male may copulate with two different females at an interval of 10 minutes.

This description of changes of partners must be accepted as correct for Lamto. An experienced observer, Thiollay is not likely to have made a mistake on such a matter. But there are some features of his account that are surprising to a visitor from Sénégal.

He does not mention any reversed mountings. It would be remarkable if reversals, fairly common in the Basse Casamance, did not also occur in the Ivory Coast, not very far away (by continental standards). One wonders if some of the supposed copulations of the Lamto birds were not really pseudocopulations. There is indirect support for this hypothesis. Thiollay (1985) says that, although successful reproduction is limited to the end of the dry season, the frequency of apparent copulations and of feedings of the female by the male (also supposedly sexual) are much the same throughout the year. It is possible, therefore, that movements of copulation or copulatory origin are used for effectively non-copulatory purposes at Lamto as well as in the Basse Casamance, even though the derived usage(s) may not be quite the same in the two regions.

THE MAINTENANCE OF PAIR BONDS.—For most of the year, mated Blue-bellied Rollers in the Basse Casamance maintain their relations with one another most frequently by joinings and re-joinings. Simple approaches and encounters occur and reoccur every day. They are several orders of magnitude more numerous than overtly sexual or pseudosexual performances. They also are more frequent than other patterns that might be (have been) expected to be relevant in the context. I did see instances of the feeding of one individual by another individual. Such performances were not common and they did not usually occur in revealing circumstances. With one or two exceptions, they were not the immediate preludes to copulations. The species seems to lack special "soliciting" patterns. At most, one individual might assume a hunched posture as another individual started to mount.

The poor development or absence of special soliciting displays is characteristic of many rollers and kingfishers, but perhaps not bee-eaters (Emlen and Wrege, 1986; Fry, 1984).

Interpretation and Discussion

What questions are raised by the preceding account?

COMPARISONS

Copulations with different partners are not a problem in theory. They are known to occur among individuals of different species in various circumstances for several different reasons.

Homosexual mountings are common in some animals such as macaques and baboons (see, for instance, references in Kummer, 1968; Imanishi and Altmann, 1970; Altmann and Altmann, 1970; Rowell, 1972; Fa, 1984).

Reversed mountings, perhaps even reversed copulations, have been recorded in such diverse groups as domestic pigeons (Craig, 1911; Whitman, 1919), European Cormorants (Kort-

landt, 1940) and grebes (Storer, 1969).

What is unusual, but not unique (see below), in the Blue-bellied Rollers of the Basse Casamance is a particular combination of form (unmistakably sexually derived tail movements, with possible cloacal contacts) and frequency, regularity of performances in non-sexual situations. It is this combination that needs to be explained. As evolutionary biologists, we should assume that the behavior is functional and advantageous. But how or why? To attempt to answer these questions, even tentatively, one must compare different kinds of data.

One set of data is almost parenthetical. Cormorants, grebes, the wild ancestors of domestic pigeons, and Blue-bellied Rollers are sexually monomorphic in plumage, if slightly dimorphic in size and weight. Appearances cannot be irrelevant to social behavior; but they do not seem to be a sufficient explanation of reversals. None of the other rollers or bee-eaters have been seen or recorded to perform pseudosexual behavior, even though they also are sexually monomorphic in plumage. (Much the same can be said of *Halcyon* and many dacelonine kingfishers). There must be special factors at work among Blue-bellied Rollers.

They can hardly be concerned with identification of sex as has been suggested or implied for other forms. Pair bonds seem to be so long-sustained in Blue-bellied Rollers that problems of sexual identification can occur only rarely, much less frequently than do reverse mountings. The bonds also are so strong that they probably do not need to be reinforced in this peculiar and energetically expensive way. (If it occurs at all, reinforcement may be only a "by product.")

There were no indications that the pseudosexual performances of the species are "rape" attempts at forced or stolen copulations by either one or both partners. The nature of the relations between the individuals involved, at least in the Basse Casamance, would seem to make such attempts unnecessary if not socially dangerous and counterproductive.

What is left then? I would like to suggest that the reversals, pseudocopulations of Blue-bellied Rollers, have the *principal function of "canalizing" aggression, not only between or among the members of a mated pair or nuclear family, but between pairs and families, on the one hand, and their neighbors or intruders on the other hand.* It is easy to imagine why Blue-bellied Rollers might need to have more outlets for aggression, or to use them more frequently, than do other coraciiforms. One can also imagine why they might need to use particularly "strong" outlets. The ecology and correlated spatial arrangements are pertinent. The argument is as follows.

Individuals, pairs, and small families of other species of rollers usually are widely and evenly dispersed throughout suitable habitats. There are, of course, adventitious feeding flocks among Abyssinian and Broad-billed Rollers (Moynihan, 1978, 1988). They may include numerous individuals (larger aggregations than nuclear or even extended families) but these groupings are transitory and are immediate and temporary responses to sudden flushes of prey. They are not quite the same as the large groups of Blue-bellied Rollers, which are more coherent and more frequently recurrent, and which are not immediate responses to flushes. Doubtless, groups of Blue-bellied Rollers are as concerned with feeding and the availability of prey as are groups of Abyssinian or Broad-billed Rollers; but the concern is of a different kind and on a different time scale. Blue-bellied Rollers seem to be basically more gregarious, potentially more capable of becoming gregarious, than their closest relatives. They maintain more social relations more consistently or recurrently.

The two most distinctive features of the social behavior of the species, increased gregariousness and the performance of frequent pseudocopulations, are correlated in time and space. It is tempting to suggest, therefore, that they are causally related to one another. They do not, however, seem to be related simply. Sexual identification does not need to be considered further. Reinforcement of pair bonds probably can be discounted as a major impetus. The principal function of the pseudosexual performances of Blue-bellied Rollers must be something else. They seem to be less concerned with bonds than with repelling approaches or transgressions. They are "meant" to be hostile rather than friendly.

Blue-bellied Rollers are more often clumped in space than are their close relatives. This can only, I think, be explained by historical factors. Historical explanations are usually to be distrusted in discussions of ecology and ethology. One should always try to tie present phenomena to present conditions. Yet there are occasional discrepancies or *décalages*. Blue-bellied Rollers would seem to provide a plausible example.

Even if individuals of the species could "afford" to be dispersed at the present time, they must have been less free a few thousand years ago before the development of agriculture, when patches of bare ground and low sparse vegetation were relatively rare and scattered. The Blue-bellied Rollers of that time were confronted with a dilemma. Nesting sites and other resources provided by tall trees must have been abundant, while clearings, prime feeding sites, must have been in short supply. In the circumstances, there probably was selection pressure upon the birds to cluster around the feeding areas and to make the best of a bad job, to allocate or to appropriate the available food as efficiently as possible with a minimum of physical combat. Again, it should be remembered that Blue-bellied Rollers are too powerful to be able to fight safely.

Since individuals must remain irritable and aggressive for competitive purposes, the avoidance of contact fights is difficult. At least, it has to be managed carefully. For some reason, perhaps a consequence of past history, the original coraciiform heritage, Blue-bellied Rollers have not evolved a system of repulsion by vocalizations alone. Nor have they developed anything very much in the way of special appeasement patterns. (Many birds of other groups use an extension of infantile food-begging for appeasement. Nestling coraciiforms, confined to dark holes, have relatively simple

begging behavior, only one or a few calls without elaborate postures or movements.)

The pseudocopulations of Blue-bellied Rollers may function as threat. At the same time, they also seem to control aggression and the dangerous consequences of overt fighting.

The initial stages of this system of dual functions must have been difficult. Even mated males and females show hostility toward one another. It is remarkable that they could have come to tolerate close contacts, patterns of sexual origin, in the absence of real and strong copulatory motivation. Yet they have done so. Why? Why this, rather than some other thing? And why *C. cyanogaster* and not related species?

Pseudocopulations as both a manifestation and control of hostility offer certain advantages. They are conspicuous enough to be effective as displays. The reciprocal attention between the performers may decrease the probability, the time available, for actual attacks upon opponents. Above all, they are demonstrations of both possession and capability. Any individual that performs a pseudocopulation is showing to the onlooking world that it has a willing and acquiescent partner. Crowded as they are or were, Blue-bellied Rollers might find (or have found) it advantageous to make frequent demonstrations.

There is a partial analogue, involving different patterns, among other coraciiforms. Males of some dacelonine kingfishers; *Halcyon smyrnensis* and the Guamanian race of *H. cinnamomina* among the forms that I have observed, go through elaborate "showing of a nest hole" behavior toward actual or potential mates at the beginning of the breeding season. This demonstrates the possession of a vital breeding resource, a nest site. Usually, the demonstration seems to be solely designed to impress a female; but there is no obvious reason why it might not also discourage male rivals in the neighborhood.

There are several factors in play. (1) Blue-bellied Rollers, like other *Coracias* species and most kingfishers, are predators upon relatively large prey that cannot easily be shared (2) In correlation with their particular predatory habits, all *Coracias* rollers have evolved large, powerful bills and irritable, aggressive temperaments. (3) Their bills, their principal offensive and defensive weapons, are powerful enough to make fighting dangerous. (4) Most rollers have adapted by evolving dispersed social structures. (5) This option was not open to Blue-bellied Rollers to the same extent. They prefer to feed on or near the ground in humid habitats. A few thousands of years ago, before the spread of human agriculture, such habitats must have been largely forested, with only occasional patches of bare ground in clearings, treefalls, landslides, etc. (6) In order to take advantage of clearings, Blue-bellied Rollers must have had to gather or cluster around relatively few sites. For rollers, they must have been crowded. (7) Presumably as a result, they have become slightly more gregarious than most of their relatives. (8) They have not, however, become very much less aggressive. Presumably their methods of feeding do not allow cooperation. (9) The need for gathering around sites must have put a severe strain upon aggressive temperaments. (10) Blue-bellied Rollers have had to find a way out of an apparent impasse. Different pairs and family groups must manage to live "together" without becoming unduly "friendly." (11) They have developed special signals to permit coexistence in these circumstances. (12) As it happens, the signals have taken the form of pseudosexual reversed copulations. (13) These performances have special advantages. Most notably, they can serve as threat without precipitating face-to-face (or bill-to-bill) contact fighting.

This argument implies that the peculiarities of the social behavior of Blue-bellied Rollers, at least in the Basse Casamance, were evolved as adaptations to past conditions, and that they have not changed promptly as environmental circumstances have been transformed by human activities during the last few hundreds or thousands of years. Complex social systems among animals such as birds cannot always keep completely up to date.

More comparisons can be added. Some refer to other coraciiforms and to certain woodpeckers of the order Piciformes. Among the coraciiforms, two types are particularly interesting for comparison with Blue-bellied Rollers.

Many species of bee-eaters of the genus *Merops* are gregarious, nesting in colonies and scattering in "clans" (Fry, 1984; Emlen and Wrege, 1986). At the same time, they are, remain, rather aggressive and often squabble among themselves. (It may be a general rule, among colonial birds, that gregariousness tends to increase disproportionately more than hostility decreases. Breeding colonies of gulls and terns exhibit such behavior.) Some individuals of several species of gregarious bee-eaters attempt copulations with individuals other than their usual mates. In the case of the White-fronted Bee-eater, *M. bullockoides*, these attempts seem to be forced copulations by males upon females (Emlen and Wrege, 1986).

Some of the social stresses in groups of bee-eaters cannot be very different from those in groups of Blue-bellied Rollers. Yet, as briefly noted above, reversals have never been recorded in bee-eaters. (Several species have been studied at length and in detail.) One might speculate on why reversals are absent. Bee-eaters are different from rollers in morphology and ecology. They feed upon smaller items of prey (hymenoptera and diptera, perhaps other small insects). Typical bee-eaters have, therefore, less powerful bills and, therefore again, less dangerous weapons than do rollers. Most bee-eaters usually catch their prey in the air (they are, of course, "flycatchers" in the generic sense). Their prey often occur in swarms. Swarms can be shared. The catching of small flying prey often entails a great deal of aerial maneuvering. Bee-eaters of the genus *Merops* are highly mobile. They often follow high energy strategies. As a result of this mix of features and adaptations, individuals of the known species of *Merops* are seldom pressed into the long, slow, tense, deceptively stolid confrontations that are so characteristic of *Coracias cyanogaster*. Apparently, the

bee-eaters can organize their social relations by simpler and more conventional, if more expensive, means than can the rollers.

Pied Kingfishers have even more powerful bills. These birds, for some reason (not self evident) tend to occur in groups or clusters in some places and at some times. Males often outnumber females. In the Basse Casamance, "supernumerary" males can be bonded to one another and/or establish dominance relations by homosexual copulation attempts (pers. obs.). I did not see reversals among Pied Kingfishers, but individuals of the species are hyperactive, frequently moving from place to place, and occasional reversals might be difficult to detect in unmarked populations.

Woodpeckers share several features of habitus with some coraciiforms. Many species have powerful bills, use trees when available, and nest in holes. There is some sexual dimorphism in plumage, usually in colors around the head; but the differences in appearance between males and females are often not very great. Most of the larger species occur in pairs and small family groups. They tend to be aggressive and highly territorial. A few species are more sociable. Gregariousness is carried to an extreme in Acorn Woodpeckers, *Melanerpes formicivorus*. The known agonistic, sexual, and pseudosexual behavior of woodpeckers is well summarized by Short (1982). There are several kinds of interferences and extrapolations.

A detailed account of a single species or population, the Acorn Woodpeckers of central California, is provided by MacRoberts and MacRoberts (1976). The authors can be quoted directly: "Mounting occurs before the birds retire to their roosts" and "may involve any group member mounting any other. Males mount females and other males; females mount males and other females.... Mounting is very brief and does not involve cloacal contact or special movements of the tail." Obviously, the behavior cannot be firmly established as sexually derived. Still, the mere fact of mounting is suggestive. Other patterns of other woodpeckers would appear to be of unequivably sexual origin. They are not, therefore, easy to interpret.

Kilham (1961), describing the behavior of Red-bellied Woodpeckers, *Melanerpes c. carolinus*, says that females mount males before true copulations. Apparently they do so only once during each interaction. Given the circumstances, the true copulations might be considered to be reversals, although they are skewed sideways (see above) or sometimes even upside down. There are brief published references to single reverse mountings in Black-cheeked Woodpeckers, *Melanerpes pucherani* (Eisenmann, in litt., cited by Short, 1982) and Lesser Flame-bodied Woodpeckers, *Dinopium benghalense* (Neelakantan, 1962). In this last instance, the movements were definitely copulatory but the two individuals involved were males. It should be mentioned that "false" copulations, apparently without reversals, have been seen to be performed by Red-cockaded Woodpeckers, *Picoides borealis*, and Hairy Woodpeckers, *P. villosus*, well outside the breeding season (Short, 1982; Kilham, 1966). These patterns probably do help to reinforce bonds.

The orders Coraciiformes and Piciformes have been supposed to be related phylogenetically (the early literature is summarized in Sibley and Ahlquist, 1972). Yet the two lineages have been distinct from the early Tertiary (Feduccia, 1980). Some species in both lineages have mixed agonistic and sexually derived patterns. The mixes have been achieved in different ways, apparently for different purposes. Hence, they are not directly homologous. The use of behavior patterns of copulatory origins in a variety of social situations would seem to be a recurrent tendency in both coraciiforms and piciforms. This may be because the birds have little other material to work with.

The use of patterns of hostile origin in basically friendly or sexual situations (e.g., the human smile) is well known in many kinds of animals. Transferences in the opposite direction are comparatively, perhaps not actually, rare. Blue-bellied Rollers have transferred in a particularly elaborate way.

The Hammerkop

Among the conspicuous sights of the African countryside are individuals of the stork-like "Hammerkop." The vernacular name comes from Afrikaans. The scientific name is *Scopus umbretta*. These birds are large predators, mostly upon aquatic prey. They have large and powerful bills (hammers indeed). They have been studied by many ornithologists. A list of relevant publications is given in Brown et al. (1982). I have also seen a graphic film by Joan and Alan Root. Hammerkops certainly are not closely related to Blue-bellied Rollers phylogenetically. Equally certainly, they have evolved similar behavior patterns.

Individuals are found singly, in pairs, or small, apparently nuclear family groups, although larger assemblages have been recorded on occasion. Individuals and pairs usually are territorial except when attracted to particularly rich food sources.

Multiple reverse mountings are characteristic of the species. They are described by many observers in almost identical terms, i.e., upside down and right side up. Unfortunately, there is a slight degree of imprecision. Up and down tail movements do occur in the courses of some reverse mountings. Whether or not cloacal contacts might occur is still unclear. The problem may not be significant in terms of general social rather than specifically sexual relations.

It is entirely clear, on the other hand, that reverse mountings are hostile responses to the appearance or approaches of potential rivals or competitors. They are never performed between the members of a pair when there are no other Hammerkops in the immediate neighborhood.

Why in the world should Hammerkops be so similar to Blue-bellied Rollers? Part of the answer, again, may be the distribution of resources. Access to food can hardly fail to be

relevant. In the case of Hammerkops, however, there may be another factor to be considered. Individuals of the species build enormous nests. They often spend enormous amounts of energy and long expanses of time (six weeks or more) in order to do so. Why are nests so important in their lives is a difficult question to answer. They build more and larger nests than they need simply to protect their own eggs and young during a single breeding season. Perhaps the huge accumulations of nesting materials serve several purposes. The masses could be deceptive, even decoys. They are visually conspicuous. Most of them are used sooner of later by other animals including barn owls, falcons, Egyptian Geese, small mammals, monitor lizards, and snakes. Is this the point of the whole operation?

Whatever the point, any construction of the size of a Hammerkop nest must be considered to be a scarce resource. How many weeks or months can a bird afford to carry twigs back and forth? The animals may not be crowded but they are concentrated upon a limited number of foci.

CONCLUSIONS

Scarce resources should be protected. The process may be complicated. Various elaborations can be used. Blue-bellied Rollers and perhaps some other species have used derivatives of sexual behavior.

RÉSUMÉ

Les Rolliers à Ventre Bleu (*Coracias cyanogaster*) vivent en Afrique occidentale. Elles sont des *Coracias* typiques puisque elles s'assoient et attendent pour piller ou chasser. Elles s'abattent sur des proies relativement grandes (arthropodes et vertébrés) sur terre nue ou de végétation basse et clairsemée. Elles diffèrent de leurs parents les plus prochains, les autres éspèces du même genre, parceque elles préfèrent des habitats humides ou demi-humides. En Afrique occidentale tels habitats sont naturellement boisés. Souvent, les Rolliers à Ventre Bleu, perchent haut sur les arbres. Mais elles préfèrent se jetter bas. Cela signifie, effectivement, que en certains temps, elles doivent avoir dépendues des clairières. Probablement, les parcelles de terre nue avec végétation basse et claisemées étaient rares et peu répandues avant la diffusion de l'agriculture. Dans ces premières circomstances, les Rolliers à Ventre Bleu, auront dû se concentrer sur tout terrain ouvert disponible. Probablement elles se trouvaient plus entassées que d'autres éspèces de Rolliers.

Toutes les *Coracias* sont grandes, puissantes, et agressives. En conséquence, la concentration et l'entassement doivent avoir étés difficiles de conduire ou soutenir. Les ancêtres des modernes Rolliérs à Ventre Bleu semblent avoir développés certains mécanismes de conduite pour faire face à leurs problèmes. On suppose qu'elles sont devenues plus (fréquemment ou régulièrement) grégaires que leurs parents. Dans la région de Basse Casamance du Sénégal et peut-etre des autres terrains, elles ont aussi développées l'habitude, unique entre les Rolliers, d'éxécuter des pseudocopulations, montages renversés, parfois avec contact cloacal parfois à plusieurs reprises. Les patrons dérivés du comportement sexuel sont capables potentiellement d'etre usés pour controler des rencontres agonistiques indépendamment du sexe actuel. Ils semblent le faire de 2 manières. Ils peuvent fonctioner comme menace. Mais aussi ils canalisent l'agression pour minimiser les risques du combat physique avec leurs voisins et intrus.

Les adaptations aux conditions boisées ont survécues alors même que les terrains ont étés éclairés pendant des centaines ou peut-etre des milliers d'années.

RESUMEN

Las Carracas de Vientre Añil (*Coracias cyanogaster*) habitan el oeste de Africa. Son típicas del género *Coracias* en cuanto a ser depredadores que acechan y esperan. Asaltan presas relativamente grandes (artrópodos y vertebrados) en vegetación baja y dispersa, o sobre suelos relativamente descubiertos. Se diferencian de sus parientes más cercanos, otras especies del mismo género, prefiriendo habitats húmedos o semi-húmedos. En el oeste de Africa, estos habitats son por naturaleza boscosos. Las Carracas de Vientre Añil se emperchan frecuentemente en las partes altas de los árboles. Sin embargo, suelen zarpar por lo bajo. Esto significa, en efecto, que debieron alguna vez depender de claros en los montes. Parcelas de tierra pelada y de vegetación dispersa probablemente escaseaban antes de extenderse la agricultura. Bajo estas circunstancias, las Carracas de Vientre Añil debieron haber tenido que concentrarse sobre cualquier espacio abierto que pudieran encontrar. Probablemente se encontraban más apiñadas que otras especies de Carracas.

Todas las especies de *Coracias* son grandes, poderosas, y agresivas. De modo que la concentración y falta de espacio deben haber sido difíciles de manejar o soportar. Los antepasados de las Carracas de Vientre Añil parecen haber evolucionado mecanismos de comportamiento para contrarrestar este problema. Se supone que se volvieron (más frecuentemente o regularmente) gregarios que sus parientes. En la región de Basse Casamance en Sénégal y quizás en otras áreas también desarrollaron el comportamiento, único entre *Coracias*, de practicar seudo-copulaciones, montajes invertidos, algunas veces con contacto entre cloacas, algunas veces repetidamente. Los patrones sexuales derivados tienen la capacidad potencial de ser usados para controlar encuentros agonísticos (hostiles) sin consideración a la reproducción efectiva. Pueden realizarlo en dos maneras. Pueden funcionar como amenaza. También pueden canalizar la agresión para minimizar los riesgos de pugna física con vecinos e intrusos.

Aparentemente, la adaptación a condiciones selváticas ha sobrevivido a pesar de que gran parte de la tierra ha sido desmontada durante siglos de años o quizás milenios.

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