

A REVIEW OF DUETTING, SOCIALITY AND SPECIATION IN SOME AFRICAN BARBETS (CAPITONIDAE)

LESTER L. SHORT

AND

JENNIFER F. M. HORNE

ABSTRACT.—Our East African studies have focused on the sociality, duetting and intra- and interspecific systematics of barbets (Capitonidae). The Afrotropical barbets include 14 duetting, social species and 22 non-duetters, both social and non-social. In this review of them, comparisons are broadly conducted, but centered about the ground barbets (*Trachyphonus*) and some species of *Lybius*.

The sexually dichromatic Red and Yellow Barbet (*T. erythrocephalus*) occurs in pairs and in social groups; duetting is by the pair, or mainly by the primary pair of a group. Within groups, secondary adults and young may join in part of the duet but their roles are limited by the dominance of the primary pair. The sexual songs are not very different. Subspecies of *erythrocephalus* differ little morphologically except in color tone and size. Darnaud's Barbet (*T. darnaudii*) is sexually monomorphic with races morphologically somewhat divergent. Sexual duetting roles are distinctive, and in groups the primary pair actively prevents duetting of secondary adults or young birds. Removal of a duetter leads to instant replacement from within the group, another bird assuming the duet role of the lost bird. In the Red-faced Barbet (*Lybius rubrifacies*), the Black-collared Barbet (*L. torquatus*) and the Black-billed Barbet (*L. guifsobalito*) the sexes are alike, pairs and social groups occur, and duetting is by the primary pair, with distinct sexual duet roles, following a greeting ceremony in which other individuals may take part. Secondary "pairs" occur in some groups; these may duet when apart from the primary pair, but not in the presence of the latter. Allopatric *torquatus* and *guifsobalito* show no or modest geographic variation and have similar though distinctive duets. *Lybius rubrifacies* shows no morphological geographic variation, and marginally overlaps *torquatus*; its duet markedly differs from that of *torquatus*.

The duet songs, whatever the degree of genetic control, are species-specific. Only paired duetting birds hold territories. Systematic comparison and studies of sociality and duetting in Afrotropical barbets suggest that the nature of their social systems and their duets, where these exist, has affected their speciation, and vice versa.

Duet-singing in birds can be intricately timed and complex (Thorpe 1972, 1973). Duets are usually between paired birds and may be precisely alternating (antiphonal), or in unison (polyphonic). Unison-singing may simply be the simultaneous singing of two birds at their own individual rhythms with overlapping songs, or more precise singing together in a coordinating rhythm. Additionally, the songs of the duetters may be identical, they may differ somewhat, or may be strikingly different. These categories of duetting are modified here from those of Thorpe (1973).

Although the relative importance of the different functions of duetting is arguable (Wickler 1976), the complexity and coordination of many duets clearly shows close interplay between the duetters. Studies of the development of duets in young barbets also indicate the complex nature of duets. Such works suggest

the genetic bases and experiential background that go into precisely timed duetting songs (Tyroller 1974). It seems logical that the evolution of species in avian groups that are social and regularly duet has been affected by their sociality and duetting habits. More particularly, the ability of individuals of one population to duet appropriately—and hence to pair with individuals of another population—ought to be of importance in relation to speciation. Generalizations must be tempered, however, by the fact that each avian species has its own unique distribution, ecology, history, and particular relations with congeneric, distantly related, and even unrelated sympatric species.

We have studied various Afrotropical barbets in the field, devoting attention especially to their sociality, vocal habits and related behavior. Barbets generally are aggressive, omnivorous or frugivorous, hole-nesting and hole-

TABLE 1. Duetting features of barbets.

Species	Pre-duet greeting ceremony	Post-duet greeting ceremony	Partner's notes differ	Simultaneous singing	Synchronized duetting
<i>Stactolaema olivacea</i>	0*	0	pitch	mainly	occasionally
<i>Lybius melanopterus</i>	0	0	0	0	0
<i>Lybius leucocephalus</i>	(+)	0	0	+	(0)
<i>Lybius vieilloti</i>	+	0	pitch	+	0
<i>Lybius rubrifacies</i>	+	+	+++	0	+
<i>Lybius torquatus</i>	+	0	++	0	+
<i>Lybius guifsobalito</i>	+	0	++	0	+
<i>Trachyphonus margaritatus</i>	+	0	+	0	+
<i>Trachyphonus erythrocephalus</i>	+	0	+	0	+
<i>Trachyphonus darnaudii</i>	+	0	+++	0	+

* 0 indicates absence, + presence; in the third column the pluses indicate the degree of difference in form (+, some difference, to +++, very marked difference). Parentheses mean that the data are not conclusive or certain for all subspecies.

roosting, sedentary piciform birds. The species we have investigated in some detail that form the subject of this article are: the Green Barbet (*Stactolaema olivacea*, Short and Horne 1980b); the White-headed Barbet (*Lybius leucocephalus*, two subspecies; unpubl. data); the Black-billed Barbet (*L. guifsobalito*; unpubl. data); the Black-collared Barbet (*L. torquatus*; Short and Horne 1982); the Red and Yellow Barbet (*Trachyphonus erythrocephalus*; Short and Horne 1980a, in press); and Darnaud's Barbet (*T. darnaudii*, three subspecies; Short and Horne 1980a, in press). Fewer details are available from our less extensive (Short and Horne, unpubl. data) studies of the Brown-breasted Barbet (*L. melanopterus*), the Yellow-billed Barbet (*T. purpuratus*) and the Crested Barbet (*T. vaillantii*). We also have been supplied by C. Chappuis with tape recordings of duets of the Vieillot's Barbet (*L. vieilloti*; Payne and Skinner 1970), and the Yellow-breasted Barbet (*T. margaritatus*; Short and Horne, unpubl. data). The duetting features of these barbets are summarized in Table 1. Our field researches mainly have been in Kenya for several months of each of the years 1976–1982; the Red-faced Barbet (*L. rubrifacies*) was investigated in Rwanda during January 1982.

Ecological, distributional, morphological, social and vocal information on the African barbets mentioned above forms a background for consideration of the interrelationship among their sociality, form and complexity of singing, and evolution, particularly speciation. In this paper we treat *Lybius* and *Trachyphonus* in special detail, as their species are widespread and vary interspecifically and intraspecifically in the parameters just noted. The ecology and sociality of duetting and non-duetting barbets are compared. Within this framework we explore the possible effects of speciation on the occurrence and complexity of duetting in the African barbets.

Tape recordings were made by Horne using a Stellavox SP-7 recorder, 72-cm parabolic reflector, and Schoeps CMC-45 microphone, with playback conducted by Short using a Sony cassette recorder. Audiospectrographic analysis involved use of a Kay Elemetrics SonaGraph 6061B to produce about 2,500 sonograms of voices of the barbets discussed. The various analyses took place in the American Museum of Natural History.

DUET FUNCTION, SEASONALITY, AND THE DUETTERS

Duetting barbets are sedentary and they clearly employ the duet in territorial defense and maintenance. At a distance, only the loud notes of the duet can be heard, and thus they can be effective in those functions. Only at ranges up to 20 or 30 m are the pre- and post-duet notes and the softer duet notes audible to humans, and presumably to the duetters themselves and to any members of their group closely associated with them. This suggests that these softer notes function in pair relations and pair maintenance.

Duets are uttered to some extent the year-round, although less frequently when the birds are not breeding. Duetters, as well as other members of a barbet group, even including subadults, have enlarged gonads all year (gonads over 2.5 mm in diameter, pers. observ.). Individual barbets of duetting species do not sing alone; when one bird rarely does so under exceptional circumstances, it sings only its particular duet song, and that haltingly. Thus, the singing of these barbets is virtually entirely in the form of duets, and in most species these are uttered only by the primary pair. Darnaud's Barbets who are members of a group other than the duetting pair are prevented by aggressive actions of that pair from duetting (Short and Horne 1980a). In groups of *Lybius rubrifacies* and *L. torquatus*, sub-pairs (pairs other than the primary pair) occasionally duet.

However, they do so only in the absence of the primary pair, which if within hearing, usually approach the sub-pair, causing them to cease duetting. Single barbets in the wild do not utter both duet parts. The duets sung by the pair are crucial for the establishment and holding of a territory. Hence, a barbet is likely to maintain a territory, and to breed, only if it finds a duet partner of the opposite sex and the two manage to synchronize their duet.

The non-duetting members of a group are exposed to frequent duets of the primary pair, and to some extent to those of distantly duetting adjacent pairs. This exposure may influence the form of duet song and the ability to pair with a duet partner later in life. As a pair duet, they may be surrounded by the often conspicuous, associated birds of a group (the duetters' presence stressed, in the cases of *Trachyphonus margaritatus* and *T. erythrocephalus*, by loud rattling calls of incoming group members who may actually join in singing part of the duet). The group may reinforce the duetters' ability to hold or add to the size of a territory. Our meager data suggest that groups, and especially larger groups, of barbets occupy and maintain larger, ecologically more favorable territories than do pairs.

In our barbet studies we frequently used playback techniques, despite their problems (different seasonal schedules of birds tested, duplication of social situation, etc.). We have encountered diverse responses to playback, which can be categorized hierarchically as follows: many barbets and woodpeckers call, sing, or even, after some time, duet as a response to playback of calls or duets of unrelated or distantly related species. Part of these "weak" responses may be due to the quality and general resemblance of their voices, but part also is likely to relate to competition for nesting and roosting cavities. Thus, playback of several duets of *Lybius guifsobalito* might elicit a "nyah" call or two from a Spotted-flanked Barbet (*Tricholaema lachrymosa*) and duets played back of *Trachyphonus erythrocephalus* sometimes got such a response from the African Black-throated Barbet (*Tricholaema melanocephala*). Also, the calls of Cardinal Woodpeckers (*Dendropicos fuscescens*) often evoked a response by *T. melanocephala*, and the loud, ringing calls (songs) of the Nubian Woodpecker (*Campethera nubica*) might stimulate *Trachyphonus erythrocephalus* to duet (Short 1982). None of these responses involve more than a vocal utterance; the respondent usually does not approach the caller unless the latter is near its roosting or nesting cavity. At a somewhat different level, as discussed below, interspecifically territorial duetters may show a

"moderate" response, reacting either to playback or to actual duets of a related duetting species by some approaching and mainly counter-duetting (see *Lybius rubrifacies* and *L. torquatus*, below). So far in our researches, however, very close, instant and consistent approaches to a playback duet (i.e., a "strong" response), followed by search behavior and counter-duetting mark only conspecific interactions. For example, this occurs among subspecies of *Trachyphonus darnaudii* (see below). Red-fronted (*Pogoniulus pusillus*) and Yellow-fronted (*P. chrysoconus*) tinkerbirds also react in this manner to playback of each other's two main calls, (not duets or songs as such). In fact, we regularly used the calls of the allopatric tinkerbird to elicit immediate, aggressive responses within the range of its counterpart. Although these reactions are indistinguishable from those of conspecifics, we do not consider the specific status of these non-duetters as established.

COMPARISON OF DUETTING AFRICAN BARBETS

Differentiation and speciation (see, e.g., Mayr and Short 1970) can be compared in 14 duetting and 22 non-duetting species of the 36 (of 42) Afrotropical barbets whose vocal habits are known (Table 2). Among the non-duetters, 7 are monotypic, 11 are simply polytypic, 4 have megasubspecies (i.e., are strongly polytypic, see Amadon and Short 1976), and 12 are involved in five superspecies. In contrast, of 14 duetters, 2 are monotypic, 6 are simply polytypic, 6 have megasubspecies, and only 3 are involved in two superspecies. These data suggest that: (1) duetters show considerably more differentiation, especially strong differentiation, than non-duetters; and, (2) speciation may be completed more rapidly in duetters (i.e., duetters tend to be more polytypic and have more megasubspecies but fewer allospecies).

Despite their appeal, such generalizations have complications. For example, genera such as *Gymnobucco* (non-duetters), *Pogoniulus* (non-duetters), *Lybius* (many duetters) and *Trachyphonus* (all duetters) differ greatly in their morphology and ecology. Approaching these data ecologically for duetters and non-duetters (Table 2), one finds that 14 of 22 non-duetters are forest barbets, whereas only 3 of 14 duetters are forest birds. Within *Trachyphonus* the sole forest species is the only weak (infrequent) duetter, but largely non-forest *Lybius* has both duetters and non-duetters. Hence, ecological and behavioral factors, as well as phylogenetic factors are likely to influence duetting and speciation (but see Discussion).

TABLE 2. Duetting, sexual dimorphism and systematics of Afrotropical barbets.

Species	Duetter	Sexually monomorphic	Sexually dimorphic	Monotypic	Simply polytypic	Megasub-species	Superspecies relations
<i>Gymnobucco calvus</i>	0	X	0	0	X	0	0
<i>G. bonapartei</i>	0	X	0	0	X	0	0
<i>G. peli</i>	(0)	X	0	X	0	0	
<i>G. sladeni</i>	(0)	X	0	X	0	0]
<i>Stactolaema anchietae</i>	0	X	0	0	X	0	
<i>S. whytii</i>	0	X	0	0	0	X]
<i>S. leucotis</i>	0	X	0	0	X	0	0
<i>S. olivacea</i>	X	X	0	0	0	X	0
<i>Buccanodon duchaillui</i>	0	0	X	0	X	0	0
<i>Pogoniulus scolopaceus</i>	0	X	0	0	X	0	0
<i>P. simplex</i>	0	X	0	X	0	0]
<i>P. coryphaeus</i>	0	X	0	0	X	0]
<i>P. leucomystax</i>	0	X	0	X	0	0]
<i>P. "makawai"</i>	?	?	?	X	0	?	?
<i>P. bilineatus</i>	0	X	0	0	0	X	0
<i>P. subsulphureus</i>	(0)	X	0	0	X	0	0
<i>P. atrofasciatus</i>	(0)	X	0	X	0	0	0
<i>P. chrysoconus</i>	0	X	0	0	X	0	
<i>P. pusillus</i>	0	X	0	0	0	X]
<i>Tricholaema hirsuta</i>	0	0	X	0	0	X	0
<i>T. melanocephala</i>	X ±	X	0	0	0	X	0
<i>T. lachrymosa</i>	X ±	0	X	0	X	0	0
<i>T. diademata</i>	0	X	0	0	X	0	
<i>T. "frontata"</i>	0	X	0	X	0	0]
<i>T. leucomelaina</i>	0	X	0	0	X	0]
<i>Lybius undatus</i>	?	X	0	0	0	X	0
<i>L. vieilloti</i>	X ±	X	0	0	X	0	0
<i>L. leucocephalus</i>	X ±	X	0	0	0	X]
<i>L. chaplini</i>	?	X	0	X	0	0]
<i>L. rubrifacies</i>	X	X	0	X	0	0	0
<i>L. guifsobalito</i>	X	X	0	X	0	0	0
<i>L. torquatus</i>	X	X	0	0	0	X	0
<i>L. melanopterus</i>	0	X	0	X	0	0	0
<i>L. minor</i>	?	X	0	0	0	X	0
<i>L. bidentatus</i>	X ±	0	X ±	0	X	0]
<i>L. dubius</i>	?	0	X ±	X	0	0]
<i>L. rolleti</i>	?	0	X ±	X	0	0]
<i>Trachyphonus purpuratus</i>	X ±	X	0	0	0	X	0
<i>T. vaillantii</i>	X	X	0	0	X	0	0
<i>T. margaritatus</i>	X	0	X	0	X	0	
<i>T. erythrocephalus</i>	X	0	X	0	X	0]
<i>T. darnaudii</i>	X	X	0	0	0	X	0

The nature of duetting itself renders somewhat simplistic a dichotomous classification of duetters and non-duetters. Some duetters actually achieve duets infrequently (e.g., *Stactolaema olivacea*, *Trachyphonus purpuratus*). Others, such as *Lybius leucocephalus* vary racially in their "duetting" (Short and Horne, unpubl. data). The more specialized duetters have different duet roles (i.e., the sexes may have separate songs), and their helpers may sing in the duet. Social groups within the complex duetters may include up to eight individuals, although in all these species the majority of such groups probably consists of pairs. That is, social groups are common but do not represent the usual situation, except, of course, immediately after fledging of the young when

the "groups" are families. The non-duetter category also presents complications. We believe it significant that the non-duetters include the extremes of the more solitary, less social barbets (e.g., species of *Pogoniulus*), as well as the most social of Afrotropical barbets (e.g., species of *Gymnobucco*, *Stactolaema*, *Lybius melanopterus*, pers. observ.). Thus, the duetters include neither the least, nor the most social barbets. Where there is intrageneric variation in duetting, duetters often are close relatives with allopatric ranges. In contrast, sympatric congeners often are more distantly related and the sympatry involves a duetter and a non-duetter (e.g., *Lybius torquatus*, a duetter, and *L. melanopterus*, a non-duetter).

THE GROUND BARBETS, GENUS
TRACHYPHONUS

Among the ground barbets (*Trachyphonus*), duets of the forest Yellow-billed Barbet are uncommon, and appear from limited data to be associated with the roosting or nesting cavity (Short and Horne, unpubl. data). The woodland Crested Barbet duets more frequently, especially in response to playback of its calls (Rwanda, 1982 experiments, unpubl. data). In each of these two species the sexes are alike, and so are their duet notes, except for some variation in pitch. Morphological geographic variation in the Yellow-billed Barbet is slight, except that the West African forest isolate *T. purpuratus goffinii* is morphologically distinctive and is sometimes treated as a separate species. Known vocalizations of *goffinii* (C. Chappuis, copy tapes) differ only in some minor details from those of the other forms, but the bird's duet is not yet known. Geographic variation in *T. vaillantii* is very slight indeed (Short and Horne, unpubl. data).

The two large ground barbets, *T. margaritatus* and *T. erythrocephalus*, are parapatric, closely related species whose exact distribution and interactions where they meet in Somalia and Ethiopia are unknown. In both these species, the sexes differ in head pattern (males with black crown patch, lacking in females). Both nest and roost in holes excavated in stream-beds or termite mounds. The coordinated polyphonic duets are very similar in these two species (pers. observ.; Short and Horne, in press: Fig. 1), the sexes having slightly different notes. Matching sexes, the notes of the two taxa parallel one another in form and pitch. Geographical variation in morphology of both species is relatively slight, featuring size shifts and brightness of color (Short and Horne, unpubl. data). We lack recordings of the duets of *T. erythrocephalus* and of *T. margaritatus* from Ethiopia and Somalia, where their ranges meet. Kenyan *erythrocephalus*, however, sings duets very like those of Chadian *margaritatus*. Their songs are so similar that unless these species vocally diverge where they meet, there exists a reasonable possibility of their interbreeding.

Trachyphonus darnaudii is smaller than either *T. erythrocephalus* or *T. margaritatus*. It overlaps broadly in range with *erythrocephalus* but not with *margaritatus*. In contrast to the latter two species, the sexes are alike in *darnaudii*. Its two duet song-forms and associated visual displays differ from those of the other two species (Wickler and Uhrig 1969, Fernald 1973, Kalas 1973). However, the two duet song types of *darnaudii* are not always sexually specific (Short and Horne 1980a, in press; see below). All four subspecies of *T.*

darnaudii have two distinctive duet roles, a phrase or set of the song of one duet partner precisely fitting within the several-note set of the other duet partner. In all races of *darnaudii*, groups are smaller than in its two relatives. Subordinates rarely sing or duet with adults. The subspecies of *T. darnaudii* also are morphologically distinctive. Those races (*T. d. darnaudii*, *T. d. bohmi*) that are sympatric with large *T. erythrocephalus* are smaller than are the others, and the two subspecies differ vocally from one another only in the temporal pattern of their duets (Short and Horne, in press: Fig. 4). The southern race, *T. d. emini*, is distinctively colored and slightly larger than *darnaudii* and *bohmi*; it partly overlaps with much larger, and ecologically divergent (more arboreal, tree-nesting) *T. vaillantii*. In its West Kenyan-West Tanzanian range, *T. d. usambiro* is known to meet a congener, *T. erythrocephalus* at only two points (we have explored much of the eastern fringe of the range of *usambiro* in Kenya, and examined all relevant literature). Apparently *erythrocephalus* disperses casually into areas outside its normal range, as indicated by sporadic occurrences in Nairobi suburbs, and one Serengeti record (Schmidl 1982). Not distinctive in color (it is no more marked than is *T. d. bohmi*), *usambiro* is considerably larger in size. We consider it significant that the race of *T. darnaudii* that is most like *T. erythrocephalus* in body size and in size of bill is the race allopatric with *T. erythrocephalus*, i.e., it may be showing "release" in the absence of a larger congener. By similar logic, the simpler, divergent duet form may be due to "release" from possible confusion of duet song with that of a congener (Short and Horne, in press). Unlike all other congeners, but exactly like the other three races of *T. darnaudii*, *usambiro* excavates a nesting hole straight down into the earth on flat terrain.

The duet of *Trachyphonus darnaudii usambiro* is composed of two distinct songs. One of these closely resembles duet songs of *T. d. bohmi*, *T. d. darnaudii* and *T. d. emini* (Short and Horne 1980a; in press: Figs. 3–6); the other is a structurally simpler, grating rattle overlapping the partner's duet-note sets about as do the two duet forms of the other races. Playback experiments in the field indicate strong reaction (close approach to the person playing the tape, counter-duetting and following the sound consistently) of *usambiro* to *bohmi* duets, and vice versa. The visual displays of duetting *usambiro* analyzed from motion pictures are identical to those of the other races. Experimental removal of one duet partner of a pair in *bohmi* and in *usambiro* resulted very soon (within 3–5 min) in replacement of the missing

TABLE 3. Comparison of duets of three species of *Lybius*.^a

Species	Duration— full duet (s)	Duration— pre-duet greeting ceremony (s)	Duration— duet (s)	Duration— post-duet greeting ceremony (s)	Number of duet sets	Tempo of duet sets (per second)
<i>rubrifacies</i> (n = 5)	18.47	5.49	6.55	6.49	12.5	0.52
<i>torquatus</i> (n = 29)	9.04	3.47	5.57	0	10.8	0.51
<i>guifsobalito</i> (n = 7)	8.65	2.78	7.55	0	16.1	0.47

^a The *n* indicates the number of full, clear duets analyzed; a duet set includes a single pair of coordinated notes of the two duetters.

duetter by a subordinate member of the group, who in all cases sang the appropriate duet role. Two, and as many as three, consecutive removals in five experiments resulted in appropriate, quick replacement from within each group (the groups had four–seven individuals). We also obtained males that sang the duet part usually ascribed to the female, as well as females that sang the supposed male role (Short and Horne, in press). Hence the vocal duet roles are not sexually absolute, but vary. The supposedly sexual, visual display roles can vary as well, independently of the vocal roles (Short and Horne, motion pictures; in press). Also, *usambiro* varies greatly in duet form (more so than in *bohmi* and *darnaudii*), such that some duets contain a “grating” song whose formed notes are nearly identical to those of the other song (Short and Horne, in press; Fig. 6).

Our data for *T. darnaudii* show that geographic variation in duet form coincides generally with morphological divergence (there is also some local variation within races, especially in *usambiro*; Short and Horne, in press). The intraracial variation and strong playback reactions of *darnaudii*, *bohmi* and *usambiro* to each other's duets suggest that some structural shifts in the duet do not preclude reaction to it as if to members of the same population. Whether or not effective interbreeding can occur between a young, potential duetter of the vocally most divergent race, *usambiro*, and an appropriate partner of the other races is not known. We are presently engaged in seeking points of contact between *usambiro* and *bohmi*. On the basis of its duet form, Wickler (1973) considered *T. d. usambiro* as a species distinct from *T. darnaudii*. However, we concur (Short and Horne, in press) with Payne (1971:136) that such separation is unwarranted. The latter view is supported by: the lack of strong color differences of *usambiro* from other races of *T. darnaudii*; the apparently identical nesting habits and visual displays of *usambiro* and those of the other races; resemblance of one duet role (song) to the duet songs of the others; and playback responses of the races to each other's duets.

COMPARISON OF SOME SPECIES OF *LYBIUS*

The species of *Lybius* we have studied offer useful information concerning duetting and systematics (Tables 1, 2). Three well-studied antiphonal duetters are *L. rubrifacies*, *L. guifsobalito* and *L. torquatus* (Tables 1, 3). Of these, *rubrifacies* inhabits a very small area of Rwanda, northwestern Tanzania, and southwestern Uganda; *guifsobalito* has a larger but not very extensive range in Uganda, Ethiopia and westernmost Kenya; and *torquatus* is widely distributed from Angola, Zaire, Rwanda and Kenya to South Africa. In terms of geographic morphological variation, *rubrifacies* is monotypic, and we also consider *guifsobalito* monotypic (Short and Horne, unpubl. data). In contrast, *torquatus* is morphologically variable, with one major variant (the subspecies *zombae*) distinctive, if only by virtue of replacement of red color on its head by black and white. The other morphological variation in *torquatus* is chiefly in intensity of color and in size. *Lybius rubrifacies* especially, and probably *L. guifsobalito*, are not apt to vary greatly in their vocal repertory, although each has been studied at only a relatively few sites. Despite morphological geographic variation in *torquatus*, its duet does not vary greatly (personal experience in Rwanda, Kenya, Malawi; Payne and Skinner 1970:174, South Africa). Kenyan birds tend to have higher-pitched notes than larger, more southern birds, and Rwandan duets show longer type B notes (Short and Horne 1982). The three species are closely related, *rubrifacies* having been allied especially with *guifsobalito* (White 1965). All are sexually monomorphic, and sing antiphonal duets in pairs with two distinct (least so in *rubrifacies*) duet roles (songs), but their associated visual displays generally are similar. Some differences are that *rubrifacies* bill-snaps distinctly, unlike the others, and *rubrifacies* and *torquatus* use more wing and flight displays than does *guifsobalito*.

When studying the systematics of related species, one should consider interspecific contacts and possible interactions that may affect

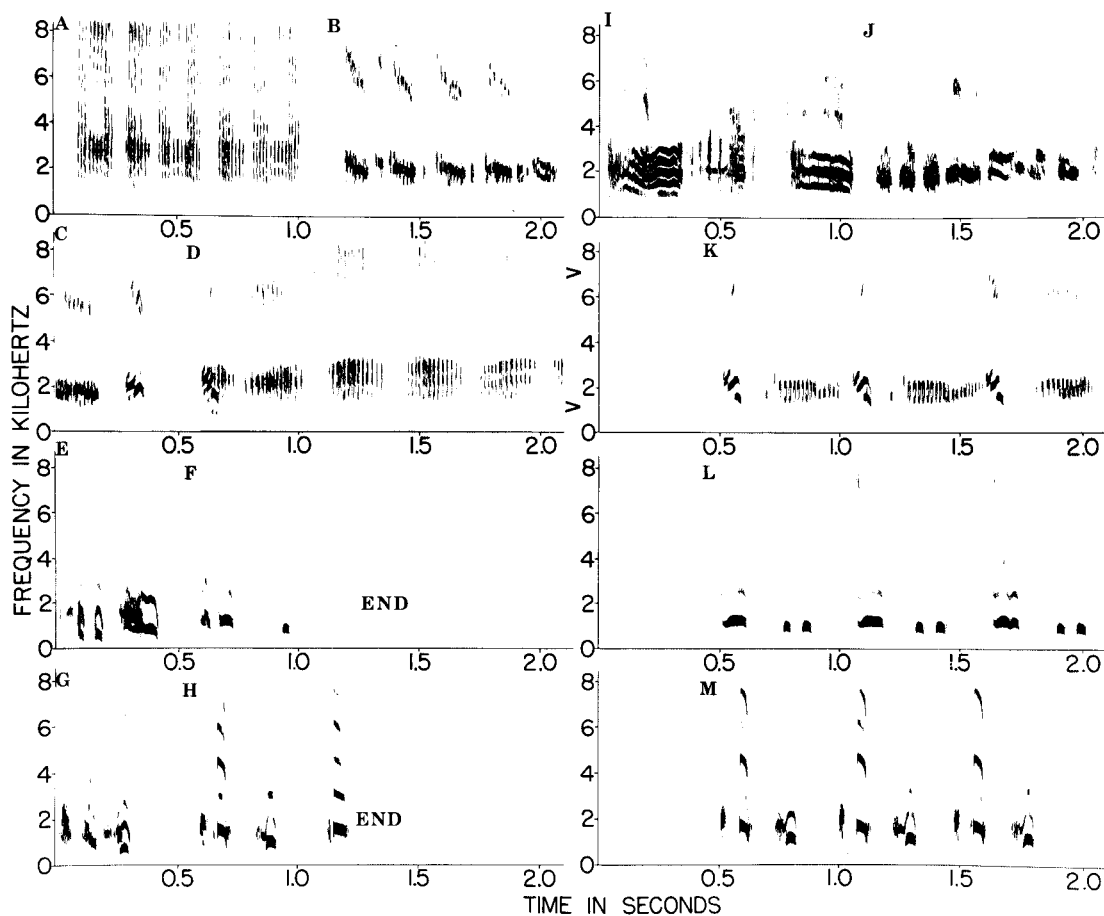


FIGURE 1. A, B, parts of pre-duet, C, start of duet and D part of post-duet of Red-faced Barbet. E, start, and F, end of duet of Black-collared Barbet. G, start, and H, end of duet of Black-billed Barbet. I, part of pre-duet of Black-collared Barbet. J, part of pre-duet of Black-billed Barbet. K, three duet sets from middle of duet of Red-faced Barbet. L, three duet sets from middle of duet of Black-collared Barbet. M, three duet sets from middle of duet of Black-billed Barbet. All sonograms made with wide-band filter.

their morphology and behavior (Short 1969, 1973). *Lybius guifsobalito* is entirely allopatric with *L. torquatus* and *L. rubrifacies*, but *rubrifacies* meets *torquatus* and its pairs and groups hold interspecific territories against that species in eastern Rwanda. Comparing the duet forms of these three species (Fig. 1, see also Table 3) reveals structural differences among them, *guifsobalito* and *torquatus* having somewhat similar duet songs (both roles) and a pre-duet greeting ceremony. The duet songs of *rubrifacies* differ markedly from those of the other two, and this species places its duet within a framework of pre- and post-duet notes (greeting ceremony notes). Not shown on the figure are the characteristic preliminary bill-snaps of *rubrifacies*, which are lacking in the others. Within all three species, the birds of a group other than the primary pair participate, if they are present, in the greeting ceremonies (pre- and post-duet), but only the primary pair duets in the vast majority (90%) of cases.

It is tempting to view the extreme duet form of *rubrifacies* as possibly related to its sympatry with *torquatus*. However, in the area of Rwanda where both are present, each utters greeting ceremonies with or without duets in response to greeting ceremonies and duets of the other, and to playback of the other's duets (both also respond to *guifsobalito* duets played to them). These playback responses involve counter-duetting or greeting ceremonies uttered at a distance, with no close approach or overflying of the playback recordist, or of the birds of the other species. This moderate response to a congener's duet does not preclude the functioning of the precise details of duet structure to prevent mixed matings. Barbets generally tend to call or even duet when they hear the distant duets or calls of other sympatric barbets, whether or not they are closely related, as noted above. The notes of the greeting ceremony (pre- and post-duet) calls are very much alike in the three species of *Lybius* (Fig.

1). The ecology of these species is similar, and it may be mutually advantageous for them not to overlap territorially. Of course, the responses may be learned, in order to function interspecifically. All of these birds duet conspicuously from tree-tops, dead trees, tops of bushes, etc. Any group of one of these species gathering conspicuously and uttering notes of a greeting ceremony with associated visual displays is bound to attract the attention, and elicit reaction, of either territorial conspecific individuals or sympatric barbet species who may see or hear the calling, displaying birds. The form and timing of the duet notes and sets of *rubrifacies* and *torquatus* are so dissimilar that their interbreeding is unlikely. It is conceivable, but unlikely that the vocally more similar but equally morphologically different *guifsobalito* and *torquatus* might interbreed, were they to meet.

We must examine the very precise nature of the duets, the structure and timing of their notes, and differences between the species in these parameters in order to consider the effects of vocal variations on the evolution of the individual species. The duet notes of the Red-faced Barbet have a very different structure from those of the Black-collared and Black-billed barbets (Fig. 1). *Lybius rubrifacies* (Table 3) also has a long pre-duet, almost as long as its duet, in addition to a long post-duet that is wholly lacking in the others. *Lybius torquatus* has a short pre-duet and its duet is short with few notes. *Lybius guifsobalito* has an even shorter pre-duet (resembling that of *torquatus*) and its duet is longer, faster, and contains more notes than do those of the others. Although the duet notes of *torquatus* and *guifsobalito* are similar, the low-pitched duet note (type A note, Short and Horne 1982) of *torquatus* is double (versus single in *guifsobalito*), and the notes of both *guifsobalito* duet parts have distinct, noisy pre-note elements generally lacking in the clearer songs of *torquatus* (Fig. 1).

Effects of interspecific interactions on the duetting of barbets are likely. Strongly duetting species of *Lybius* are largely or entirely allopatric with one another, but often are broadly sympatric with: (1) non-duetters (e.g., *L. torquatus* with *L. melanopterus*, and with *L. minor*); (2) simultaneous polyphonic duetters (e.g., *L. guifsobalito* with *L. leucocephalus*, although the latter often is ecologically isolated from its congeners); or (3) rarely duetting species (e.g., *L. guifsobalito* and *L. rubrifacies* with *L. bidentatus*). Even though duetting *L. rubrifacies* and *L. torquatus* meet in Rwanda, they are but narrowly parapatric, their contacts being very limited. *Lybius torquatus* there is at the extreme northwestern point of its range, is re-

stricted to wetter habitat, and is not numerous. *Lybius rubrifacies* (as is its dry woodland habitat) is more widespread in eastern Rwanda, with a larger population than that of *torquatus*, and it occurs beyond the range of *torquatus*, considerably to the north and west of their area of contact in southern Akagera Park.

Placing the data on these three *Lybius* species in context (see Table 1): *Lybius melanopterus*, which is highly social, does not duet and has no song as such, individually uttering interactive and noisy, loud location notes; *L. vieilloti* sings simultaneous polyphonic "duets" with a "pre-duet" greeting ceremony, but does not actually duet in a coordinated fashion; and *L. leucocephalus* varies racially, but tends to have raucous greeting ceremonies, frequently calling near potential nesting cavities (Table 1). Races of *L. leucocephalus* show strong vocal differences, for apparently populations from Cameroun (*L. l. adamauae*; C. Chappuis's tapes) east to western Kenya (nominate *L. l. leucocephalus*, unpubl. 1982 studies) show clear, formed polyphonic duets, the songs sung in unison. These differ from the unison-calls of Kenyan *L. l. albicaudus* and *L. l. senex* much more than do duets of *Trachyphonus darnaudii usambiro* from those of *T. d. bohmi* and *T. d. darnaudii*. Preliminary playback experiments show at least approach responses and unison-calling of *senex* to the duets of nominate *leucocephalus*.

DISCUSSION

Undifferentiated polyphonic, unison-sung duets and duet roles intuitively seem less complex—requiring less coordination of the caller—than the precise, antiphonal duets, and coordinated polyphonic duets with different songs and roles of the duetting barbets. Long association of secondary birds with a primary duetting pair provides an intimate arrangement for the "fine-tuning" of the duet songs that they will eventually sing. Much remains to be learned about the experiential overlay of the genetic background for duetting. Certainly we have heard no resemblances of particular duets of one species to those of sympatric congeners, as of *T. darnaudii* and *T. erythrocephalus*, so there are somewhat narrow limits of modifiability. Data are needed regarding the sexual nature of the barbets' duet roles, and the conditions under which the roles may be switched. Such "switching" is possible in shrikes (*Laniarius*, Thorpe 1972). Elsewhere, however, we have stressed the difficulties of comparing duetting in so phylogenetically divergent and behaviorally different birds as barbets and songbirds (Short and Horne 1982).

However sexual the duet roles may be, duet-

ting in the species of *Trachyphonus* and *Lybius* that we have discussed always involves but two duet roles; the two may be distinctly different or essentially similar (in a few cases, see below). The precision with which duet sets fit together, especially in such species as *T. darnaudii* (Short and Horne 1980a; in press: Fig. 2), suggests a strong requirement for the matching of appropriate duet roles, however they may develop through the experience of the birds within a family or broader group. A barbet leaving its group should have to either match its song with that of a potential mate, or find a potential mate who can match its duet song appropriately, with or without some practice. Further, not only must the duet songs match, but the intricate regulation and synchronization of the songs, shown for *L. torquatus* (Short and Horne 1982:36–37; also Greenewalt, Horne and Short, unpubl. data), and apparently important in the other coordinated duetters discussed, must be established and maintained. If these requirements are not met, a barbet that leaves its group is apt to be unsuccessful in mating, and in holding a territory. Lone singers are uncommon to rare in duetting barbets (unpubl. data), and appear to represent attempts of subordinate birds to find a mate. Thus, there would seem to be severe constraints placed upon the degree of divergence in duet songs within the species, although the exact nature of such constraints and the magnitude of the allowable divergence that does not preclude mixed matings remain to be established.

As to how distinctive the duets must be in order to prevent interbreeding of speciating taxa, we need more information on the development of duets, for there is some variation in notes of the two duet songs in barbets having distinct song-forms. The notes of the two songs composing the duet resemble one another very closely in some duets of *Lybius torquatus* (Short and Horne 1982: Plate 5d), and of *Trachyphonus darnaudii usambiro* (Short and Horne, in press: Fig. 6). The partner's songs in duets of *Trachyphonus erythrocephalus* and *T. margaritatus* in each case also show close resemblance in form. If an adult bird could indeed alter its duet role, it might more readily accept a duet partner singing a song that was somewhat to markedly different. The development and modifiability of visual display elements of duetting also have to be considered.

The comparison of museum specimens (Short, unpubl. data) suggests that *Lybius leucocephalus albicaudus* and *L. l. senex* interbreed over much of southern Kenya and northern Tanzania, despite the distinctive unison calling of each; neither form sings duets. Sym-

patric *Trachyphonus darnaudii* and *T. erythrocephalus* have different duets, whereas parapatric, closely related *T. erythrocephalus* and *T. margaritatus* have almost indistinguishable duets. *Lybius torquatus* meets and interacts strongly with *L. rubrifacies*; these species differ markedly in duets as well as in coloration. However, related *L. guifsobalito*, which is allopatric with both *torquatus* and *rubrifacies*, has a duet resembling that of *torquatus* and coloration approaching that of *rubrifacies*. Other sympatric duetters with very divergent duets are congeneric *L. guifsobalito* with *L. bidentatus* and unrelated *Tricholaema lachrymosa*, and *Lybius vieillotii* with *Trachyphonus margaritatus*. In a sense even more divergent in "songs" are sympatric *L. torquatus*, a duetter, with *L. melanopterus*, a non-duetter, and *Stactolaema olivacea*, a duetter, with non-duetting *S. leucotis*. These examples show circumstantial evidence but correlation nevertheless between the occurrence and divergence of duetting and speciation.

We earlier cautioned against broad systematic generalizing from data involving duetters and non-duetters because of ecological parameters (forest or non-forest habits) that seem related to duetting. Some problems can be overcome by comparisons of congeneric, sympatric (hence under similar ecological regimes) species. The allopatric occurrence of the taxa having similar duets, and the sympatric occurrence of congeners having very diverse duets (or no duets, e.g., *L. melanopterus* with complex duetting *L. torquatus*) strongly support the view that speciating taxa (megasubspecies to allospecies) undergo major shifts in their duetting during late stages of speciation (the stages involving reinforcement of isolating mechanisms, competitive interactions and range overlap). Enhancing this view is a comparison of species for which duetting data are available, using non-duetting *Gymnobucco* and *Pogoniulus* and duetting *Lybius* and *Trachyphonus* (Table 2). *Gymnobucco* shows no megasubspecies, and two species form a superspecies among its four species. Only two of nine *Pogoniulus* have megasubspecies, although five species seem involved in two superspecies. Two of the six duetters, but not the non-duetter (*melanopterus*) of *Lybius* have megasubspecies, and two of five (duetting) *Trachyphonus* show megasubspecies. The megasubspecies with divergent songs (duets) occur only in the duetters among *Lybius* and *Trachyphonus*.

Investigations are needed: (1) of the duets of populations or individuals morphologically intermediate between vocally and morphologically distinct taxa such as *Lybius leucocephalus leucocephalus* and *L. l. senex*, and *Tra-*

chyphonus darnaudii bohmi and *T. d. usambiro*; and (2) of the duets of the vocally similar allopecies *T. margaritatus* and *T. erythrocephalus* from the regions of Ethiopia and Somalia where they are likely to meet.

The more complex antiphonal and coordinated polyphonic singing duetters with strong behavioral correlates of the duetting (suppression of singing of subordinate group members) seem to have diverged vocally when historical factors fostered geographic isolation and thus morphological differentiation. Sympatric, related duetters appear to have mutually influenced the nature of each other's duets and the course of their evolution (i.e., of their ecology and morphology as well as their vocalizations), as in the likely case of *Trachyphonus darnaudii* and *T. erythrocephalus*. These effects seem to be greatest during the later stages of speciation. Barbets of duetting groups seem either to speciate fully and rapidly, or to remain differentiated at the level of megasubspecies. Further data on additional species should lead to firmer conclusions about the relationship between duetting and speciation in the African barbets.

ACKNOWLEDGMENTS

The Leonard C. Sanford Fund and the Gerald and May Ellen Ritter-Eugene Eisenmann Fund of the American Museum of Natural History supported Short's field work. G. R. Cunningham van Someren was helpful in Kenya, and J.-P. Vande weghe assisted us in Rwanda. This review is based upon a symposium lecture presented at the XVIII International Ornithological Congress. We are grateful to J. David Ligon and Robert Payne for suggestions benefiting the manuscript, and to C. Chappuis for use of his recordings.

LITERATURE CITED

- AMADON, D., AND L. L. SHORT. 1976. Treatment of subspecies approaching species status. *Syst. Zool.* 25:161-167.
- FERNALD, R. D. 1973. A group of Barbets. II. Quantitative measures. *Z. Tierpsychol.* 33:341-351.
- KALAS, K. 1973. A group of Barbets. I. Some ethological observations. *Z. Tierpsychol.* 33:335-340.
- MAYR, E., AND L. L. SHORT. 1970. Species taxa of North American birds. A contribution to comparative systematics. Nuttall Ornithol. Club Publ. 9.
- PAYNE, R. B. 1971. Duetting and chorus singing in African birds. *Ostrich, Suppl.* 9:125-146.
- PAYNE, R. B., AND N. J. SKINNER. 1970. Temporal patterns of duetting in African barbets. *Ibis* 112:173-183.
- SCHMIDL, D. 1982. The birds of the Serengeti National Park Tanzania. British Ornithologists' Union Checklist 5.
- SHORT, L. L. 1969. Taxonomic aspects of avian hybridization. *Auk* 86:84-105.
- SHORT, L. L. 1973. Hybridization, taxonomy and avian evolution. *Ann. Mo. Bot. Gard.* 59:447-453.
- SHORT, L. L. 1982. Woodpeckers of the world. Monograph 4. Delaware Museum of Natural History, Greenville, DE.
- SHORT, L. L., AND J. F. M. HORNE. 1980a. Ground barbets of East Africa. *Living Bird* 18:179-186.
- SHORT, L. L., AND J. F. M. HORNE. 1980b. Vocal and other behaviour of the Green Barbet in Kenya. *Ostrich* 51:219-229.
- SHORT, L. L., AND J. F. M. HORNE. 1982. Vocal and other behaviour of Kenyan Black-collared Barbets *Lymbius torquatus*. *Ibis* 124:27-43.
- SHORT, L. L., AND J. F. M. HORNE. In press. Aspects of duetting in ground barbets. Proc. V Pan-African Ornithological Congress.
- THORPE, R. H. 1972. Duetting and antiphonal song in birds. *Behaviour Suppl.* 18.
- THORPE, R. H. 1973. Duet-singing birds. *Sci. Am.* 229:70-79.
- TYROLLER, G. 1974. Duett-Entwicklung bei handaufgezogenen Bartvögeln (*Trachyphonus darnaudii emini*). *Z. Tierpsychol.* 35:102-107.
- WHITE, C. M. N. 1965. A revised check list of African non-passerine birds. Govt. Printer, Lusaka, Zambia.
- WICKLER, W. 1973. Artunterschiede im Duettgesang zwischen *Trachyphonus darnaudii usambiro* und den anderen Unterarten von *T. darnaudii*. *J. Ornithol.* 114:123-128.
- WICKLER, W. 1976. Duetting song in birds: biological significance of stationary and non-stationary processes. *J. Theor. Biol.* 61:493-497.
- WICKLER, W., AND D. UHRIG. 1969. Bettelrufe, Antwortzeit und Rassenunterschiede im Begrüssungsduett des Schmuckbartvogels *Trachyphonus darnaudii*. *Z. Tierpsychol.* 26:651-661.

American Museum of Natural History, New York, New York 10024. Address of second author: P.O. Box 24622, Karen, Nairobi, Kenya. Received 17 September 1982. Final acceptance 31 March 1983.