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Mate-Guarding and other Functions of Antiphonal Duets in the Slate-coloured Boubou (*Laniarius funebris*)¹⁾

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With 7 figures

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Abstract and Summary

Antiphonal duets between male and female of a mated pair have been described for many bird species. Most authors admit that duetting may have different functions in different species, but they usually treat it as a uniform phenomenon within one species, although the same pair may duet with a variety of different songtypes. This paper presents evidence that in *Laniarius funebris* different duettypes indeed serve different functions.

In the study population at Lake Baringo (Kenya) males duet with four songtypes, females with only one. By means of multivariate analyses it was found that the occurrence of the four male songtypes cannot be explained by a single, uniform tendency for duetting, but only by 3—4 factors representing different functions. These functions were analysed by studying the frequency of songs initiated by males and females, the frequency of answers in different situations, and the effect of songs and answers on other behaviours. The following result emerged:

One male songtype is used to reach a breeding synchrony in mates. Two other types both have territorial functions but their relative frequencies seem to change with the extent of threatening by other pairs and cooperation between mates.

For the fourth type a mate-guarding hypothesis is proposed: in this case the duet is not performed in the common interest of two mates, each informing the other about its intentions; rather, each answers the mate's song to prevent solo-singing, which could attract other birds as competitors.

The analysed functions are discussed in the light of sociobiological reasoning and with respect to the higher number of duetting species in the tropics than in temperate zones.

I. Introduction

In many birds and some mammals male and female of a mated pair adjust their vocalization with respect to time and/or motif. Such duetting is

¹⁾ Dedicated to Professor KONRAD LORENZ on the occasion of his 80th birthday.

particularly frequent in monogamous pairs inhabiting permanent territories in tropical environments (for lists see KUNKEL 1974 and FARABAUGH 1982). Suggested functions of duetting include acoustical contact in dense vegetation, synchronization of reproductive activities, territorial advertisement, reinforcement of the pairbond and facilitation of mate, sex or species recognition (VON HELVERSEN 1980; FARABAUGH 1982). Most authors agree that several of these, as well as other functions, are not mutually exclusive, and that duetting may have different functions in different species. But they usually treat duetting as a uniform phenomenon within one species, although the same pair may use a variety of different elements. In some species, including the bush-shrikes *Laniarius ferrugineus* and *L. funebris*, "the birds' selection of particular patterns could not be correlated with environmental events or situations" (HOOKER and HOOKER 1969). Such a correlation is not required for hypotheses which see a main function of duets in a pair-specific exchange of code-words helping in mate recognition and the pairbond (WICKLER 1972, 1980). But in some species, including the same two *Laniarius* shrikes, other authors did find a relationship between specific duet elements and specific situations, though the precise functions remained obscure (TINGAY 1974; WICKLER 1976; HARCUS 1977; SEIFT and WICKLER 1977; TODT et al. 1981, and this study). This suggests that the "absence" of situation-specific elements may rather reflect the difficulty of getting sufficient behavioural data, especially in the dense vegetation of tropical habitats. In this paper we analyse the adaptive significance of various songtypes in duetting *L. funebris*. The functions are inferred from the general biology of the birds, the ecological conditions under which they live, the physical structure of the duets, the contexts in which different duettypes occur and the quantitative relationships between them.

II. General Biology and Ecology

1. Material and Methods

In East Africa *L. funebris* is a common bushshrike (Laniidae) inhabiting thick woodland cover and semi-arid bushland, usually at altitudes below 1500 m (BRITTON 1980). The sexes are uniformly slate-coloured and nearly similar in size. This monomorphy and the birds' cryptic habits and preference for dense thickets render observation difficult. But their loud, sex-specific vocalizations at all times of the day and year usually leave no doubt about their presence and sex. Over the months March, April, May, June and September in 1980, 1981 and 1982, one of us (E.S.) observed 7 pairs for a total of 205 days, with special focus on duets. Vocalizations were recorded with a directional microphone (AKG D 900 C) and a Uher 4200 IC tape recorder. Sonagrams were produced on a Kay Electric 6061 B sonagraph.

2. Study Area

The observations were carried out near Lake Baringo (Kenya; 36° 05', 0° 37' N) which lies some 65 km north of the equator at an altitude of 900 m. The climate in this area is characterized by an annual mean temperature of 25 °C and a low average rainfall of 645 mm/year, about 60 % of which occurs between April and August (values for Marigat from BROWN and BRITTON 1980; STEVENSON 1980). While temperatures do not change much, variation in rainfall pattern is pronounced, both between and within years (Fig. 1). Low rainfall, high

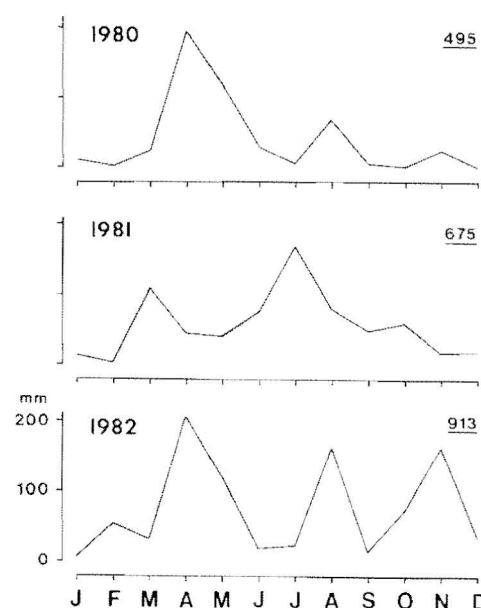


Fig. 1: Rainfall pattern in the three years of study. Underlined figures (right) represent the total amount in mm for each year. (Data recorded by J. H. E. LEAKEY at Snake Farm, Lake Baringo)

temperatures, and in recent years increasing erosion have made the area semi-arid, with thorn-bushes predominating. But in some places bush vegetation can be thick (in the rainy season almost impenetrable), interspersed with several high trees (*Acacia spec.*) (SONNENSCHNEN 1981).

3. Territoriality

In these pockets of dense vegetation pairs of *L. funebris* live in territories defended throughout the year, most vehemently at the beginning of the breeding season and during nest construction. These fluctuations in defense are mirrored in the response to conspecific song played from a tape recorder. In the dry season and during incubation birds may not react at all, while in the early stages of the breeding cycle they usually answer readily with duets and fly towards the recorder excitedly, even transgressing the boundaries of their territories. Because of these fluctuations in responsiveness, playback experiments are not too qualified for testing the presence of a pair or determining territory size (cp. DABELSTEEN 1980).

4. Breeding Biology

In our opinion the main ultimate factors causing *L. funebris* to prefer dense vegetation are food supply and nest protection, both are most important during the breeding season.

Nests are built 1–1.8 m above ground. Both sexes may take part in nest building, though male contribution is often less and in some cases lacking altogether. Male and female take regular turns incubating the 2 or 3 eggs and brooding the young but (as in nest building) some males have a minor share. They sit on the nest for shorter periods or, as in one pair, shirk altogether.

Juveniles hatch after 17 days of incubation and are thereupon brooded until about one week old. Both parents bring food, during the first days green caterpillars exclusively, later on other insects as well. Begging of the young is quiet and perceptible to humans from nearby only.

Although the nest is thought to be left at the age of 14 days, a successful fledging could unfortunately never be observed. Sooner or later all eggs or nestlings were robbed, some nests

being destroyed as well. The most likely candidates for this high predation pressure are snakes, monitor lizards (*Varanus niloticus*), mongooses (Herpestinae) and birds such as hornbills (Bucerotidae). If a clutch is lost the birds immediately start building a new nest. Some initially unsuccessful pairs produced three, perhaps even four clutches in one season.

A more detailed description of the biology of *L. funebris* will follow in another publication.

III. Vocalizations

1. Single Calls

Besides the striking sex-specific duet songs (see below), *L. funebris* disposes over a variety of other vocalizations (Fig. 2), all of which occur in both sexes. When excited (e.g. by playback of conspecific song, disputes with rivals or during copulation) the birds utter a noisy “kch” or more rarely a shrill “rrrh”. Both calls can be followed by a complete duet. Another harsh call (which could not be recorded) was given when a cuckoo appeared near the nest. A fourth call, sounding like “teck teck . . .”, is also known from other

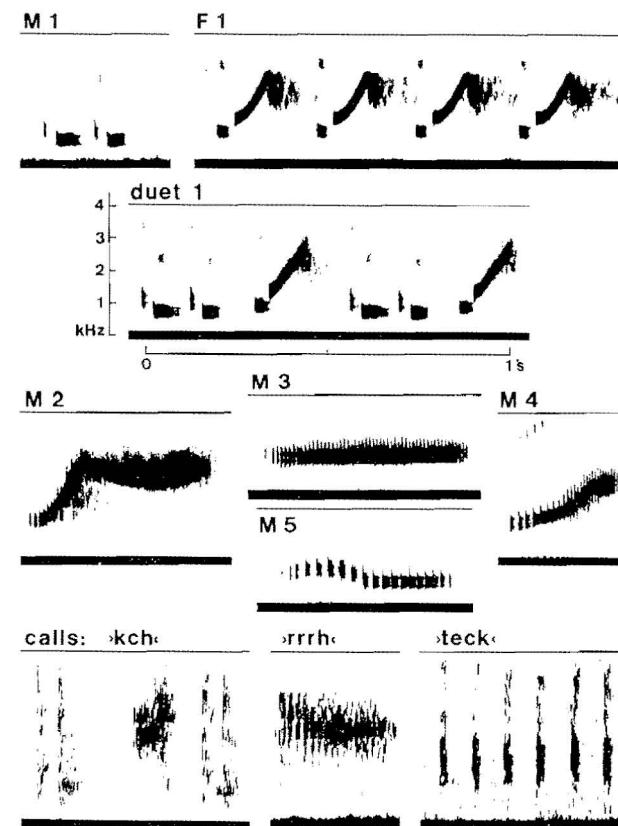


Fig. 2: Songtypes and calls of *Laniarius funebris* at Baringo

species of bushshrikes. It increases in repetition rate with increasing excitement and is frequently given when a bird approaches its nest; it was also heard when a conspecific caught in a trap uttered anxiety calls, and when a cobra (*Naja spec.*) appeared near the nest. The precise functions of these calls are not known, but according to circumstances they probably signal different intensities and/or situations of excitement, alarm and/or warning. This is corroborated by the physical characteristics of the calls, including an abrupt start, a wide frequency range, and frequent repetitions in the case of "teck", all of which make it easier for conspecifics to localize the caller (cp. MARLER and HAMILTON 1966). A further type of vocalization consists of soft contact calls almost inaudible to the human ear. They are used when mates are close together, e.g. at the nest, and when nestlings fail to gape while being fed.

2. Duets

a) General

Mates of *L. funebris* pairs frequently combine their sex-specific song into duets, audible throughout the year in varying frequencies. Either sex may initiate and end a duet. The song of one bird is not always answered by the mate; long series of solo song are no exception, especially in males. Unlike many other duetting birds such as *Trachyphonus*-species (WICKLER and UHRIG 1969), *Lybius torquatus* (SHORT and HORNE 1982), *Dicrurus adsimilis* (VON HELVERSEN and WICKLER 1971) and *Cichladusa guttata* (TODT and FIEBELKORN 1980), mates of *L. funebris* need not come together to perform a duet. They usually sing and answer at some distance, separated by dense vegetation and without visual contact. We never observed mates sitting as close together as those depicted in SEIBT and WICKLER (1977), doing nothing but duetting and making the accompanying conspicuous movements of bowing and stretching. SEIBT and WICKLER interpreted these movements as visual appeasement of the acoustically aroused duet-partner. We feel that this bowing and stretching is rather primarily, an inevitable effect of song production. Two points support this hypothesis:

- The same movements occur when duetting mates cannot see each other.
- The intensity of the movement seems to increase with the effort necessary to produce the song; e.g. it is more pronounced with the loud elements in songtypes 2 and 4 than with the softer one in type 3.

Moreover, as bowing and stretching also occur during aggressive interactions, then usually combined with an open bill and "kch" calls, they may rather serve a threatening than an appeasing function. Similarities between threat and duetting postures were also noted by HUXLEY and WILKINSON (1979) and BAPTISTA (1978). Though SEIBT and WICKLER's hypothesis, based on captive *L. funebris* attracted to a certain perch, may still be true, it can apply only to situations with visual contact, extremely rare in our study population.

b) Duet Structure

In the actual study area the males of all 6 pairs investigated used the same four well-defined songtypes (= M1 to M4, Fig. 2). All females had only one identical songtype (= F1). The song may be given as a duet or as solo song. In most cases one song is comprised of two or more single elements; a duet may have up to 14 elements sung by male and female in varying sequences, e.g. "FFFF MM F MM" or "MM F" or any other arrangement.

F1 sounds like a lengthened "queet" or a short "quitt". Up to 8 elements may rapidly succeed one another in one song (Fig. 2). M1 sounds like "kong" and is always given 2 or 3 times in rapid succession, treated in the analysis as one song. M2 and M4 again usually consist of 2 elements, whereas M3 is a one-element song.

In another population, only a few km from our study area, males had the same four songtypes but an additional fifth (Fig. 2). At the beginning of the 1982 breeding season this type occurred for some days in our population but then disappeared again. Except for this case the repertoire in the population remained constant from 1980—1982.

Several duets (and solo songs as well) can be combined into one "song series". In such a series the intervals between two successive songs are clearly longer than the intervals between two elements within one song and clearly shorter than the intervals between two song series. We designate duets, solo song and song series according to the male songtype as duet 1 to 4, solo song 1 to 4 and song series 1 to 4. This is possible as within one duet and within one series males always use the same type.

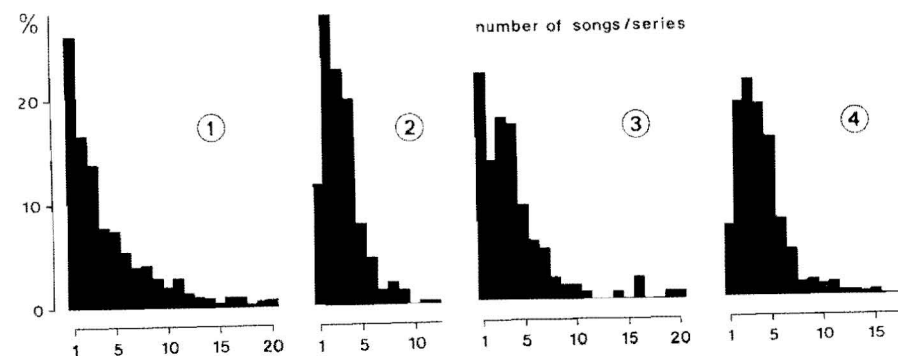


Fig. 3: Frequency distribution of songs 1—4 in relation to length of song series.
 $n_1 = 1066$, $n_2 = 283$, $n_3 = 149$, $n_4 = 379$

Among other factors the length of a series depends on the type of song. Fig. 3 gives the frequency distribution of M1 to 4 in relation to series length. (Series length > 20 are rare enough to be disregarded.) All distributions are significantly different ($p < 0.05$ and < 0.01 ; Kolmogorov-Smirnov test, two-tailed). The longest series are performed with M1 (max. 350 songs with 218 F1 answers in 23 min), followed by M3 (max. 24), M4 (max. 23) and M2 (max. 12).

IV. The Functions of Different Song-types

1. Material and Methods

For the functional analysis we considered the frequency/h of the following 11 variables:

- 1) total number of duets,
- 2) answers of females (= duets initiated by males),
- 3) answers of males (= duets initiated by females),
- 4) song series initiated by males,
- 5) song series initiated by females
- 6) total songs of males (= duets initiated by males plus solo songs),
- 7) total songs of females (= duets initiated by females plus solo songs),
- 8) total number of songtype M1,
- 9) total number of songtype M2
- 10) total number of songtype M3
- 11) total number of songtype M4.

Variables 4)–11) are irrespective of whether the mate responded or not. Three sets of data were used:

Data set 1: absolute song frequencies/h, collected *simultaneously* from several pairs in relation to date.

During the transition period from dry to rainy season we recorded the singing activity of 3–5 pairs audible from a certain spot. Observations were from 16. 3. 82–18. 4. 82 with daily records of one h shortly after sunrise and one h just before sunset. No breeding activity occurred during that period so that singing activity of different pairs was taken to be fairly equal and lumping of the data seemed justified. The frequencies/h of songtypes M1 to M4 were averaged over two days to form data set 1 (Fig. 6a).

Data set 2: absolute song frequencies/h, collected *successively* from individual pairs in relation to the reproductive stage.

Frequencies of variables 1)–11) were recorded during 148 independent observations lasting from 1 to 5 h with an average of 2.5 h. These observations usually lay in the early morning hours and covered the following stages: dry season in March, beginning of the rainy season, the subsequent periods of nest building, incubating, brooding, feeding and nest loss, as well as the following non-breeding season in September.

Each observation concerned only one pair. Sufficient data were collected from three different pairs; roughly similar results seemed to justify pooling the data from identical reproductive stages.

Since the frequencies/h (= data set 2) were not normally distributed for most of the variables, and thus did not fulfil the requirements of factor analysis, we transformed them with the formula $x' = \log(x+1)$ (FREY and PIMENTEL 1978; SOKAL and ROHLF 1969). After this transformation 9 of the 11 variables no longer differed from a normal distribution ($p > 0.10$; Lillifors-modification of the Kolmogorov-Smirnov one-sample test, SACHS 1978). Only variables 7 and 10 differed slightly ($0.05 < p < 0.10$).

The actual factor analysis was based on Pearson correlation coefficients between all variables. For computation we used SSP-program FACTO of IBM, with subsequent VARIMAX-rotation.

The log-transformed frequencies of songtypes M1 to M4 were averaged within each reproductive stage. Means were retransformed from log- to linear-scale and log-standard deviations were converted into 95 % confidence limits (Figs. 4 and 6b; SOKAL and ROHLF 1969).

Data set 3: relative frequency of responses, calculated from data set 2.

The relative frequencies of responses to a particular songtype were calculated by dividing the number of answers by the total frequency of that type. This was usually done for each of the 148 observations separately, or even for each song series within one observation. But such ratios can be biased when sample sizes are small. Therefore consecutive observations with low numbers of songs were combined to $n \geq 10$. These ratios were transformed, averaged within each reproductive stage and re-transformed as mentioned above.

Table 1: Distribution of songtypes M1 to M4 in duets initiated by males and females and in solo songs of males. Data pooled over several pairs. χ^2 and p-values indicate whether the compared rows differ in the relative frequency of songtypes

	% of song type				n
	M 1	M 2	M 3	M 4	
1. duets initiated by females	93.9	0.9	0.3	5.0	1 434
2. duets initiated by males	79.0	5.5	5.0	10.5	11 880
3. solo songs of males	67.8	9.6	6.6	16.0	10 126

	χ^2	df	p
comparison 1 / 2	296.5	3	< 0.001
2 / 3	370.3	3	< 0.001
1 / 3	422.5	3	< 0.001

Statistics: If not stated otherwise, differences were tested with the Mann-Whitney-U-test (two-tailed) and correlation coefficients were computed from Spearman-rank-correlations (r_s). In cases where parametric t-tests and Pearson-correlation-coefficients (r) were used, data previously were tested for normal distribution and — if necessary — transformed as described under “data set 2”.

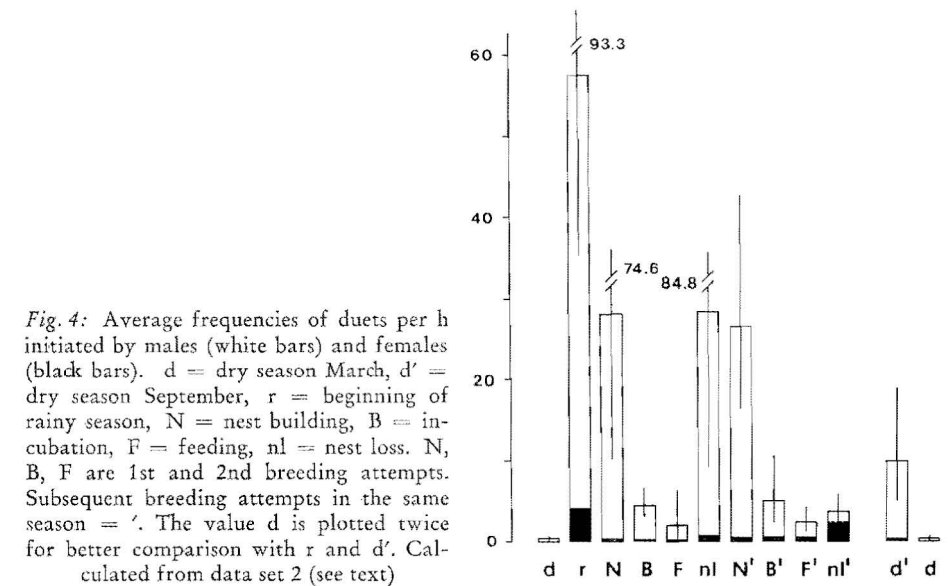


Fig. 4: Average frequencies of duets per h initiated by males (white bars) and females (black bars). d = dry season March, d' = dry season September, r = beginning of rainy season, N = nest building, B = incubation, F = feeding, nl = nest loss. N, B, F are 1st and 2nd breeding attempts. Subsequent breeding attempts in the same season = '. The value d is plotted twice for better comparison with r and d'. Calculated from data set 2 (see text)

2. Results

Altogether we recorded 13,314 duets. Only 10.8 % of them were initiated by females, 89.2 % by males. Although the initiative of both sexes varies within the year, in all periods of the study males started considerably more duets than females did (Fig. 4; data set 2 for variables 2 and 3).

If females begin, males almost never answer with M2 or M3, only occasionally with M4 but usually with M1 (Table 1, first row). If males begin, again M1 is the most frequent songtype, followed in descending order by M4, M2, and M3 (Table 1, second row). But the relative proportions of M2, M3 and M4 are higher in duets initiated by males. In duets initiated by both males and females, the distributions of M1 to M4 differ from the distribution in those male songs not answered by females (Table 1, third row). This suggests that both sexes preferentially duet with M1.

These findings were corroborated and specified by results from factor analysis. According to a common rule, first only factors with an eigenvalue of ≥ 1.0 were extracted (VAN DE GEER 1971; BALTHAZART 1973; ASPEY and BLANKENSHIP 1977). This resulted in three independent factors accounting for

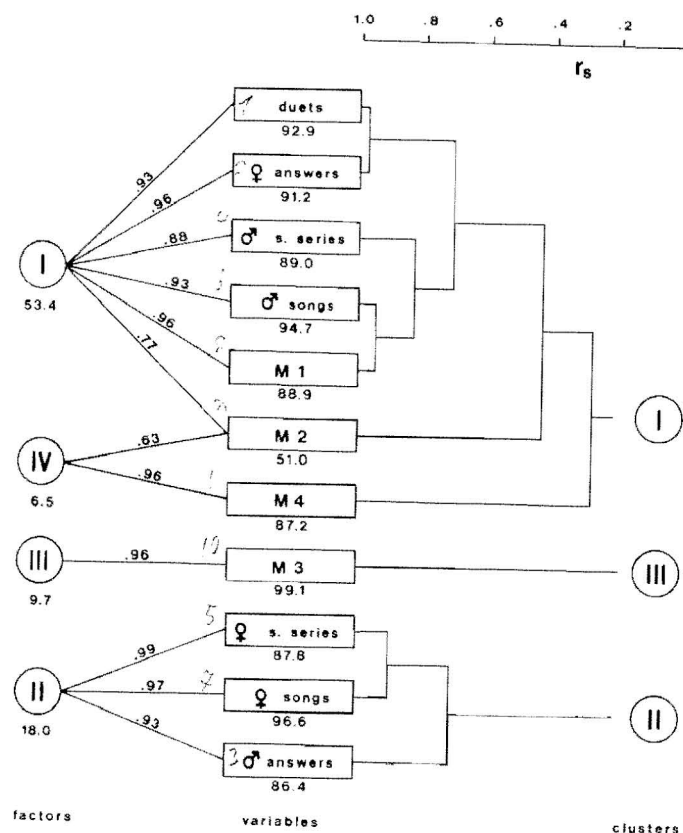


Fig. 5: Result of factor analysis (left) and cluster analysis (right). Numbers under factors I—IV represent the percentage of total variance explained by the particular factor. Numbers under the variables show the percentage of variance in the particular variable accounted for by the four factors. Numbers between factors and variables are factor loadings. They represent the extent each behaviour correlates with the extracted factor after VARIMAX rotation. Following a suggestion of ASPEY and BLANKENSHIP (1977) only factor loadings > 0.45 have been considered relevant. According to their rating all loadings are "very good" or "excellent". For further explanation and for cluster analysis see text

81% of the total variance but for only 51 and 55% of the variance in the interesting variables M2 and M3. A fourth factor was therefore extracted with an eigenvalue of 0.7. This 4-factor solution is shown in the left half of Fig. 5.

M1 is clearly associated with factor I, also accounting for the total number of duets and so may be termed "duet factor". This factor also explains the total number of songs and song series initiated by males and the number of answers from females. But to account for the frequency of songs and song series initiated by females, and the number of answers from males, we need a separate factor II, independent of the total number of duets. This is consistent with the low number of duets initiated by females (Table 1), fluctuating over the year by a factor of 15 only, whereas duets initiated by males fluctuate by a factor of ca. 115 (Fig. 4).

M3 appears on a factor of its own (III). M2 and M4 are grouped into the same factor (IV) but M2 also belongs to factor I. However, only 51% of the variance in M2 is accounted for by the 4-factor system in Fig. 5. This can be improved by extracting a fifth factor with an eigenvalue of 0.64. In this case M2 is separated from factors I and IV and appears on its own factor with a loading of 0.87 (not shown).

To check whether the result was biased by the non-normal distribution of variables 7 and 10, even after transformation, a cluster analysis was also performed (FREY and PIMENTEL 1978; ÜBERLA 1968; BALTHAZART 1973). This was based on the same set of data using non-parametric Spearman rank correlation coefficients (r_s) as a measure of similarity and a "complete linkage algorithm" as a decision rule for defining clusters (DE GHETT 1978). In the right half of Fig. 5, the association between variables and groups of variables can be deduced from the position of the connecting vertical lines. The further left these lines are, the closer the association, represented by r_s values in the upper scale. Since $r_s < 0.162$ is no longer significant ($df = 146$, two-tailed), groups of variables with still lower associations have not been connected. This results in three main clusters.

The solution only slightly differs from factor analysis: instead of appearing in a separate factor, M2 and M4 are grouped into cluster I. But their correlations with the other variables of that cluster are weak. In all other aspects both multivariate techniques yield the same result.

As according to these results at least some songtypes require separate factors or clusters to explain variances in their frequencies, it seems unlikely that all duetting in *L. funebris* is caused by the same proximate factor and/or serves the same ultimate function. To find out the differences, we analysed the contexts in which the songtypes occurred. This analysis is presented in the order of increasing frequency from M3 through M2 and M4 to M1.

Male Songtype M3

M3 starts and ends gradually and its frequency band is narrow and constant (Fig. 2). This minimizes clues from time-, phase- and intensity differences, thus making it hard to locate the caller (MARLER and HAMILTON

1966). Moreover, it is the quietest of all songs, not usually reaching beyond the boundary of the caller's territory. Therefore M3 probably conveys an information to the mate for which the singer's location is unimportant. The assumption that the mate is addressed is supported by the fact that M3 song series lengthen as the relative frequency of female responses to M3 decreases ($r_s = -0.344$, $df = 48$, $p < 0.02$; data set 3): males seem to expect their females to answer.

Frequency of M3: The highest frequency of M3 occurs at the very beginning of each reproductive period. In the evening of March 31st 1982

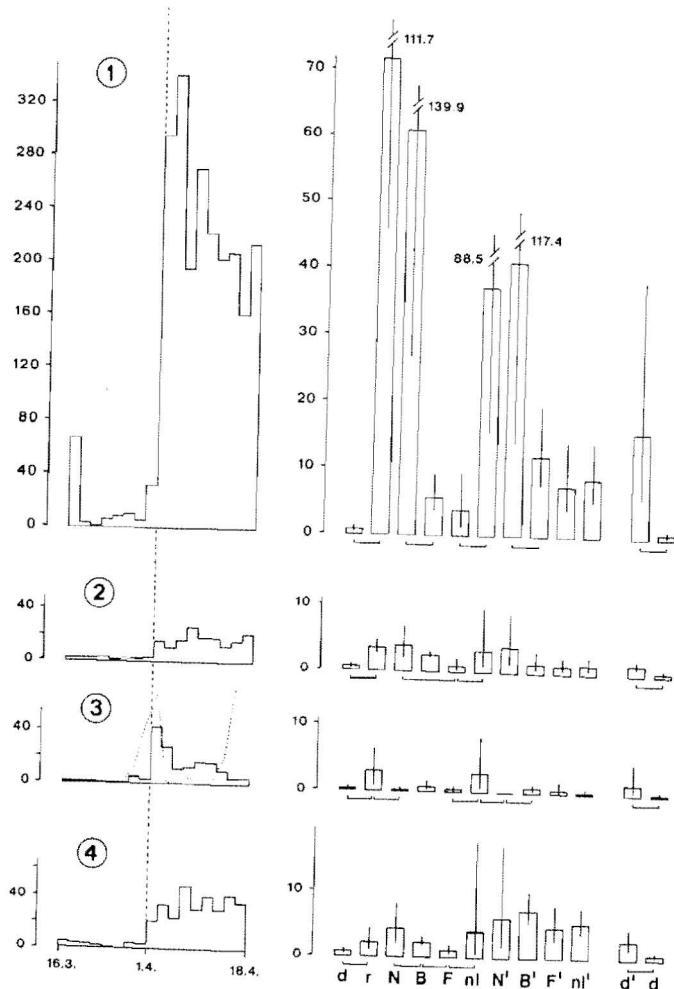


Fig. 6: a. (left) Transition from dry to rainy season. Bars: number of male songs 1-4 (from top to bottom) averaged over 2 days, calculated from data set 1 (see text). Vertical broken line: date of first heavy rainfall. Dotted line in distribution of song 3: rainfall averaged over two days; b. (right) average frequency of male songs 1-4 during different periods as in Fig. 4; calculated from data set 2 (see text). Adjacent values of significant difference ($p < 0.05$) are connected by brackets

heavy rain set in and lasted all night long; singing of M3 immediately shot up the next morning (Fig. 6a, third row). Though this was also true for M1, M2 and M4, the distribution of M3 differs significantly from all other songtypes (all $p < 0.01$; Kolmogorov-Smirnov two-sample test, two-tailed). M3 reaches its peak earlier and retains it much more briefly than the other types. Though peak singing of M3 was apparently released by the first heavy rain and precisely coincides with the rains peak, subsequent rains did not produce similar effects (Fig. 6a, third row). But M3 did increase again, even without rain, whenever a new breeding attempt commenced. This was usually the case after losing the first two clutches. After losing subsequent clutches breeding ceased and so did M3 (Fig. 6b, third row). On renesting, again M3 reaches its peak earlier and retains it for shorter periods than M1, M2, and M4. This suggests that M3 is the first signal indicating a male's readiness to breed.

Relative frequency of female answers: However, in September 1980 M3 was sung significantly more often than in the dry season in March, and not much less than during the rains in April and after nest loss (Fig. 6b). Yet no breeding occurred. But September differed from all other periods of high M3 in the relative frequency of female responses: they answered only 19 % of this songtype as opposed to 72 % during the rains ($p = 0.014$) and 61 % after nest loss ($p = 0.095$; data set 3). Thus whether breeding will actually occur depends not only on the frequency of M3 but on an agreement between the sexes, reached and manifest in duetting with M3. Once an agreement is established, M3 seems superfluous, in fact as soon as nest building starts its frequency drops sharply from one day to the next (Fig. 6b).

Male Songtypes M2 and M4

Several similarities between M2 and M4 allow a joint treatment. They have almost the same volume, and of all songtypes they are the loudest, reaching far beyond the caller's territory boundary. Their sonagrams look similar, with M4 resembling the ascending part of M2 (Fig. 2). They also resemble M3 in their gradual start and end, so that again clues from time differences are minimal. But their wider frequency range allows some location of the singing bird on the bases of phase- and intensity differences (MARLER and HAMILTON 1966). Thus M2 and M4 probably signal a bird's presence and approximate position to others outside the territory.

The assumption that the mate is not the main addressee is based partly on volume, which seems unnecessarily high for conveying information within a territory (cp. SEIBT and WICKLER 1977). And there is no significant correlation between the length of male song series and the relative frequency of female responses (M2: $r_s = 0.016$, $df = 107$, n.s.; M4: $r_s = 0.115$, $df = 136$, n.s.; data set 3). Thus, contrary to M3, a male singing M2 and M4 seems not to expect its mate's answer.

Frequency of M2 and M4: Similarities between M2 and M4 also apply for frequencies. These variables were grouped relatively close in the multivariate analysis (Fig. 5). Their distributions are quite similar, both in the

transition period (Fig. 6a; data set 1) and during the various reproductive stages (Fig. 6b; data set 2).

Unlike M1 and M3, peak singing activity of M2 and M4 is maintained over several weeks after the onset of the rains (Fig. 6a). M2 and M4 are also more evenly distributed over the year than M1 and M3, whose peaks rise sharply above the surrounding values (Fig. 6b). This suggests that the functions of M2 and M4 are less closely linked to breeding than those of M1 and M3. The highest frequencies of M2 and M4 coincided with the most likely periods for attacking and chasing intruders.

One pair, not included in the overall analysis of data set 2, had no direct neighbours and so probably suffered less boundary violations. In this pair both songtypes were less frequent than in pairs with neighbours over the same time span (M2: $p < 0.002$; M4: $p = 0.05$; data set 2).

When actually involved in territorial disputes with neighbouring pairs, males increased the frequency of M2 and M4. These observed disputes were not real fights, but pairs usually stayed close to their common boundary and clearly reacted to their neighbours' vocalizations. In such "singing contests" the relative frequencies of M2 and M4 were significantly higher than in the overall distribution of songtypes, and in playback experiments (Table 2). Compared with overall distribution the relative frequency of M4 increased more in singing contests than that of M2. The corresponding relative decreases in M1 and M3 were not significantly different from each other. These relationships may apply only for territorial disputes in which rivals are not in visual contact. If they are, M1 seems to predominate. But we have no supporting quantitative data.

The results suggest that M2 and M4 help in territorial advertisement. As *L. funebris* pairs live in permanent territories all year round the higher frequency of M2 and M4 (as compared with M1 and M3) throughout the year is to be expected; and so are the pre-breeding peaks when territories become most crucial. Moreover, the differential increase in relative frequencies of M2 and M4 in singing contests (Table 2) makes it unlikely that both songs are

Table 2: Distribution of songtypes M1 to M4 overall (= sum of Table 1), in singing contests with neighbours and during playback inside the territory. Data pooled over several pairs. χ^2 and p-values indicate whether the relative frequency of compared songtypes in singing contests differ from the overall distribution

	% of song type				n
	M1	M2	M3	M4	
1. singing contests	45.5	12.7	1.5	40.3	134
2. overall distribution	75.1	7.0	5.4	12.5	23 440
3. answers to playback	70.7	7.0	9.6	12.7	157

comparison	χ^2	p	comparison	χ^2	p
M1 / M2	17.432	<0.001	M2 / M3	8.383	0.004
/ M3	1.255	0.263	/ M4	4.353	0.037
/ M4	98.829	<0.001	M3 / M4	18.684	<0.001

Table 3: Frequency of female responses to male songtypes M2 and M4 while male or female incubates. All data from one pair

		on eggs		
		♀	♂	
♀ responds to	M2	10	17	$\chi^2 = 2.181$ $p = 0.140$
	M4	3	15	

mere variations of the same type. This will become more apparent when we consider the reaction of females.

Relative frequency of female responses: Females respond to M4 relatively more often than to M2:

- During periods directly preceding a potentially reproductive phase; the reverse is true during periods in which activities focus on the nest (building, incubating, brooding and feeding) ($p < 0.001$, $df = 43$, t-test).
- During singing contests at the boundary as opposed to the overall distribution (Table 2).
- During incubation periods when males are on the eggs, as opposed to when females are on the eggs (Table 3).

One common feature of contexts a)–c) is that the ratio of M4 to M2 answers seems to increase with the females' participation in territorial defence (a, b), and/or as her engagement in other activities decreases (a, c). Thus joint engagement in territorial defence increases the frequency of duet 4 over duet 2. Also, during incubation, leaving the nest (to join the mate in defence?) was found to occur more often when the female responded to M4 than when she did not, whereas no such difference became apparent for duet 2 (Table 4).

From these results we conclude: duet 4 represents the strongest vocal territorial advertisement and is used mainly when a pair is actually threatened. Duet 2 probably represents a weaker form, used in "routine" advertisement. By shifting the relative frequencies of M2 and M4 a male can signal the degree of threat, and whether the female's help is needed. By shifting the relative frequencies of her answers to M2 and M4 a female can signal whether she will join her mate immediately or is otherwise occupied. But both duets proclaim to other birds that the territory is occupied by a mated pair.

Table 4: Frequency of leaving the nest in relation to female answers to male songtypes M2 and M4. All data from one pair. Differences were tested by χ^2 (right) and Fisher exact probability test (left)

		leaving the nest			
		yes	no	yes	no
♀ answers	yes	3	24	7	11
	no	4	35	4	42
χ^2		-		8.296	
p		0.308		0.004	
		M2		M4	

Male Songtype M 1

Because of abrupt starts and endings in the single elements and their high repetition rate a bird singing M1 can probably be easily located on the basis of time differences (MARLER and HAMILTON 1966). This and the volume of M1 (intermediate between the louder M2 and M4 and the quieter M3) allows conveyance of the general information "Here I am!" to the mate and to conspecifics outside the territory.

From this basic meaning, and from the various situations in which such information is advantageous, a variety of more specific functions seem to have arisen. Three situations will be considered here: 1. Disturbances; 2. territorial advertisement, courtship and mate-guarding; 3. brood relief.

Disturbances

Various disturbances inside the territory seem to elicit vocalization with M1. Such disturbances can be caused e.g. by an obtrusive scientist, noisy people or a conspecific intruder, be it a real one or a playback. HOOKER (1969) mention similar observations for *Laniarius aethiopicus*. And HARCUS (1977), who quantified disturbances and vocalizations in *L. ferrugineus* and other species, suggested that in a duet mates communicate a heightened awareness of a potential danger. Such awareness, he argues, could afford increased protection, especially from predators. HARCUS' interpretation has been questioned by FARABAUGH (1982) and our results do not support it either because:

- Predators and other alarming situations are not signalled by M1 but by different calls never occurring in duets.
- The relative frequencies of female responses to M1 are lower during incubation, brooding and feeding (when increased awareness and protection are most crucial) than at other times (0.40 vs. 0.60; $p < 0.01$; data set 3).
- Although disturbances such as playback experiments inside the territory do increase total M1 vocalization, the relative amount of duets is not different from undisturbed situations in the same season (63 % vs. 58 %; $\chi^2 = 0.932$, n.s.). Re-analysing HARCUS' data for *L. ferrugineus*, we found that in this species too the percentage of duets during disturbance is not significantly higher than expected from undisturbed situations.

Thus increased awareness seems primarily to manifest itself in increased vocalization of one sex; a constant response rate of the other sex results only secondarily in more duets. Therefore some duets 1 rather seem to follow from increased awareness instead of leading to it.

Territorial Advertisement, Courtship and Mate-guarding

L. funebris males sing M1 particularly often at the onset of the rainy season, during nest building and after nest loss (Figs. 6a and b). And they initiate duets 1 about 7 times more often than females do (Table 1). This suggests that "disturbances" mean more to males than to females, especially at the beginning of any reproductive attempt. Other males, e.g. singing, approaching

Table 5: Percentage of cases in which males matched the songtype of other males in singing contests and playback experiments. Differences between the two situations were tested with Fisher exact probability test. Data pooled over several pairs. Since only male-male interactions and reactions to M1—M4 were considered, sample sizes differ from those in Table 2

	% identical responses to songtype				n
	M 1	M 2	M 3	M 4	
singing contests	57.1	57.1	-	95.2	42
playback	81.0	22.7	17.4	22.7	88
$p \leq$	0.080	0.092	-	0.001	

or trespassing, could pose a threat to the resident's reproductive prospects. This is supported by results from playback experiments.

Every second day a tape recorder was placed inside each of 7 territories and 7 songtypes (no duets) were played to the resident pair. These included the four male songtypes under investigation, M5 from a neighbouring population (see Fig. 2), one type from the Serengeti population (Tanzania) and the female songtype F1.

To facilitate interpretation of results from playback experiments (see LABELSTEEN 1980) we tried to make conditions for all pairs as similar as possible. This included:

- All songtypes used in playback had been recorded outside the study area and did not belong to any of the pairs.
- Experiments were carried out in September 1980 when none of the pairs was reproductively active.
- All experiments started at 07.00 h.
- The sequences of songtypes and pairs were shifted daily in such a way that each pair had finally heard each songtype once in 1st, 2nd, 3rd, ... 7th position and had once been the 1st, 2nd, 3rd, ... 7th pair in the sequence of playback.
- To ensure that birds were within hearing distance the first songtype in each sequence was repeated until one mate answered. The following types were played only once with a two-minute interval. In the intervals we recorded any answers, and their character: solo, duet, songtype.

Table 2 shows the results. The relative frequencies of M1 to M4 in the 157 first answers to playbacks did not differ from the overall distribution of these types ($\chi^2 = 5.334$, $df = 3$, $p = 0.149$), indicating that the experiment roughly mirrored the natural situation.

But reactions to playback of solo songs clearly differed from reactions to duets of neighbours during singing contests (Table 5). In singing contests between pairs there was a strong tendency for males to use the same songtype as the neighbouring male ("songtype matching"). This is especially true for M4. During playback, however, M2 and M4 elicited only low percentages of matching. Usually they were followed by M1, as was M1 itself. Thus one function of M1 probably lies in territorial advertisement to keep out single rivals, whereas M2 and M4 prevail during joint defence by both sexes against other pairs.

In singing contests between pairs, first vocal responses usually came from the same sex as the neighbouring bird which had started singing (Table 6). Thus birds of the same sex seem to represent a greater threat than birds of the opposite sex. This is also supported by the following observation: At the beginning of the 1982 breeding season, two females were heard in a territory

Table 6: Number of cases in which males and females matched the singing of other males and females ("models") in singing contests and playback experiments. Data pooled over several pairs

model \ answer	singing contests		playback	
	male	female	male	female
male	42	9	133	15
female	3	7	24	2
χ^2	11.843		0.150	
$p \leq$	0.001		n. s.	

duetting with the resident male. In the course of duetting one of the females was seen chasing and vigorously attacking the other. When actual breeding started, only one female remained on the territory.

Surprisingly, this sex-specific competition was not supported by results from playback. No matter whether male or female songtypes were played, in most of the experiments the first answer came from males (Table 6). As it is highly unlikely that single females pose a greater threat to males than mated ones do, we assume that M1 not only serves in deterring other males, but also in attracting additional females, especially non-mated ones. Such a multiple function has been attributed to male songs of many non-duetting species in temperate zones. The sexual character of the male response is supported by the relatively high number of M3 during playback (Table 2). The above interpretation is consistent with the finding that, during the first breeding attempt, M1 decreased from the onset of the rain until nest building (Fig. 6). With most birds fairly well synchronized by the rain, the decrease in courting may reflect the decreasing availability of females not yet occupied with breeding. With clutch loss occurring at different times, synchronization between neighbours lessens as the breeding season advances, so that in subsequent breeding attempts at any time males may have a certain chance to attract females ready to copulate. This could be one reason why M1 is more frequent during subsequent incubation, brooding and feeding periods than during the initial ones (Fig. 6b). Thus discouraging rival males and attracting females seem to be important functions of male songtype M1.

Female Songtype F1

Volume, abrupt starts and endings, repetition and the wide frequency band of F1 seem well qualified for conveying information about the presence and position of a female to the mate, and to birds outside the territory. Year-round, females initiate very many fewer songs than males do. But singing increases in both sexes prior to breeding (Fig. 4). This is consistent with all functions proposed for male songtypes: synchronization (M3), joint territory defence (M2 and M4), territorial advertisement and courting (M1). But the fact that vocalizations initiated by females are answered almost exclusively with M1 (Table 1) suggests a functional similarity between M1 and F1. We suggest that F1 serves to discourage same-sex conspecifics and to attract those of the opposite sex, but to a much lesser extent than singing M1 in males does.

Attracting additional mates may improve the reproductive success of a male, but not usually of a female. He can fertilize many more eggs whereas she can lay only one clutch, no matter how many males she has copulated with. Nor does she gain by copulating with another male who invests only his sperm. If at all, females should therefore court only at the very beginning of the breeding season when there may still be chances to attract a better mate. This may explain why, at the beginning of the rainy season, females initiate songs only about 14 times less often than males, but during nest building about 75 times less often (Fig. 4).

Relative frequencies of male and female responses: For immediately pre-reproductive periods a negative correlation exists between the lengths of male song series 1 and the relative frequencies of female responses ($r_s = -0.111$, $p < 0.02$; data set 3 pooled over periods r, N, nl, N' and d'). The corresponding correlation between the length of female song series and male response could not be tested, as female series are rare. If females start singing, males usually answer immediately. At the beginning of the rainy season the relative frequencies of male response to songs of their females was higher than vice versa (0.74 vs. 0.66; $p < 0.05$, data set 3). Female response then decreased from 0.66 at the start of the rainy season to 0.48 during nest building ($p < 0.001$). Significance of the corresponding decrease in males from 0.74 to 0.67 could not be tested because of the few songs initiated by females in most periods (Fig. 4). But throughout the year male mean response in each reproductive stage was higher than for females ($p = 0.01$; Wilcoxon matched-pairs signed-ranks test, two-tailed), just as with total singing activity (see above and Fig. 4).

These results suggest the following hypothesis: By singing M1 and F1 male and female *L. funebris* repel same-sex conspecifics but attract those of the opposite sex. As these are potential competitors, the mate should try to make the courtship signal ineffective, to avoid impairment to its reproductive success. It can be done by turning the song into a duet, informing potential competitors that the courting bird is already mated. This hypothesis, also mentioned by WICKLER and SEIBT (1980) and FARABAUGH (1982), we term the "mate-guarding hypothesis".

A male's genetic contribution to the next generation can decrease if he is cuckolded, whereas a female's need not if her partner mates with others also. Having more to lose, the male should guard more, which is consistent with the higher relative frequency of male response to female song than vice versa. The female would suffer loss only if her mate left her altogether, or invested in other females' progeny. This danger is probably higher at the beginning of the breeding season than later, when the male has already invested in territorial defence and nest building, and the availability of females has decreased. Thus the decrease in female response from the start of the rains until nest building is to be expected. So is the negative correlation between length of song series and relative response frequency if a singing bird stops courting others because its own mate scotches its chances by joining in.

According to the mate-guarding hypothesis duet 1, unlike duets 2, 3 and 4, does not reflect the mates' common interest. It originates because each sex tries to prevent the mate from singing alone. Although the answering bird is trying primarily to guard the singer, the answer also helps the singing bird to guard the answering one since this answer cannot help but inform the singer about his mate's presence.

Brood Relief

Brood relief can occur in different ways:

- The bird on eggs remains in the nest until his mate comes to take over ("immediate relief"). Only 6.5 % of these situations were preceded by duets, as recorded in the last two minutes before changeover ($n = 77$).
- The incubating bird leaves the nest before the other shows up ("delayed relief"). In such situations duets preceded 68.4 % of all cases ($n = 64$), many more than in immediate relief ($\chi^2 = 59.7$, $p < 0.001$).

Thus when birds do not see each other the changeover is coordinated acoustically, the vast majority with duet 1. This delayed brood relief bears some relationship to mate-guarding.

Frequency of M1 and F1: A female on eggs never initiates singing, but only responds to songs of her mate. Therefore a male receives no acoustical information whether his female is still incubating unless he "asks" her. As outlined above, the songtype most likely to elicit her answer is M1, which also has the potential of attracting other females. As the likelihood that a female con-

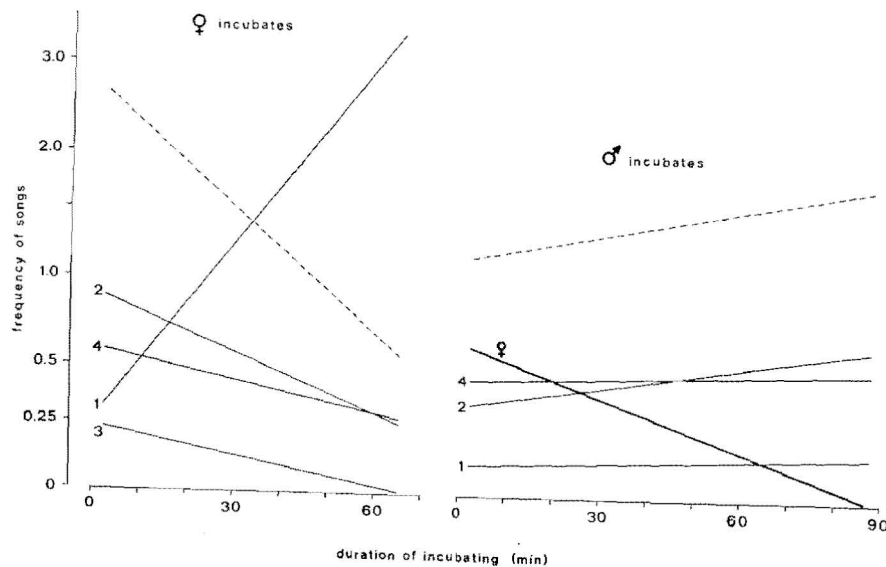


Fig. 7: Frequency of songs in relation to duration of incubating. a. (left) female incubates; lines 1–4: regressions for male songs 1–4; broken line: regression for sum of male songs 2–4; b. (right) male incubates; lines 1, 2, 4, and female: regressions for male songs 1, 2, 4, and female song (male song 3 is extremely rare in this situation); broken line: regression for sum of male songs 1–4. For calculation and significances see text

tinues incubating probably decreases with the time she is already on eggs, the frequency of asking should increase. And indeed, the longer a female is incubating the more M1 her mate sings (Fig. 7a; $r = 0.308$, $df = 101$, $p < 0.01$). With the total frequency of male songs (M1 to M4) remaining approximately constant, this increase occurs at the expense of M2 to M4. Although none of these decreases significantly alone, together they do ($r = -0.293$, $p < 0.01$).

When the male himself is incubating the overall frequency of M1 is much lower than during female incubation ($p < 0.001$). Nor does the frequency change significantly with time for any of the male songtypes or for the total number of male songs, although these tend to increase slightly (Fig. 7b). This very low and constant frequency of M1 is to be expected, as a male on eggs does not need to ask his female about incubation. It is she who now needs the information. Contrary to M1 however no high and increasing frequency of F1 is to be expected, as from a territorial and courtship point of view the female's interest is less than the male's (see above). Moreover, a male on eggs does initiate singing himself, mainly the territorial songtypes M2 and M4 which occur as frequently during his own as during the female's incubation bouts (Fig. 7). Thus the female only has to ask where the male is when his own singing activity is low. This is supported by a negative correlation between songs initiated by the female and the total number of songs initiated by the incubating male (Fig. 7b; $r = -0.563$, $df = 73$, $p < 0.01$).

Relative frequency of responses to M1 and F1: With lengthening female incubation time the relative frequency of her responses to M1 increases ($r = 0.826$, $df = 5$, $p < 0.05$). This plus the increasing number of M1 (Fig. 7a) clearly results in more duets. During male incubation the relative frequency of responses (pooled over male and female and all songtypes) also seems to become more frequent but not significantly. As the total number of songs initiated by males and females decreases (Fig. 7b), the average number of duets remains approximately constant throughout male incubation time.

By responding, the incubating bird not only guards his mate in the sense mentioned above, he also indicates that he will leave the nest. This follows from the result that brood relief was more likely to occur when the mate on eggs responded (Table 7). Although this is true for both sexes, the connection between response and leaving the nest seems to be less pronounced for incubating males than for females ($\chi^2 = 3.288$, $p = 0.07$). More often than females, males initiate a changeover by first leaving the nest and then starting sing-

Table 7: Frequency of brood relief in relation to answered and unanswered songs. Left: female incubates, male starts singing; right: male incubates, female starts singing. All data from one pair

brood relief	female incubates		male incubates	
	yes	no	yes	no
answer				
yes	36	9	13	9
no	14	37	7	21
χ^2	26.450		5.966	
$p \leq$	0.001		0.015	

ing ($\chi^2 = 19.532$, $p < 0.001$, $n = 229$). The female can probably tell from the direction of the song that her partner is no longer incubating. She usually answers, then flies to the nest. In females, responding therefore usually precedes leaving the eggs, while in males leaving usually precedes singing. This is probably necessary because the low singing activity of females (especially towards the end of male incubation bouts) gives the male too few opportunities to inform the female through his answer that he will leave the nest. But both mechanisms of brood relief force the mate to take over incubation unless he wants to impair his reproductive success by leaving the eggs unattended.

3. Mutual Substitution of Songtypes

Attaching a particular function to a particular songtype does not necessarily rule out all other functions. But our results show that in their functions male songtypes M1 to M4 cannot be substituted at haphazard.

Especially M3 (synchronization) seems to be a very specific songtype, frequent for a few weeks of the year only. Because of its low volume it can fulfil neither the functions of M2 and M4 (territorial advertisement of pairs) nor those of M1 (territorial advertisement of single males, courtship and mate-guarding). Indeed, M3 was almost absent in singing contests (Table 2) and also during nest building when mate-guarding is still important (Fig. 6b). But M1, M2 and M4 (along with nest building and other behaviour patterns) may well help in maintaining mate-synchrony once M3 has decreased. M1, M2 and M4 all have territorial functions but cannot substitute for each other completely. M1 was low in singing contests with pairs (Table 2) and decreased towards the dry season (when territories are still maintained) much more than M2 and M4 (Fig. 6b). This would be difficult to explain if a purely territorial function of M1 is assumed.

On the other hand, for M2 and M4 no effect of female responses on series length could be detected. And during incubation no effect on brood relief was found (Fig. 7). Neither result is consistent with the courtship and mate-guarding function.

Thus although any solo song or duet loud enough to reach birds outside the territory may to some extent serve territorial advertisement, courting and mate-guarding, there are specific songtypes for these functions. These similarities and differences are also illustrated by the grouping of M1 to M4 in the multivariate analyses (Fig. 5).

V. Discussion

The foregoing analysis has led us to postulate three functions of duetting in *L. funebris*:

Duet 1: mate-guarding.

Duets 2 and 4: joint territorial advertisement of pairs.

Duet 3: synchronization of breeding between mates.

A problem in functional studies arises from the difficulty of distinguishing between the primary, selectively most advantageous function of a behaviour pattern and its secondary beneficial consequences which may be of minor importance (CURIO 1973; HINDE 1975; LAMPRECHT 1981; SERPELL 1981). TINGAY (1974) e.g. states that "singing together can be thought of as 'reinforcing the pairbond' if it increases or maintains the likelihood that a pair will remain together and behave cooperatively".

According to this notion all four duettypes of *L. funebris* could reinforce the pairbond. But if that were the primary function it would be difficult to explain why four different types have evolved, and in other populations even more. We feel that reinforcement of the pairbond is a secondary beneficial consequence of the primary functions postulated here.

1. Synchronization of Breeding between Mates

DILGER (1953) suggested that one important function of duetting may be "... to facilitate synchronization of the physiological sexual rhythms in birds" (see also IMMELMANN 1961; DIAMOND and TERBORGH 1968; TODT 1970). In this respect duetting resembles courtship dances and other ritualized movements which serve the same function but are less effective where visibility is poor (ARMSTRONG 1942; SERPELL 1981).

Such synchronization between mates is of particular importance where

- a) internal gonadic rhythms would be ineffective because of unpredictable environments and/or
- b) external "zeitgebers" are weak or not indicative of the best reproductive period.

These conditions are usually assumed to be more characteristic of tropical areas than of temperate zones (see FARABAUGH 1982 for a critical review) and definitely did apply for our study area, which represents a typical *L. funebris* habitat.

Vegetation was dense and fluctuation in time and amount of rain was marked during the three years of our study (Fig. 1). As vegetative cover and insect food supply are usually triggered by the rains (SINCLAIR 1978; BROWN and BRITTON 1980) optimal breeding conditions at Lake Baringo indeed seem to be neither predictable nor constantly favourable. Therefore a mainly endogenous circannual cycle of reproductive activity would be maladaptive (FARNER and GWINNER 1981; GWINNER 1981). An additional triggering through external "zeitgebers", known for many temperate zone birds, could also be misleading. Although the onset of the rains could provide such a "zeitgeber" there are years when the beginning of the rainy season is not very pronounced and the amount of rain may not suffice to improve breeding conditions. The first rain peak in 1982 e.g. was confined to two nights only, followed by a dry period of two weeks (Fig. 6a). On the other hand, after nest loss, breeding conditions may still be favourable with respect to food and cover, although there is little or no rainfall. Such environmental conditions may result in a

desynchronization of gonadic cycles between mates, known to occur in tropical species (KUNKEL 1974; SOSSINKA 1980; DITTAMI in prep.). Thus a selection pressure for synchronization of mates through behavioural mechanisms seems likely.

In *L. funebris* this is apparently the function of duet 3. It reaches its peak frequencies earlier and for shorter periods than the other songtypes, and drops to zero when nest building starts (Fig. 6). Therefore duet 3 really seems to effect synchronization instead of resulting from it. Cases of vocally induced sexual activity are known in budgerigars, ring doves and canaries (BROCKWAY 1969; LEHRMAN and FRIEDMAN 1969; KROODSMA 1976). In duetting pairs of white-browed robin chats (*Cossypha benglimi*), deafening of females does not affect the pairbond but terminates nest building and other reproductive activities (TODT and HULTSCH 1982). This supports our argument that duets may have more specific functions than maintaining the pairbond, and it suggests that in *Cossypha* too duetting helps in synchronizing mates. But although males of *L. funebris* may exert an influence on their females' physiological state by singing M3, this is definitely not the only stimulating factor. It works only in conjunction with the appropriate external factors and the appropriate female response.

The importance of external factors is indicated by the different intervals, in the three study years, between the onset of the rains and the start of nest building. The importance of female responses follows from the fact that in September 1980 M3 was relatively frequent (Fig. 6b) and yet no breeding occurred. This omission of reproductive activity was paralleled by the females' low frequency of responses, showing that the duet is really responsible for the tuning in, not the male song alone.

This is to be expected. As production of sperm is less costly than eggs and therefore implies a lower investment (TRIVERS 1974), the males' reproductive mood should be less sensitive to environmental conditions. Females, however, should signal their agreement only if conditions are favourable enough to justify their higher investment.

We therefore believe that nest loss and rain act as mechanisms triggering singing activity. The final decision whether to breed or not is reached through the joint effects of environmental factors and behavioural tuning in, mainly with duet 3.

2. Joint Territorial Advertisement of Pairs

Cooperative territorial defence by a mated pair is one of the most quoted functions of duetting, and some authors consider it the basic one (WATSON 1969; PAYNE and SKINNER 1970; TODT 1970, 1975; PAYNE 1971; TINGAY 1974; WICKLER 1976; HARCUS 1977; SEIBT and WICKLER 1977; WICKLER and SEIBT 1979, 1980; FARABAUGH 1982). The main arguments to support this hypothesis are:

1. Many duets are much too loud (and therefore unnecessarily risky) for conveying information to the mate alone.

2. Duets are often performed on treetops and other conspicuous places.
3. Hearing a duet elicits approach, counter-singing or even attack in resident pairs, just as with territorial songs in several temperate zone male birds.
4. Duets used in territorial advertisement are usually simple, and in some cases resemble territorial solo song.
5. Duets occur throughout the year, which corresponds with the fact that most duetters live in monogamous pairs defending their territories all year round.

Our study supported arguments 1, 3, and 5 for duet types 2 and 4. But why are there two different types?

A large and versatile repertoire could be advantageous if e.g. it increased nestbuilding activity and clutch size (cp. KROODSMA 1976) or conveyed the message of an exceptionally high density, thus causing roaming strangers of the own and other species to avoid the area ('Beau Geste Hypothesis', KREBS 1977; RECHTEN 1978).

However, in *L. funebris* the application of M2 and M4 was situation-specific, with M4 increasing over M2 during actual territorial disputes between pairs. This allows a different interpretation:

Joint effort in defence is probably needed only when the resident pair is actually threatened, but it seems to be superfluous for routine territorial advertisement. By using two different territorial songtypes, and changing their relative frequencies according to the degree of the threatening, a male can signal whether or not the female's help is needed. By changing her relative amount of answers to each of the two types a female can signal whether she is free to join the male in defence or is engaged in other activities such as incubating or brooding.

This provides sufficient information for both sexes and can help to avoid unnecessary cooperation and/or risk-taking. This is particularly important when eggs or young have to be cared for. This 2-song-type solution appears superior to and less ambiguous than an alternative, in which males signal the degree of threatening through differences in intensity or frequency of one songtype. Intensity differences are biased by distance and vegetation; frequency differences would require more time to pass the message. Two songtypes also seem superior to a solution in which females do not answer if they are occupied with other activities. This would weaken the territorial advertisement, as other birds could not distinguish this case from territorial defence by a single male alone.

The fact that the two songtypes are similar in their physical characteristics suggests that they may have split up from a common ancestor under selection pressure to make vocal communication as definite as necessary.

3. Mate-guarding

Probably because duetting is a cooperative display of two mated birds, most authors have described its adaptive significance in terms of a pair's com-

mon interests. This is probably true for many duets, including types 2 to 4 described in this paper for *L. funebris*. However, with unequal parental investment, each sex will tend to a reproductive strategy best furthering its own interests, and conflict here must be expected (TRIVERS 1972).

So far the only hypothesis about the function of duetting clearly allowing for conflicting interests between males and females was proposed by WICKLER (1980) and illustrated by WICKLER and SEIBT (1980). This considers the elaboration of pair-specific duets as an investment demanded by one mate to prevent the other from deserting. But this hypothesis was not applicable to our *L. funebris* results, as pair-specificity did not exist in our study population. Moreover, the hypothesis could not explain why duetting increased again after nest loss.

In accordance with our results and with the idea of conflicting interests between the sexes, we suggest a mate-guarding function of duet 1 (cp. WICKLER and SEIBT 1980; FARABAUGH 1982). In males of monogamous species a double reproductive strategy will be selected for: while closely guarding their own mates, to protect them from insemination by other males, they should strive to attract and fertilize as many additional females as they can. This prediction of TRIVERS (1972) has recently been supported by field studies on birds and mammals (BARASH 1976, 1981; HOOGLAND and SHERMAN 1976; BEECHER and BEECHER 1979; BIRKHEAD 1979, 1982; ALATALO et al. 1981; POWER et al. 1981). Polygamous tendencies in a male may lead to a reduction of his mate's fitness, e.g. if she is supplanted by a stronger bird or loses part of his parental investment to other females. Therefore females too should try to monopolize their males. This has received less attention than mate-guarding by males. But YASUKAWA and SEARCY (1982) have recently hypothesized that the function of female-female aggression is "to guard the nonshareable portion of the mate's parental investment".

Such sex-specific aggression and competition occurs in *L. funebris* as well, but the poor visibility in our study area allowed too few direct behavioural observations to estimate its extent.

Mate-guarding usually involves visual contact, close proximity, following the mate and attacking competitors, especially during egg-laying or oestrus (BEECHER and BEECHER 1979; BARASH 1981; BIRKHEAD 1982). But where visibility is reduced, as e.g. in dense vegetation, visual guarding of mates and detecting of rivals may become ineffective, even if birds are only a few m apart. Vocal supervision can be a suitable alternative. But although singing may help discourage rivals, complete guarding will only work if the mate responds. This seems equivalent to saying that the mate must have an "interest in being guarded", which sounds a paradox. But a bird can force its mate to respond if he uses a song with the potential of attracting other mates, and thus detracting from his own mate's fitness; he guards by being guarded.

This is apparently the main function of duet 1 in *L. funebris*. In accordance with the theory outlined above males sing (= court females and discour-

age males) and answer (= guard their mates) more than females do; and females answer (= guard) more when the risk of losing the mate is higher. Closely related to this territorial and mate-guarding function is the application of duet 1 in brood relief and in some (but not all) cases of disturbance.

4. Differences between Tropical and Temperate Zones

All three hypotheses outlined above are consistent with the prevalence of duetting in the tropics. Singing and answering can be restricted to males where females do not affect intermale competition for territories and mates. This is the usual pattern in many temperate zone birds with males arriving earlier than females. Moreover, resulting from strong external "zeitgebers" such as daylength most birds are well synchronized in arrival time and reproductive state. Therefore once pair formation has occurred, chances to attract additional partners and chances of being cuckolded are low for both sexes. Consequently singing can decrease markedly during and after pair formation, which indeed it does in many species (NICE 1943; ARMSTRONG 1963; THIELCKE 1970a, b).

But where males and females arrive in pairs or remain in the same area for prolonged periods, as many tropical species do, selection pressure for permanent and joint territorial advertisement must be high (FARABAUGH 1982) (*L. funebris* duets 2 and 4). Also the fitness of each sex cannot only be impaired directly by rivals of the same sex, but also indirectly by the own mate's activities bent on attracting such rivals. In addition, external "zeitgebers" and synchronization of gonadal activities are often weak. This not only necessitates a tuning in of mates (duet 3); it also has the effect that for several months of the year there may be some birds ready to copulate. Thus prolonged courtship song is promising for the singer, especially for males, but risky for the mate, who must turn the song into a duet to signal a claim on the courting bird (duet 1).

With respect to mate-guarding, duetting is functionally similar to counter-singing between territorial males. In both cases rivals of the same sex are discouraged.

It must be emphasized that our results and hypotheses on the structure and function of various duet types in *L. funebris* from Lake Baringo should not be generalized. Studies by THORPE (1972), HOOKER and HOOKER (1969), WICKLER (1972), SEIBT and WICKLER (1977) and our own investigations reveal tremendous variations between different *L. funebris* populations with respect to repertoire size in males and females, pair-specific differences in duet types, absolute frequency of solo songs and duets during the day and relative frequency of duets initiated by males and females. This calls for more detailed studies on the adaptive significance of different duet types in different populations and species. Nevertheless we feel that synchronization of mates, territorial advertisement of pairs and mate-guarding are among the most important and wide-spread functions of duetting.

Zusammenfassung

Duettgesang zwischen den Partnern eines Paares ist von zahlreichen Vogelarten bekannt. Zwar werden dem Duettieren im allgemeinen verschiedene Funktionen bei verschiedenen Arten zugestanden, aber innerhalb einer Art wird es gewöhnlich als einheitlicher Vorgang angesehen, auch wenn dasselbe Paar über mehrere Duettelemente verfügt. Diese Arbeit beschreibt an *Laniarius funebris*, wie verschiedene Gesangstypen verschiedenen Funktionen dienen.

In der untersuchten Population am Baringosee in Kenia verfügen die Männchen über vier Gesangstypen, die Weibchen über einen. Multivariate Analysen ergaben, daß sich das Auftreten der vier Männchen-Gesangstypen nicht mit einer einzigen, allgemeinen Tendenz zum Duettieren erklären läßt, sondern mit drei oder vier Faktoren, die verschiedene Funktionen repräsentieren.

Folgende Ergebnisse wurden erzielt:

Gesangstyp 3 dient der Abstimmung der Partner über den Beginn des Brütens. Die Typen 2 und 4 haben beide territoriale Funktionen, aber ihre relative Häufigkeit wechselt mit dem Grad der Bedrohung durch andere Paare und dem Grad der Kooperation zwischen den Partnern. Gesangstyp 1 wird mit einer Partner-Überwachungshypothese erklärt. In diesem Fall ist das Duettieren nicht ein Informationsaustausch im Interesse beider Partner, sondern der eine vollendet den Gesang des anderen zum Duett, um Solosingen zu verhindern, welches Rivalen anlocken könnte.

Die analysierten Funktionen werden im Rahmen soziobiologischer Aspekte diskutiert, vor allem hinsichtlich der größeren Zahl duettierender Arten in den Tropen gegenüber den gemäßigten Zonen.

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