Male-led duets in the Moho, *Hypergerus atriceps,* and Yellow-crowned Gonolek, *Laniarius barbarus*

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INTRODUCTION

Duetting, in which the male and female of a pair combine to give a single song, often with great precision, is something of an enigma (see Langmore 1998). It is more or less restricted to the tropics, and is also frequently associated with monomorphy (Catchpole & Slater 1995). Although it is known from laparotomy that the male leads the duet in certain species, e.g. in the Slate-coloured Boubou, *Laniarius funebris* (Wickler & Sonnenschein, 1989), the female has recently been found to do so in another monomorphic species, the Bay Wren, *Thryothorus nigricapillus* (Levin 1996a). This raised the possibility that female-led duets may be widespread, but as yet largely undetected. To test this we studied marked individuals of two monomorphic African duetting species, using recently developed molecular techniques to determine their sex from blood samples.

The two species chosen for the study are both common in The Gambia. While both duet, they differ quite markedly in their precise pattern of song (Fig. 1). The duet of the Moho, *Hypergerus atriceps,* also commonly known as the Oriole Warbler (Barlow *et al.* 1997), has previously been described by Grimes (1974), who compared it with that of the Grey-cappedWarbler, *Eminia lepida* from East Africa, the species' closest relative. The Yellow-crowned Gonolek, *Laniarius barbarus,* formerly called the Barbary Shrike, was one of the bush-shrikes studied by Thorpe (1972), who referred to the initiating call as 'presumably made by the male' (p. 122). A more detailed description of its duets is given by Grimes (1965, 1966). More extensive observations have been made on the closely related Slate-coloured Boubou (Sonnenschein & Reyer 1983).

METHODS

The study was carried out in The Gambia between 13 September and 3 October 1997. Birds were caught in mist nets using tape lures to attract them. Those caught were marked with colour rings and, in some cases, with small white patches of Tippex™on the wings, tail or lores, to allow identification at long range. Blood samples were taken by venipuncture of the brachial vein, stored in lysis buffer, and subsequently analysed in St Andrews to determine the sex of the bird using the method developed by Griffiths *et al.* (1998).

The songs of all pairs studied were recorded and the birds observed to determine the role each took in the duet. Allocation of elements to individual birds was easy in the Moho, as the trill of the follower only occasionally occurred to interrupt the regular singing rhythm of the leader. In the Gonolek, the contributions of the two birds were distinguishable as they could often be heard coming from quite separate locations.

In total, four Mohos from three pairs, and five Yellow-crowned Gonoleks, all from different pairs, were caught at the locations shown in Table 1. The two Mohos at Abuko could not be sexed,

and it did not prove possible to observe the role in the duet of these and of two of the Yellow-crowned Gonoleks. However, for two Mohos and three gonoleks both sex and role in duet were determined. Gonoleks duet frequently and often from exposed perches, so that between 10 and 100 duets were observed for each pair. Moho duets are less frequent and easy to observe, but the contribution of the marked individual was clearly seen during a bout of duetting in both cases.

RESULTS

Description of calls

Moho,Hypergerus atriceps

In the Moho the leading bird has several song types consisting of a repeated series of musical whistles, alongside which its partner sometimes produces a harsh rattling trill. Extensive recordings and observations of six pairs produced no instance where the second bird started to sing without the first doing so already, nor was there any evidence that the two members of a pair could adopt either role. It was thus clear that in each pair one sex is the leader and the other the follower.

Yellow-crowned Gonolek,Laniarius barbarus

In the Yellow-crowned Gonolek the bird that usually leads (Bird A) again has several different call types, but these are very brief and simple, and are very frequently followed by 1–3 calls in response from its partner (Bird B), with a remarkably short reaction time so that the calls overlap with each other. As Grimes (1965, 1966) noted, however, occasionally the call of the bird that usually follows may precede that of its partner, but this is much less frequent than the other sequence. We analysed 50 bouts of singing sonagraphically (Signal RTS system) and found six that consisted only of the contribution of Bird A and none that were only of Bird B; 34 were ofAfollowed by B and 10 of B followed by A. Thus, where both birds take part, A is much more often the leader _

$_2$=13.1, *P*=0.0003). Latencies varied considerably, with particularly long ones noted when the birds were singing far apart. Conversely, when the birds were perched together, they sometimes started near simultaneously. This raises the possibility that second bird is responding not to the sound, but to visual stimuli from the first that indicate it is about to sing.

0030-6525 Ostrich (March 2002) 73(1&2): 0–0 1

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Slater, P.J.B., Gil, D., Barlow, C.R. Graves, J.A. 2002. Male-led duets in the Moho, *Hypergerus atriceps,* and Yellow-crowned Gonolek, *Laniarius barbarus.* Ostrich 73(1&2): 00–00

Many duetting species are monomorphic and the suggestion has recently been made that duets may be female-led more often than has been supposed in the past. Observations were carried out on several marked individuals of two monomorphic duetting species, the Moho, *Hypergerus atriceps,* and Yellow-crowned Gonolek, *Laniarius barbarus,* in The Gambia. DNA analysis from blood samples revealed that in each case the male was the pair member that normally led the duet. It is suggested that duets of this sort may arise where it benefits a male to attract more than one female, but it is to the female's disadvantage that he should do so.

The role of the sexes

The results are summarized in Table 1. The three Yellowcrowned

Gonoleks that were sexed and had also been observed to duet were all males, and all of them were the usual leader (Bird A) in their duet. Of the two Mohos that were sexed, one was male and one female. The former was the leader in its duet, whereas the latter was the follower. Thus all the data obtained pointed to the male being the usual leader of the duet in both these species.

As their territories can cover several hectares, capture of all birds required tape-luring, and this probably explainswhya preponderance of those caught (6/9) were males and duet leaders; presumably the male is thus the more territorial sex. However, three of the birds that were caught were female, if one includes one of the AbukoMoho pair (see Table 1), indicating that in both species, females are also to some degree attracted to tape lures. Observations on Mohos at Marakissa and at Tanji Bird Reserve, indicated that both members of a pair are frequently attracted and reply to playback by duetting.

DISCUSSION

Both species studied here have large territories and are highly mobile, often spending their time in dense undergrowth or tall trees. Even using tape lures, catching them was not easy, and observing marked birds subsequently also presented problems.

Sample sizes are thus necessarily small, although this is not problematic with the particular question posed. From many hours of observation on both marked and unmarked pairs, there was no evidence that the two members of a pair could produce either vocalization. Nor is it likely on the basis of previous studies that pairs differ in which sex sings the two different parts. Thus it is clear from the results that the male produces the part that normally leads the duet in both species, unlike the situation in the Bay Wren (Levin 1996a,b). Levin suggested that the female is the more territorial sex in this species, that her song excludes other females and attracts males, and that the male adds his part to her song to label her as being mated and thus exclude other males. His part is therefore the equivalent of mate guarding, as found in many male animals. A similar proposal had earlier been made by Sonnenschein & Reyer (1983) on the basis of their studies of Slate-coloured Boubous, except that they argued that one duet in this species functioned in mateguarding by both sexes, while others had territorial and pair-bonding roles. These duets appear more varied and complex than those of Yellow-crowned Gonoleks or Mohos, but this may be because their study was a longer-term one, making it possible to detect changes with the stage of the breeding cycle.

In the male-led duets reported here, it is possible that something equivalent to the mate guarding Levin found may be going on, but with the less usual situation that it is predominantly the female that guards the male. Male song is likely to attract females, but it would benefit the female to label him as being mated by duetting if her breeding success would be reduced if he succeeded in attracting a second mate. This could occur if the male normally assists with incubation and care of the young, as is often the case in monomorphic species (and known

TABLE 1.Details of location, sex and role in the duet of all the birds studied.

Location	Identity (rings)	Sex	Wing length (mm)	Normal role in duet
Moho				

Marakissa Red/white F ? Follower
Kembujeh White/red M 80 Leader
Abuko Yellow/blue ? 83 ?
Abuko Pink/red ? 79 ?
Yellow-crowned Gonolek
Kembujeh Blue/yellow M 106 Leader
Kembujeh White/black M 101 ?
Kembujeh White/yellow M 105 Leader
Kembujeh Yellow/black F 95 ?
Kembujeh White/red M 103 Leader

FIG. 1. Tracings of sonagrams of duets of the two species studied, in both cases with elements of the leader (Bird A) shown black and those of the follower (Bird B) in white. The upper trace is part of a Moho song, in which the whistles of the leader are accompanied by the rapid trill of the follower. The lower trace shows two duets from one pair of Yellow-crowned Gonoleks and one from another.

to occur in Slate-coloured Boubou, Sonnenschein&Reyer 1984). It would therefore not be surprising if a male with two females left more offspring than a male with one, whereas a female left fewer if her male had a second partner than if she was his only one. It is in these circumstances thatwepredict it would benefit a male to sing to attract a second female, but it would also benefit his mate to warn off such a female and for that female to heed the warning and continue her search for an unmated male. Indeed, in addition to warning off other females, it might benefit a female to 'jam' her partner's signal by singing as near simultaneously as possible with him and in the same frequency range, as is the case in both these species (see Fig. 1). This suggestion, that males may benefit from polygyny, while monogamy is more likely to be advantageous to females, has been put forward to explain polyterritorial polygyny in the Pied Flycatcher, *Ficedula hypoleuca* (Alatalo & Lundberg 1990), and nest destruction by secondary females in Great Reed Warblers, *Acrocephalus arundinaceus* (Hansson *et al.* 1997), as well as aspects of the complex breeding system of the Dunnock, *Prunella modularis* (Davies 1992).

Little is known about the breeding systems of Mohos and Yellow-crowned Gonoleks, though we observed two females responding to the song of a male Yellow-crowned Gonolek on one occasion, and three Mohos approaching a tape lure on another. From the idea put forward here we would predict that male-led duets would occur in species where the male assists in care of the young, but where females lacking that assistance or sharing it with another can average more than half the number of young raised by monogamous pairs. It would thus benefit a male to attract a second female, while not benefiting one female to share her mate with another. The critical factor is the existence of a conflict of interest between male and female, an idea in marked contrast to the cooperative basis ofmany earlier theories of duetting (see Farabaugh 1982).

ACKNOWLEDGEMENTS

We thank the Department ofWildlife and Conservation in The Gambia for permission to carry out this work, and particularly Paul Murphy for his assistance there. Mrs Fumeke Sarr also helped us in The Gambia, and Dr Samuel Palmer gave permission for us to work at Corbola Farm, Kembujeh. We are also grateful to Richard Griffiths, both for advice and for providing

us with the primer sequences used to sex the birds, to Pat Sellar for helpwith some observations in the field and with sonagrams, and to Michelle Hall and Steve Rothstein for comments on the manuscript. This study was partly funded by a grant to P.J.B.S. from the Royal Society of London.

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Received February 2000. Accepted April 2000
Editor: R. Slotow