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An acoustic postconflict display in the duetting tropical boubou (*Laniarius aethiopicus*): a signal of victory?

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Abstract

Background: In many species of birds, pair bonded males and females precisely co-ordinate their vocalisations to form duets. Duetting behaviour, although still somewhat of an enigma, is thought to function primarily in territorial defence and mate guarding. We identify an additional function of duetting in an afrotropical bird, the tropical boubou (*Laniarius aethiopicus*), that uses one duet type as a postconflict display probably to advertise victory to other boubous.

Results: We simulated intrusions into boubou territories in the field in Ivory Coast, West Africa using playbacks of four different types of boubou duets to test the use of the presumptive acoustic victory display before, during and after playbacks. These staged encounters resulted in either retreat of the focal birds during playback or continued presence accompanied by vocal displays after playback had ceased. Losers of encounters never sung after retreating whereas 11 out of 18 pairs sung the presumptive victory duet after the encounter. Analysis revealed that the presumptive victory display was sung significantly more often after than before or during the playback treatment.

Conclusion: We conclude that, most likely, the investigated duet type is a postconflict victory display – a novel function of duets. Furthermore the duet is a rare example among birds of a context-specific song. The conspicuousness of the display suggests that it is directed not only to losers of an agonistic encounter but also to other pairs of birds in neighbouring territories.

Background

Much theoretical and empirical work has been conducted on signals and signalling behaviour before and during agonistic interactions as well as the evolution of contest behaviour [e.g. [1-3]]. In addition, signalling behaviour that occurs after an encounter has ended can be very important if it reduces the costs of further contests between rivals. Indeed, communication network theory predicts that postconflict displays should be more common than reported [4]. In song birds, it has been demonstrated that males increase their song rate after playback [reviewed in [5]] or use special quiet singing during playback and shift to normal full singing after playback [6,7]. Distinct postconflict displays have been identified as appeasement signals [8] or could be used to stabilise the pair bond [9]. When postconflict displays are used by winners of an encounter, but not by losers, such displays have been described as victory displays [10].

We describe a distinct postconflict display in the duetting tropical boubou (*Laniarius aethiopicus*) an afrotropical bird with extensive duetting behaviour in which pair-bonded males and females sing highly synchronised songs [11]. Tropical boubous are socially monogamous

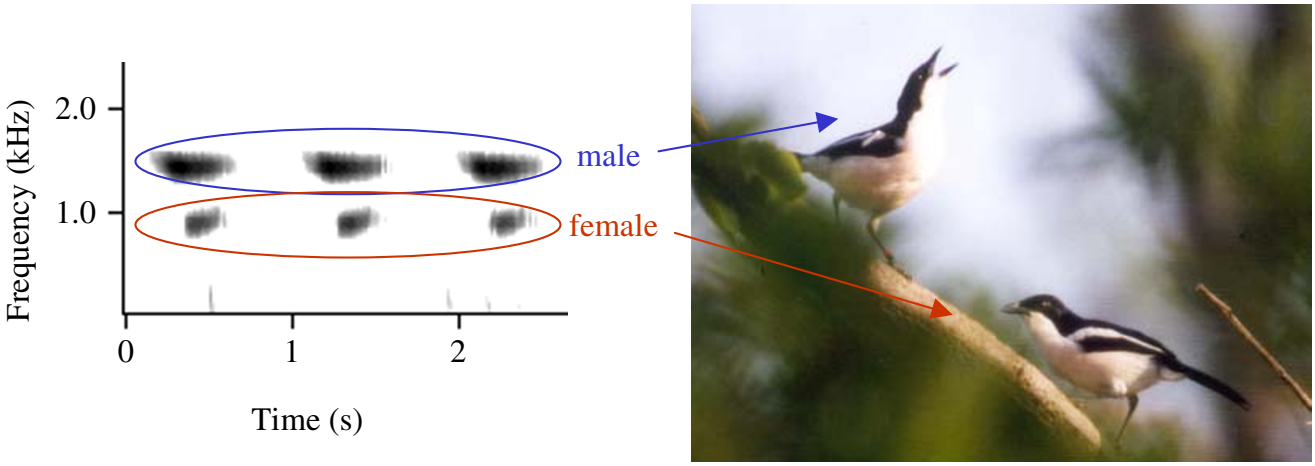

Figure 1
Spectrogram of the presumptive victory display (duet type 5) and photograph showing a pair of duetting tropical boubous, *Laniarius aethiopicus*. Only the initial three repetitions of the duet are shown. Males always sing the top notes, females the bottom notes.

and maintain territories throughout the year. The function of duets in birds is poorly understood. In general, duets could function in territorial defence, maintain the pair-bond, or be a form of acoustic mate-guarding [e.g. [12-15]].

So far we have identified a repertoire of 12 duets in the tropical boubou with each sex maintaining a sex specific role in the duet. Some duets are initiated by the male while others are initiated by the female [16]. Multiple lines of evidence suggest that both joint territorial defence and mutual mate-guarding are important functions of duetting in tropical boubous and that both co-operation and conflict between males and females have shaped duetting behaviour [17].

During our study of the function of duetting we noticed that, after simulated territorial intrusions using acoustic playbacks, one male-initiated duet (Fig. 1) was nearly never used during encounters in which birds sang between 50–200 duets. Instead, this duet was nearly always sung when we ended the playback, often after the recording equipment had been packed away and we were leaving the territory. Particularly striking was that this duet was sung from a higher perch and appeared louder than other duet types.

In this paper we describe in detail a novel duet type and the context in which it is sung. We hypothesise that this duet, termed duet type 5 [16], is used as an acoustic victory display by the winning pair after an agonistic territorial encounter. We predict that winners should sing the victory duet after but not during or preceding an encounter. In contrast, losers should never sing this duet after a territorial conflict. The use of duets as a postconflict display has not been proposed before.

Results

Duet type 5 (Fig. 1), the presumptive victory display, was sung significantly more often after than before or during the playback treatment (McNemar test, $\chi^2 = 4.9$, $p < 0.03$; Fig. 2) suggesting that this duet functions specifically as a postconflict display. 11 out of 18 pairs responded with duet type 5 as the first and only duet sung within 30 min after a distinct postencounter silent period, whereas it was sung during the pre-stimulus period in only two cases (pairs 4 and 10) and the playback period in one case (pair 7; Fig. 2). When sung after an encounter, duet type 5 was

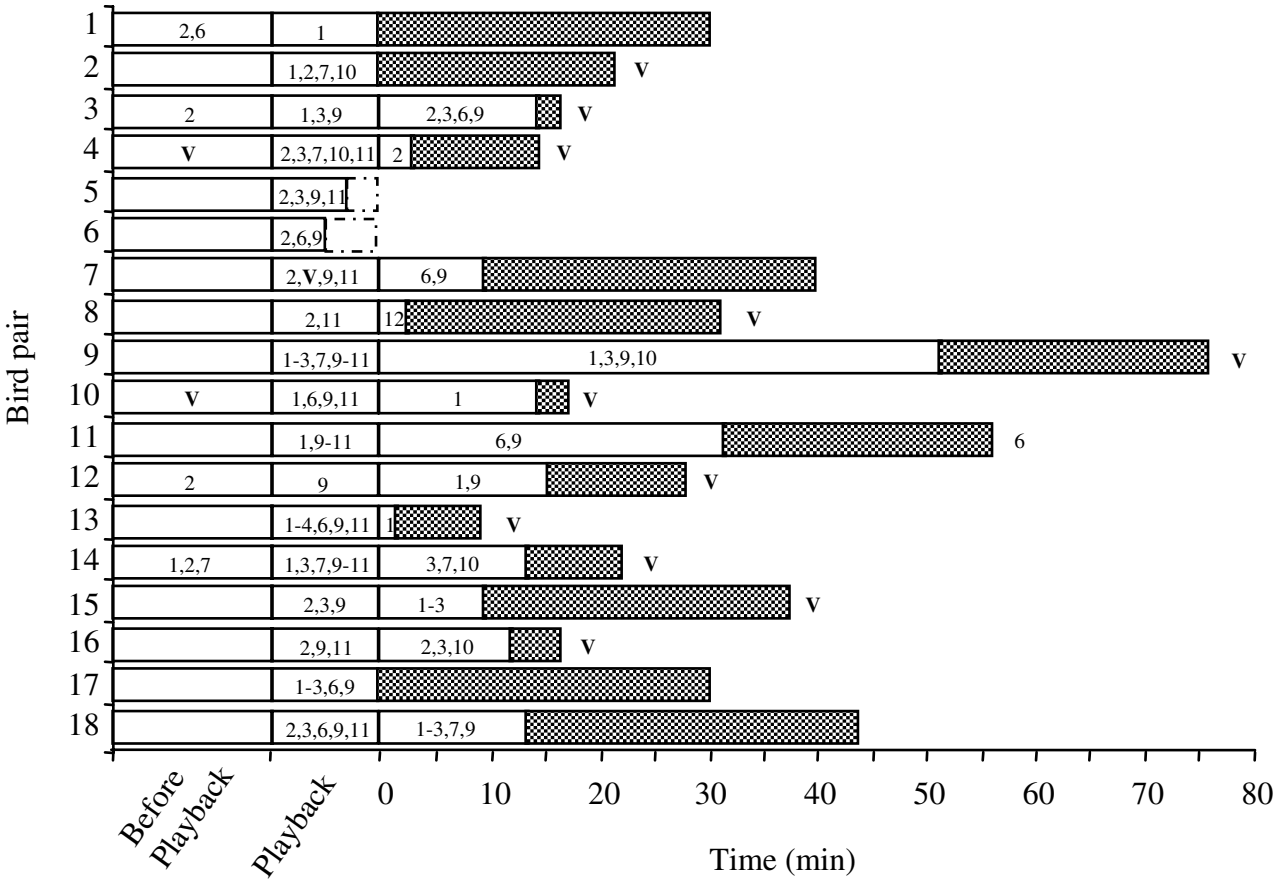

Figure 2
Occurrence of duet type 5 in tropical boubous in response to playbacks of duet types 1 (pairs 1–3), 2 (pairs 4–8), 6 (pairs 9–13), and 9 (pairs 14–18) [16]. White bars show duration of the period before playback, the playback period, and the period of continuous singing after playback. Shaded bars show duration of the silent period following playback. Numbers and letters indicate the duet types used. V stands for duet type 5. Pairs 5 and 6 stopped duetting prior to the end of the playback period (dashed lines).

always preceded by periods of prolonged silence ranging between 2.5 – 29 min. Two pairs (1 and 17) also sang duet type 5 more than 30 min after the end of the silent period (38 and 59 min, respectively), suggesting that an even stronger case could be made for duet type 5 as a postconflict display if the experimental protocol had required a longer recording period to follow the silent period. Only pair 11 sang a duet type other than duet type 5 after the distinct silent period following the encounter (Fig. 2).

Two pairs stopped responding during the playback period, disappeared from sight and were not seen or heard to vocalise 30 min after the playback ended (pairs 5 and 6). Most importantly, these pairs did not sing duet type 5 after departing. Three additional observations, unrelated to these sets of experiments (data not shown), were made of pairs leaving the vicinity of a playback after a vocal duel without these pairs singing the presumptive victory display. These pairs could be regarded as having lost the encounter.

In contrast, 16 pairs remained in the vicinity of the playback during and after the playback. These birds were given the impression of winning the territorial encounter. There was a trend for presumptive winners to sing duet type 5 after the playback (two-tailed binomial, $p < 0.07$).

Duet type 5 resembled and differed from other duets sung by the tropical boubou [16]. Like other duets, the notes sung by males and females were highly synchronised

tonal notes that were often repeated within a duet. It differed, however, in several notable design features from other duet types. First, male and female notes typically overlapped completely (Fig. 1). Second, the duet was significantly longer than other duets (33.3 ± 22.3 s, range 10.9 – 80.2 s, n = 14 and 1.3 ± 0.4 s, range 0.6 – 3.0 s, n = 56, respectively; Mann-Whitney U-test, $n_1 = 14$, $n_2 = 56$, z = -5,756, $p < 0.001$) with the motif (male and female note) sung on average 38.9 ± 25.3 times (range 14–91; n = 14). Third, male notes reached significantly higher dominant frequencies (initial male note 1535 ± 33 Hz, n = 13) than in most other duets (722 ± 21 Hz, n = 50; Mann-Whitney U-test, $n_1 = 13$, $n_2 = 50$, z = -5.52, $p < 0.001$).

Discussion

We identified one duet type of the tropical boubou as a postconflict display. Postconflict displays may have several functions. They may be appeasement signals typically used in social groups such as primates during peacemaking [8] or may be used to stabilise the pair bond after a conflict with neighbours [9]. Both hypotheses predict that both winners and losers should show the display. In primates, for example, appeasement signals are typically shown by both opponents [e.g. [18]]. Postconflict displays may also be used to signal victory. When used in this context, by definition, only the winner(s) will perform the victory display [10].

Although we have identified one duet type as a postconflict display it is less clear what the function of this duet is. Unfortunately, we were not able to rigorously classify birds as winners or losers. Birds that had left the playback area may simply have lost interest in the playback. However, our observations that pairs that fell silent and departed from the playback area, never sung duet type 5 and the trend for presumptive winners to sing this duet are consistent with the idea that this duet is used as a victory display.

Most birds continued to sing immediately after we ended the playback so that many other duet types were sung after the encounter. Interestingly, however, duet type 5 was only sung after a distinct period of silence following playback. Our interpretation is that this unusual duet was used when birds were certain that our playback had ended, i.e. the intruders had left the area. This may be more difficult to determine in the dense vegetation in which these tropical birds live than in temperate-zone songbirds that have been the subjects of most bird song playback studies.

It would appear that the long time (10–77 min) that passes between the end of the playback and the use of duet type 5 might argue against its use as a victory display because it might be difficult for receivers to associate the duet with the outcome of the encounter. However, some primate studies have indicated that postconflict behaviour may be shown one hour after the end of aggressive interactions (e.g. [19]). Furthermore, time frames of behavioural responses, in our case to termination of playback, may not be simply immediate but involve broader time frames of tens of minutes, hours or days [20].

We were able to hear the male note of the victory display across two territories, further than notes of other duet types. In addition, it was typically sung from higher perches than other duets (Grafe and Bitz unpublished). Thus, the display's conspicuousness suggests that it is directed to individuals outside the social group, potentially beyond the neighbour's territory, not at the partner, and thus is unlikely to be used primarily to stabilise the pair bond after a conflict with neighbours.

Not many victory displays have been identified because studies of agonistic interactions in animals have often focused on signals and signalling behaviour before and during the encounter and because such displays may not be as distinctive as in boubous. Funnel-web spiders manipulate the web or prey after winning an encounter [21], winning crickets stridulate after encounters [22] and little blue penguins give a bow flipper display after winning [23] while losers show none of these behaviours. More recently, Bower [5] describes an acoustic victory display in song sparrows after naturally occurring territorial encounters in which winners sang at higher rates after winning an encounter than losers.

The presumptive victory display in the tropical boubou is unique in that it is a highly synchronised duet. This suggests that there is a joint interest in deterring future intrusions. The vigour of the display, however, differs between males and female showing striking asymmetries: the duet is always initiated by the male and he sings at a higher amplitude whereas female often skips notes (Grafe and Bitz unpublished). These display features suggest that males may have more to gain from advertising their success than females.

Duetting in the tropical boubou appears to serve multiple functions. Most duet types are used for territorial defence [17], however, the duet type described in this study is used specifically as a postconflict signal. We are aware of only one other example in which a single song or song motif is used by birds in such a specific context. Sonnenschein and Reyer [12] suggest that two duet types, sung by the slate-coloured boubou, are used specifically to synchronise breeding and in mate-guarding, respectively. Generally, songs within a repertoire are used interchangeably [24-26].

Why did one pair sing the victory display during the playback period when the encounter was persisting? It appears that birds may have misidentified that the playback period was not yet over. This can occur when birds, for whatever reason, stop singing and we stopped presenting the playback stimulus according to the interactive playback protocol. It should be noted that the victory duet was shorter than average in this case (23 motif repetitions) and the focal pair switched to other duet types immediately after hearing the playback again.

There is ample evidence that communication takes place in a network of interacting individuals with reproductive decisions influenced by such information (e.g. [4,27]). The conspicuousness of the presumptive victory display in the tropical boubou, which needs to be further documented, suggests that it might be directed to an audience of receivers not directly involved in the interaction (reviewed in [28]). The presence of an audience is predicted to enhance the value of victory by reducing the number and intensity of future encounters and escalated conflicts should occur more frequently when audiences are present [3]. It will be interesting to test these predictions in the future.

Conclusions

We conclude that the tropical boubou uses one duet type as a postconflict display to signal victory. Paired birds sang the presumptive victory display significantly more after than before or during playbacks of four different duet types. This suggests that this acoustic display is a general context-specific response to a territorial encounter. Use of duet type 5 as an appeasement signal seems very unlikely because we never heard pairs of birds responding to each other with this duet. Likewise, it is unlikely to be sung to stabilise the pair bond after a territorial encounter because signal intensity suggests it is directed to receivers outside the territory. Instead, timing and conspicuousness of duet type 5 is consistent with its use as a victory display. Boubous appear to be the first bird species to use a different kind of song after playback than before or during playback.

Methods

Study area and species

The tropical boubou (*Laniarius aethiopicus*, Malaconotidae) is widely distributed throughout tropical Africa. We studied the vocal repertoire and the function of duetting in the southern Guinea savannah region of the Comoé National Park, Ivory Coast. The acoustic behaviour of the tropical boubou has been studied in East Africa [11]. Paired birds defend territories year round. The sexes cannot readily be distinguished because they are monomorphic in plumage coloration. Molecular sexing of birds in West Africa have shown that both males and females initiate duets with each sex maintaining a sex specific acoustic role [16].

Data analysis and experimental protocol

Experiments were conducted during the early breeding season in June and July 2001 after the first rains of the season. We incited territorial responses by broadcasting recordings of four different male-initiated duet types (1, 2, 6, and 9), often used by boubous during territorial encounters [17], to 18 pairs of birds. Within a duet type, a different stimulus, each from a different pair of birds from the population, was taken for each playback. Since the replicates for each duet type were small (3, 5, 5, and 5, respectively) the data were pooled to evaluate the overall effect of intrusion irrespective of duet type.

The stimulus was played from within the territory or at its border using a Sony WM D6C tape recorder, a Canton XC loudspeaker and a customised amplifier. Peak playback sound levels were approximately 76 dB SPL at 10 m (measured using a Brüel & Kjaer 2236). We started the playback at a rate of 12 duets/min. As soon as the focal pair responded, which was typically within a few minutes, we immediately switched to an interactive playback with a duet presented for each duet sung by the birds.

A pre-stimulus period of 15 min preceding the playback was observed to assess baseline activity and for comparison with post-stimulus singing behaviour. The interactive playback period lasted 10 min and typically evoked strong vocal responses by the resident pair. In most cases (13 out of 18), birds kept singing after we stopped our playback at high but decreasing levels. Preliminary playbacks had shown that duet type 5 was often sung after a period of silence in which the birds typically remained in the vicinity of the playback area. We regarded pairs that left the vicinity of the playback before it had ended as losers whereas pairs that remained close by throughout the playback were classified as winners of the encounter. To evaluate vocal activity after longer silent periods (> 2 min) we continued to record for 30 min after birds had "stopped" singing. In two cases, in which birds stopped singing before the end of the playback, the 30 min postsilence observation period started at the end of the playback session. Thus, we had an equal postsilence observation period of 30 min for all pairs. We noted the duet types sung before, during and after the playback period. We recorded vocalisations using a Sony WM D6C tape recorder and a Sennheiser MKE 300 microphone and digitised these using Canary or Syrinx.

We measured the spectral and temporal components of the elements of the presumptive victory display (duet type 5). Sample sizes vary between comparisons because not

all acoustic parameters could be equally well measured due to background noise and the quality of recordings.

Author's contributions

The project was initiated and designed by TUG who also interpreted the results and wrote the manuscript. Most of the work in the field was conducted by JHB. Data was analysed jointly by both authors.

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References

1. Maynard Smith J: *Evolution and the theory of games Cambridge: Cambridge University Press*; 1982.
2. Huntingford FA, Turner AK: *Animal conflict London: Chapman & Hall*; 1987.
3. Johnstone RA: **Eavesdropping and animal conflict.** *Proceedings of the National Academy of Sciences USA* 2001, **98:**9177-9180.
4. McGregor PK, Peake TM: **Communication networks: social environments for receiving and signalling behaviour.** *Acta Ethologica* 2000, **2:**71-81.
5. Bower JL: **The occurrence and function of victory displays within communication networks.** In: *Communication networks* Edited by: *McGregor PK. Cambridge: Cambridge University Press* in press.
6. Dabelsteen T: **Quiet singing in song birds: an overlooked phenomenon.** *Bioacoustics* 1998, **9:**89-105.
7. Dabelsteen T: **Public, private or anonymous? Facilitating and countering eavesdropping.** In: *Animal Communication networks* Edited by: *McGregor PK. Cambridge: Cambridge University Press* in press.
8. Aureli F, Cords M, Schaik CP: **Conflict resolution following aggression in gregarious animals: a predictive framework.** *Animal Behaviour* 2002, **64:**325-343.
9. Wickler W: **Vocal duetting and the pair bond. I. Coyness and partner commitment. A hypothesis.** *Zeitschrift für Tierpsychologie* 1980, **52:**201-209.
10. Bradbury JW, Vehrencamp SL: *Principles of animal communication Sunderland: Sinauer*; 1998.
11. Thorpe WH: **Duetting and antiphonal song in birds.** *Behaviour Supplement* 1972, **18:**1-193.
12. Sonnenschein E, Reyer H-U: **Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*).** *Zeitschrift für Tierpsychologie* 1983, **63:**112-140.
13. Langmore NE: **Functions of duet and solo songs of female birds.** *Trends in Ecology and Evolution* 1998, **13:**136-140.
14. Hall ML: **The function of duetting in magpie-larks: conflict, cooperation, or commitment?** *Animal Behaviour* 2000, **60:**667-677.
15. Seddon N, Butchart SHM, Odling-Smee L: **Duetting in the subdesert mesite *Monias benschi*: evidence for acoustic mate defence?** *Behavioral Ecology and Sociobiology* 2002, **52:**7-16.
16. Grafe TU, Bitz JH, Wink M: **Song repertoire and duetting behaviour of the tropical boubou (*Laniarius aethiopicus*).** *Animal Behaviour* in press.
17. Grafe TU, Bitz JH: **Functions of duetting in the tropical boubou (*Laniarius aethiopicus*): territorial defence and mutual mate-guarding.** *Animal Behaviour* in press.
18. Waal de F: *Peacemaking among primates Cambridge: Harvard University Press*; 1989.
19. Rolland N, Roeder JJ: **Do ringtailed lemurs (*Lemur catta*) reconcile in the hour post-conflict?: a pilot study.** *Primates* 2000, **41:**223-227.
20. Owings DH, Morton ES: *Animal vocal communication Cambridge: Cambridge University Press*; 1998.
21. Reichert SE: **Games spiders play: behavioral variability in territorial disputes.** *Behavioral Ecology and Sociobiology* 1978, **3:**135-162.
22. Hack MA: **The energetic costs of fighting in the house cricket, *Acheta domesticus* L.** *Behavioral Ecology* 1997, **8:**28-36.
23. Waas JR: **An analysis of communication during aggressive interactions of little blue penguins (*Eudyptula minor*).** In: *Penguin biology* Edited by: *Davis LS, Davis D. San Diego: Academic Press*; 1990:366-371.
24. Catchpole CK, Slater PJB: *Bird song Cambridge: Cambridge University Press*; 1995.
25. Searcy WA, Nowicki S: **Functions of song variation in song sparrows.** In: *The design of animal communication* Edited by: *Hauser MD, Konishi M. Cambridge: MIT Press*; 1999:577-595.
26. Burt JM, Campbell SE, Beecher MD: **Song type matching as threat: a test using interactive playback.** *Animal Behaviour* 2001, **62:**1163-1170.
27. Mennill DJ, Ratcliffe LM, Boag PT: **Female eavesdropping on male song contests in songbirds.** *Science* 2002, **296:**873.
28. Matos R, Schlupp I: **Performing in front of an audience – signallers and the social environment.** In: *Communication networks* Edited by: *McGregor PK. Cambridge: Cambridge University Press* in press.