

Territorial response to bioacoustic playback in *Copsychus albospecularis*, Madagascar magpie-robin, in Kirindy Forest

Victoria Betts, Writtle College, University of Essex, United Kingdom

Henry Massa Makuma, Makerere University, Uganda

Christine Wu, University of Vienna, Austria

**Fidelis Atuo, A.P. Leventis Ornithological Research Institute, University of Jos,
Nigeria**

Abstract

Copsychus albospecularis is a common bird endemic to Madagascar, with sub-species *C. a. pica* occurring in Kirindy dry deciduous forest. Bioacoustic playback experiments were conducted in order to observe territorial behaviours of male and female birds in eight territories. Two types of playback tracks were used for the experiments – repetitive ‘repeat-mode’ and diverse ‘serial-mode’. Four behavioural variables were recorded in order to ascertain differences between male and female territorial response, and differences in response to each mode of playback.

Male response to both types of playback was significantly higher than female, showing a significant increase compared to before playback. Male behaviour differed in response to repeat- and serial-mode playbacks, indicating distinct functional roles for the two song modes.

INTRODUCTION

The unique nature of biotic interactions in Madagascar has long attracted the focus of researchers. The combination of high levels of endemism and diversity and high rates of habitat loss make Madagascar one of the world’s conservation priorities (Pons & Wendenburg, 2004; Alder, 1994). The West Madagascan dry forest is one of the 218 Endemic Bird Areas (EBAs) in the world (Fishpool & Evans, 2007). Here we report on the song function of one of Madagascar’s endemic bird species, the Madagascar magpie-robin *Copsychus albospecularis*.

Bird songs permit efficient, long-range communication and serve a variety of functions, facilitating species recognition, mate attraction and territorial defence, mediated by male-male contests (Catchpole & Slater, 2008). In approximately three quarters of bird species, each male sings more than one type of song (Kroodsma, 1982). Kroodsma’s (1982) anti-habituation hypothesis predicts that variety should prolong the listener’s response during song presentation. Previous studies demonstrated that male territorial birds settle down faster after heavy repetitive modes than serial modes (Stoddard

et al., 1987). Large song repertoires have also been shown to be important in female mate choice (Catchpole & Slater, 2008).

Magpie-robins produce high-pitched, harmonious and variable songs from an elevated perch (Sinclair & Langrand, 2003). Our preliminary observations indicated that males sometimes produce long strings of the same song type ('repeat-mode' singing), while at other times they produce much more varied song sequences ('serial-mode' singing). Along with the abundance of the species in Kirindy, this made them an ideal subject for investigating the function of different singing modes using sound playback experiments. It should be noted that females also occasionally sing (personal observation), adding further complexity and interest to the bioacoustic communication system of the species.

Two questions were addressed. Firstly, does the territorial response of male and female magpie-robins to bioacoustics playback differ significantly? Secondly, does the territorial response of male and females differ between two types of playbacks – serial-mode and repeat-mode? These questions led to the development of two hypotheses. H₁ was that male and female territorial responses to playback differed. H₂ was that magpie-robin responses to repeat- and serial-mode playbacks differed.

METHODS

Study area

The study was conducted in the Kirindy forest (20° 03' S, 44° 39' E) (Figure 1), 60 km northeast of the city of Morondava in the Menabe region of west-central Madagascar. Kirindy forest is a dry deciduous forest, approximately 12,000 ha in size. It is a fragment of an ecosystem that was once considerably more widespread in Madagascar and is endangered worldwide, mostly due to the impact of slash-and-burn (Langrand, 1990). It has a tropical dry climate with a hot wet season (November-March/April) and a dry season (April/May-October). Mean annual temperatures are 24.7 °C with mean maximum temperatures and mean minimum temperatures of 30.7 °C and 19 °C respectively. Rainfall averages 799 mm per year.

Study species

Langrand, (1990) noted that the magpie-robin (family Turdidae) is one of only 7 species of Madagascan birds with an oriental origin, with most of the avifauna being Afro-tropical. The species has a distinctive pied plumage with some sub-species variation. In the *C. a. pica* sub-species (Langrand, 1990) at Kirindy forest, males are black and white, while females are grey-brown and white. Magpie-robins are primarily insectivorous, but also consume berries and other fruit. They

inhabit various primary forest types, as well as secondary growth, woodland savannah, mangrove, arboricultural areas (coffee and banana plantation) and wooded surroundings of towns and villages.

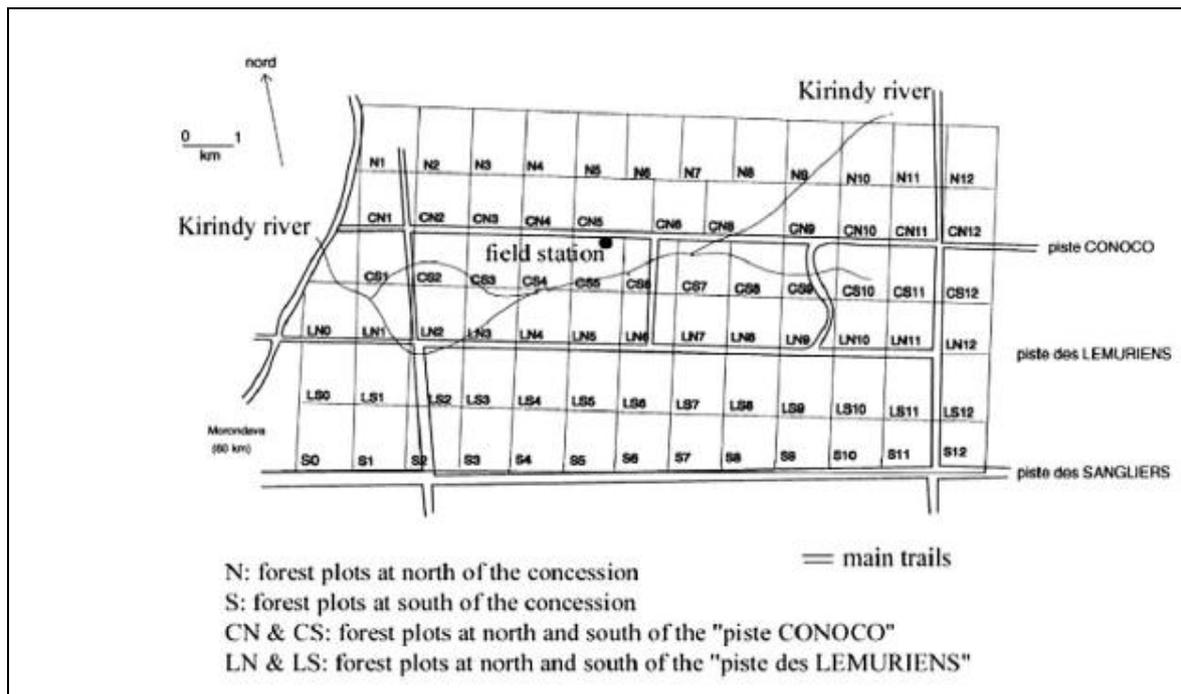


Figure 1. Map of the Kirindy forest (CFPF forest concession). The letters and numbers indicated the different forest plots. The field station was located near the 'piste Conoco'. Field studies were performed in the plots CN-4, CN-5 and CN-85 (source Chouteau, 2004).

Song characteristics and definitions

A hierarchy was used to describe components of bird song. A 'song' is comprised of multiple phrases separated by short pauses. A 'phrase' is a discrete unit comprised of 2 or more adjacent syllables. A 'syllable' is a discrete unit of 2 or more individual notes. Figure 2 shows a labelled magpie-robin sonogram of this hierarchy.

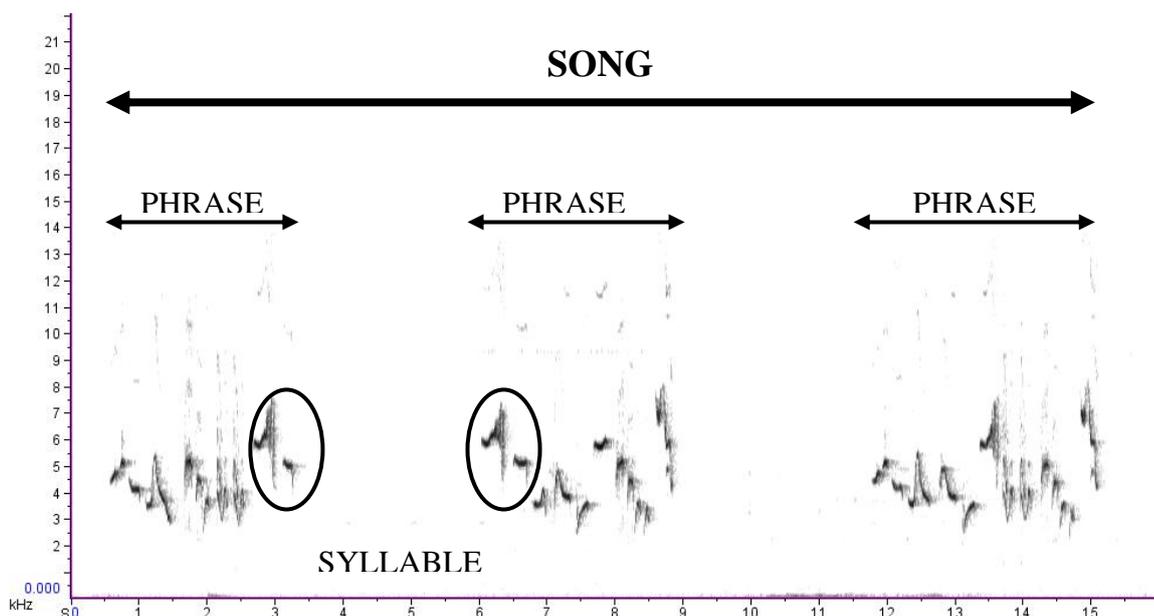


Figure 2. Labelled magpie-robin sonogram showing definitions of song, phrase and syllable.

Preliminary observations and bioacoustic recording

Pilot observations of the behaviour of the magpie-robins were undertaken in Kirindy forest for nine days between 2nd and 10th November 2010. Male songs were recorded using a Marantz PMD 660 recorder and Sennheiser ME66 directional microphone. Recordings were processed using Raven Lite 1.0 (Maher *et al.*, 2009), GoldWave (Craig, 2001) and Avisoft-SASLab Pro (Specht, 2006) bioacoustic software to create tracks suitable for bioacoustic playback. Territorial response to bioacoustic playback was tested during pilot studies.

Mist-netting and colour ringing

Colour rings were applied to male magpie-robins in 8 territories to permit future identification and confirmation of territories. Birds were trapped by luring them into mist nets with the use of playback. Individuals were weighed and measurements of wing length, tarsus and beak length were recorded. Approximate age of each individual was established prior to release by means of feather moult patterns.

Bioacoustic playback format

‘Serial’ (a series of different song phrases) and ‘repeat’ (one repeated song phrase) mode playback sequences were constructed from the recordings. 5 serial and 5 repeat tracks were made using 15 distinct song phrases clipped from the species song recordings. Sound was filtered below 1.5 KHz and above 9.0 KHz frequency and the amplitude approximately equalised across tracks by altering the volume of phrases. Each repeat-mode track consisted of a 60 second lead-in of low-level background noise followed by 4 cycles of a single randomly selected song phrase repeated 10 times. Serial-mode tracks consisted of a 60 second lead-in followed by 4 cycles of 3 three randomly selected song phrases, with 10 phrases in each cycle. Phrases were separated by 3 second gaps of low-level background noise, consistent with the natural song tempo, and the 10 phrase cycles were separated by 20 second gaps (see Figure 3).

Repeat-mode

-----A---A---A---A---A---A---A---A---A-----A---A---A---A---A

Serial-mode

-----A---C---B---C---A---B---B---C---A---C-----A---C---B---C---A---B---

Figure 3. Schematic representation of repeat- and serial-mode playback track construction. ‘A’ represents a single song phrase and ‘-’ denotes a one second background noise gap.

Experimental observation methodology

Each of the 8 focal territories received two playback trials. In one of these a repeat-mode bioacoustic playback was performed, while the other comprised serial-mode playback. These were randomly allocated to control for order effect. Each territory received its two playbacks on different days (1-2 days apart) to reduce habituation effects. Observations were conducted between 05:00 and 08:00 from 18/11/2010 to 21/11/2010 inclusive. A Marantz PMD 670 recorder was used with a Sony portable speaker for playback. A Marantz PMD 660 was used in conjunction with a Sennheiser ME66 directional microphone to record the vocal response to playback. A 5 m radius was marked around the speaker to aid judgement of distances.

Responses of both male and female birds to the playbacks were recorded. A short pre-observation playback was performed prior to each experiment in order to ensure the male bird was in the vicinity. A settling-in period of 5 minutes allowed any response to this lure to drop before the focal observation began. Data were then collected from 5 minutes pre-playback, 5 minutes during playback and 10 minutes post-playback. Observers maintained positions at least 6 m from the speaker at all times.

For each male and female presence/absence was recorded as point observations every 30 seconds, with proximity from the playback speaker, estimated to the nearest metre if <5 m, or as >5 m if the bird was further away. Within each continuous 30 second interval the number of discrete song phrases by each individual and the number of flights within a 20 m radius were recorded. The number of tail flicks (a discrete rapid vertical movement of the tail) was also recorded for the pre-playback, playback and post-playback periods using a tally counter. This was subsequently adjusted to a rate per unit time for the period in which the bird was in full view.

Data were analysed using non-parametric statistical tests (Kruskal-Wallis, Wilcoxon Signed Rank and Two Sample Sign).

RESULTS

Difference in territorial response between male and female magpie-robins

In all experiments and all time periods, male birds were more apparent than female birds, as shown in Figures 4 and 5. Percentage presence was calculated as the percentage of each time period that the bird was present within a 20 m radius of the playback speaker. Male response to playback shows an increase from before to during of 45.7% for repeat-mode and 42.5% for serial-mode. For the same time period, females show a small drop in presence of 1.5% for repeat-mode playback and 2.5% for serial-mode playback. Between during and after playback, males show a decrease in presence of 0.3%

for repeat-mode playback and 31.3% for serial-mode playback. Contrastingly, between during and after playback females show an increase in presence of 10.9% for repeat-mode playback and 12.2% for serial-mode playback.

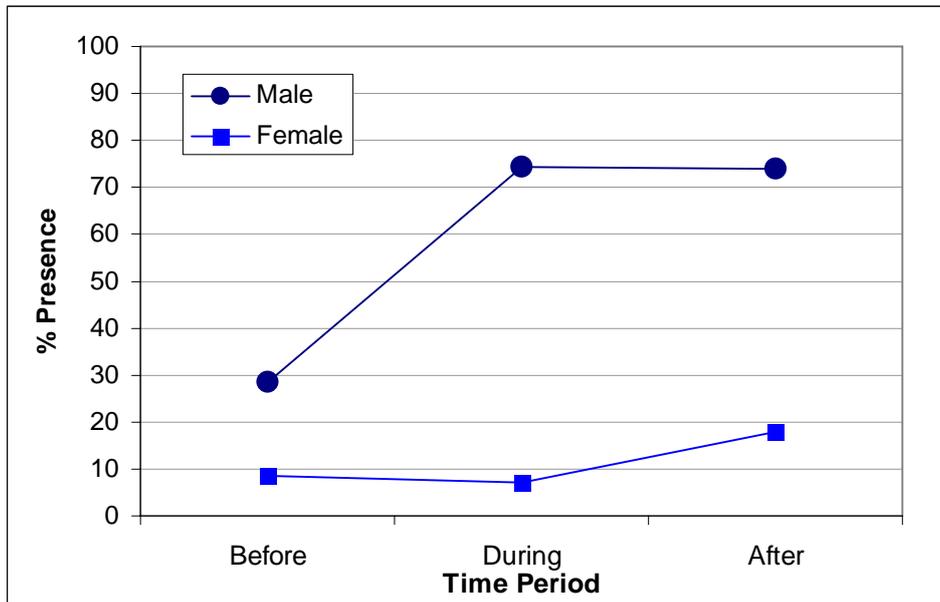


Figure 4. Male and female percentage presence of repeat-mode playback.

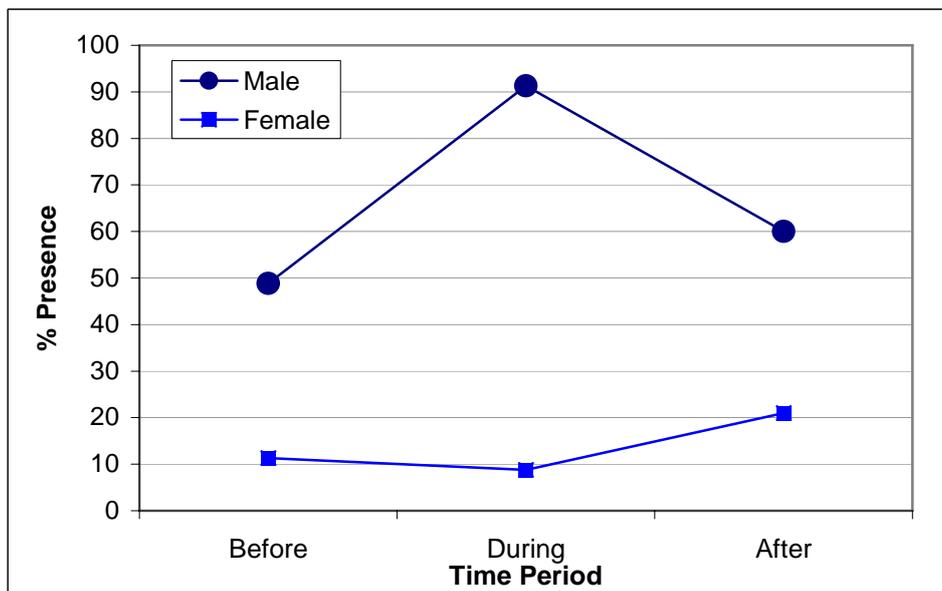


Figure 5. Male and female percentage presence of serial-mode playback.

A single observation of a female singing alongside the male in response to serial-mode playback was made for Territory 2.

Differences in male territorial response to repeat- and serial-mode playbacks

The result for the repeat-mode playback in territory 2 was 'no response' and was therefore excluded from further analysis. In all measured variables there was a clear response to the initiation of both repeat- and serial-mode playback, as demonstrated by the difference between the 'before' and 'during' columns in figures 6-9.

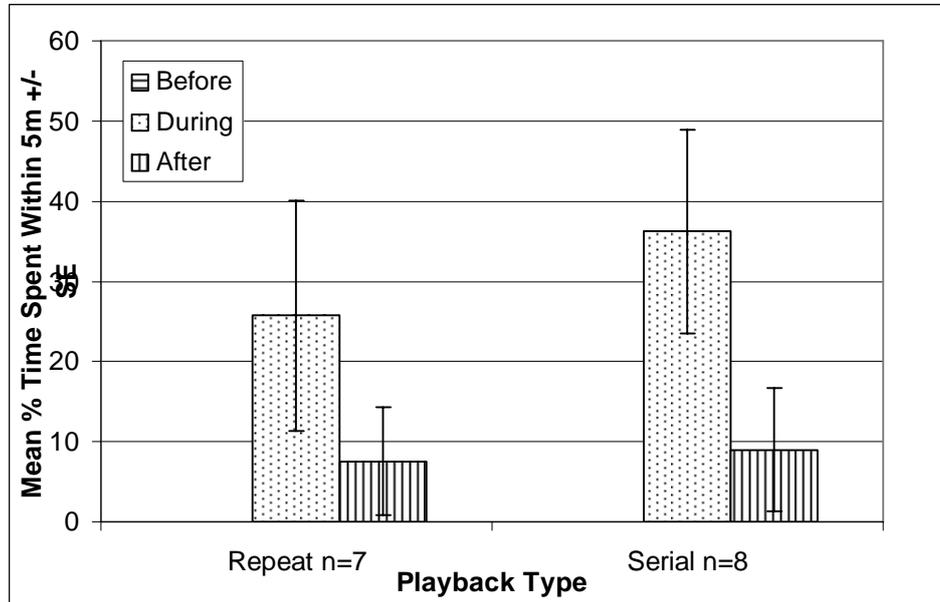


Figure 6. Mean percentage time spent within 5 m of the speaker (male).

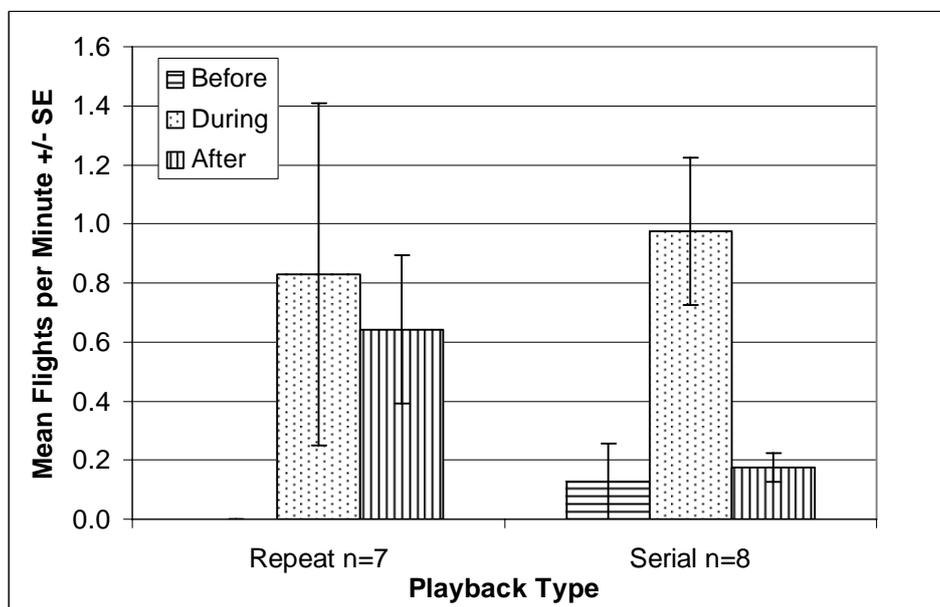


Figure 7. Mean number of flights per minute (male).

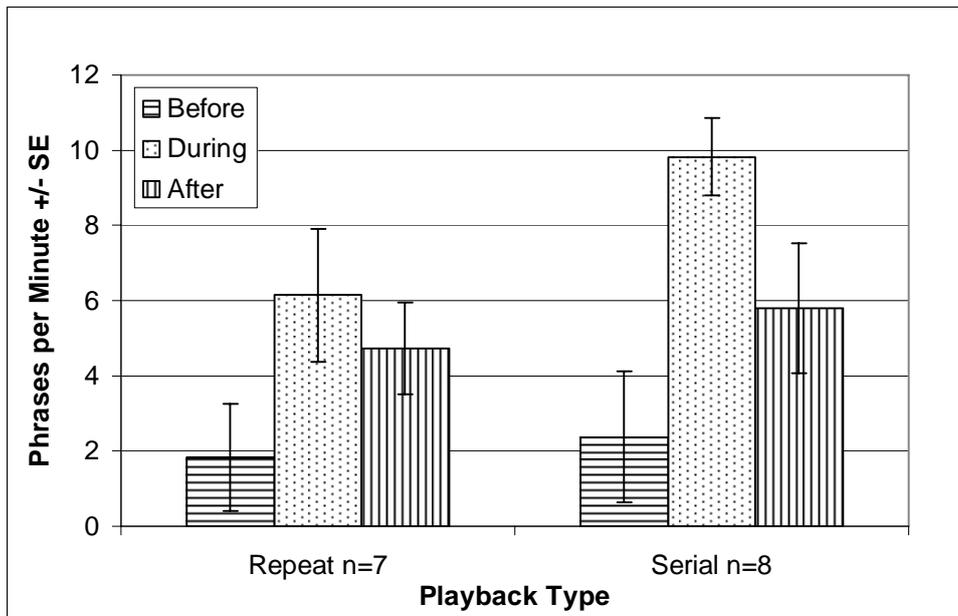


Figure 8. Mean number of song phrases per minute (male).

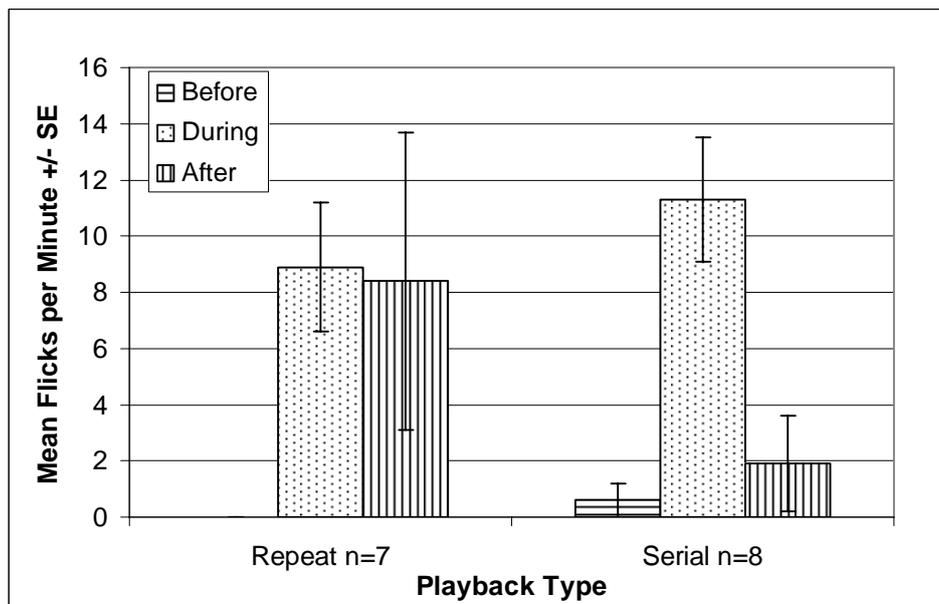


Figure 9. Mean number of tail flicks per minute (male).

For repeat-mode playback, there was a significant difference between the number of flights per minute over the three playback phases (Figure 7: Kruskal-Wallis test, $H = 8.59$, $df = 2$, $P = 0.014$) and also between the number of tail flicks per minute (Figure 9: $H = 9.31$, $df = 2$, $P = 0.010$). Non-significant differences were found for the percentage of time spent within 5 m of the speaker (Figure 6: $H = 3.75$, $df = 2$, $P = 0.153$) and the number of song phrases per minute (Figure 8: $H = 4.54$, $df = 2$, $P = 0.104$).

For serial-mode playback, significant differences existed across the 3 time periods for all measured variables: percentage time spent within 5 m of the speaker (Figure 6: $H = 7.36$, $df = 2$, $P = 0.025$), number of flights per minute (Figure 7: $H = 11.14$, $df = 2$, $P = 0.004$), number of song phrases per minute (Figure 8: $H = 9.59$, $df = 2$, $P = 0.008$) and number of tail flicks per minute (Figure 9: $H = 14.83$, $df = 2$, $P = 0.001$).

Response levels to repeat-mode playback in the during and after phases of the experiment showed no significant differences: percentage time spent within 5 m of the speaker (Figure 6: Mann-Whitney test, $W = 6.0$, $N = 3$, $P = 0.181$), number of flights per minute (Figure 7: $W = 10.0$, $N = 6$, $P = 1.000$), number of song phrases per minute (Figure 8: $W = 10.0$, $N = 7$, $P = 0.554$) and number of tail flicks per minute (Figure 9: $W = 20.0$, $N = 7$, $P = 0.353$).

Response levels to serial mode playback in the during and after phases of the experiment showed significant or borderline-significant differences: percentage time spent within 5 m of the speaker (Figure 6: $W = 15.0$, $N = 5$, $P = 0.059$), number of flights per minute (Figure 7: $W = 35.0$, $N = 8$, $P = 0.021$), number of song phrases per minute (Figure 8: $W = 32.0$, $N = 8$, $P = 0.059$) and number of tail flicks per minute (Figure 9: $W = 36.0$, $N = 8$, $P = 0.014$).

In the ‘during’ phase of the experiment the number of song phrases per minute increased for serial-mode playback relative to repeat-mode playback in all territories – a significant pattern (Table 1: Two Sample Sign Test, $N = 7$, $P = 0.016$). Results for percentage of time spent within 5 m of the speaker (Table 1: Two Sample Sign Test, $N = 6$, $P = 0.688$) flights per minute (Table 1: Two Sample Sign Test, $N = 7$, $P = 0.126$), and tail flicks per minute (Table 1: Two Sample Sign Test, $N = 7$, $P = 0.454$) were not significant.

Table 1. Two sample sign test for response variable levels during playback. ‘+’ shows an increased response to serial versus repeat mode playback, ‘-’ shows a decreased response to serial versus repeat mode playback and (0) shows no difference

Territory	% time within 5 m of speaker	Flights per minute	Song Phrases per minute	Tail flicks per minute
T1	+	+	+	+
T3	+	+	+	+
T4	-	+	+	+
T5	-	+	+	+
T6	(0)	+	+	+
T7	+	-	+	-
T8	+	+	+	-
N for test	6	7	7	7
P-value	0.688	0.126	0.016	0.454

In the 'after' phase of the experiment there were no significant differences in response levels between repeat- and serial-mode playback: percentage of time spent within 5 m of the speaker (Table 2: Two Sample Sign Test, $N = 4$, $P = 1.000$), number of flights per minute (Table 2: Two Sample Sign Test, $N = 7$, $P = 0.454$), number of song phrases per minute (Table 2: Two Sample Sign Test, $N = 7$, $P = 1.000$), and tail flicks per minute (Table 2: Two Sample Sign Test, $N = 5$, $P = 0.376$).

Table 2. Two sample sign test for response variable levels after playback. '+' shows an increased response to serial versus repeat mode playback, '-' shows a decreased response to serial versus repeat mode playback and (0) shows no difference

Territory	% time within 5 m of speaker	Flights per minute	Song Phrases per minute	Tail flicks per minute
T1	(0)	-	-	-
T3	+	+	-	+
T4	-	-	+	-
T5	(0)	-	+	(0)
T6	(0)	-	-	(0)
T7	-	-	+	-
T8	+	+	+	-
N for test	4	7	7	5
P-value	1.000	0.454	1.000	0.376

DISCUSSION

Male and female roles in territorial defence

Response to male bioacoustic playback is evident and differs significantly between male and female *Copsychus albospecularis pica*. One example of possible duet singing in response to playback was observed although this may have been a courtship interaction related to the breeding season. Females are known to sing throughout the tropics for a variety of reasons, a behaviour rarely observed in temperate regions (Slater & Mann, 2004).

Males show a significant response to playback, increasing their apparency and exhibiting a number of territorial behaviours. Males increase their proximity to the playback speaker, initially moving within 5 m in order to seek out the source of the song before moving to a nearby high perch. The number of flights increases as the bird searches for the perceived intruder. Tail flicks increase and are a visual signal directed at the perceived intruder. A significant increase in the number of song phrases vocalised per minute represents an audio-communication signal, in this case for the purpose of defending and marking territory (Catchpole & Slater, 2008).

Male response to repeat-mode and serial-mode playback

Observations and recordings show that songs sung by the male in response to playback begin in repeat-mode and gradually transition into a serial-mode song as time after playback increases. This suggests that each song mode may have a different role. Our experiments showed that serial-mode playback elicits a stronger response than repeat-mode playback in the period during playback. This difference was statistically significant for the number of song phrases sung each minute. Significant differences may have been achieved for other response variables given a larger sample size. The levels of response to repeat-mode playback were maintained for a longer time whereas the levels of response to serial-mode playback decreased significantly in the period after serial-mode playback. Changes in response levels after playback varied between individuals rather than with playback mode.

These different responses provide further evidence for a functional difference between song modes, an effect observed in other avian species (Beebee, 2004). Serial-mode songs are usually sung to attract females, at territory boundaries and at dawn (Beebee, 2004), representing a general declaration of fitness and affirmation of territory (e.g. “here I am/I am seeking a mate/this is my territory”). Repeat-mode songs are thought to represent a more aggressive and defensive message (e.g. “get out, get out, get out”). This suggests that the pattern of vocal response to playback by the bird of repeat-mode singing followed by serial-mode singing represents a transition from high-priority defence to a more general reinforcement of territory ownership.

Challenges and limitations of study

The effect of habituation was evident as a zero response to repeat-mode playback in territory 2. This territory had received a higher number of playbacks during the preliminary studies. Data from the territory 4 repeat-mode playback was affected by the presence of a sparrowhawk predator in the after playback phase. The response of the male altered from songs to alarm calls, and it exhibited a large increase in the number of tail flicks and flights per minute. This represents a prioritisation of predator response over territorial defence response.

The use of a pre-experiment playback to lure the bird into the area had some impact on the before playback level number of songs per minute, as the level did not fully return to zero prior to the experiment starting in several cases, despite the 5 minutes settling in period.

Time of day was not adequately controlled for and may account for some of the variance in the results. Although the playbacks were all conducted within a 3 hour time window, different playbacks to each territory were not conducted at the exact same time. A further challenge was the possibility of

variation of the location of the playback speaker within each territory as a confounding variable. The strength of the response observed may differ in relation to whether the playback was conducted at the heart of a territory or close to a boundary.

CONCLUSION AND RECOMMENDATIONS

This study found that males exhibit a stronger territorial response to male song bioacoustic playbacks than females, supporting hypothesis H₁. In addition, there is evidence to suggest that repeat-mode and serial-mode songs in Madagascar magpie-robins perform different functions, as they elicit different types and levels of territorial response. This supports hypothesis H₂.

The experimental design could be improved by taking steps to reduce the habituation effect, such as ensuring no experimental territory received pilot/preliminary playbacks. Additional time would allow for an increased interval between playbacks to the same territory, again minimising habituation. Playbacks to the same territory should be conducted at the same time of day for different treatments to reduce confounding variables. Territory maps would enable placement of the playback speaker in equivalent positions within each territory. Data clearly affected by the presence of predators should be discarded and the experiment repeated at a later date. A pre-experiment lure should be used with caution and elevated response levels allowed to drop to zero before initiation of experimental observation. Detailed recordings of the vocal responses would permit quantifiable bioacoustic analysis to back-up the observation that males sing in different modes during and after playback.

Repetition of this experiment outside of the breeding season may produce different results for species behaviour. Areas for further research include the use of female song playbacks to territories and observing the response of males and females to see if this differs. Removal of the female from the territory and observation of the male response to both male and female song playbacks and different playback modes may yield additional insights into the roles of different behaviours and song modes.

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