

Spatial and temporal variation in song rate and song duration in the Little Greenbul *Andropadus virens*

Abigail Bunker, Anglia Polytechnic University, UK

Ellinor Lillieholm, University of Stockholm, Sweden

Abstract

We studied variation in the singing behaviour of the little greenbul *Andropadus virens* at two sites in Amani Nature Reserve, over a period of 6 days. Variation was measured in terms of singing rate per minute and mean song duration. The effects of differences in population densities, neighbouring birdsong and playbacks were measured over time. Our results show a significant peak in singing activity in the early morning. Singing rate and duration show a similar but non-significant trend. Neither measure of song co-varied with population densities. We found a weak, marginally significant correlation in rate of singing between neighbouring birds and some evidence of a sequential pattern in song. Playback experiments elicited varied responses but there was no significant difference in song before and after playback. Temporal variation over the course of the day occurs even though the little greenbul sings all day. The results of song interactions between neighbours and of playback experiments suggest that their song is signalling both territorial and mate attraction messages.

INTRODUCTION

Auditory signals are widely used by many animal groups for communication but birdsong is perhaps one of the best known examples. The advantages and disadvantages of using song are varied: for forest dwelling birds, for example, sound is much more easily perceived than visual signals and in comparison to other channels, has a relatively long range and ability to bypass obstacles (Alcock, 1984, cited in Krebs & Davies, 1993). It also provides great flexibility in terms of rate of delivery, song duration, pitch, loudness and harmonic structure, elements that may be changed quickly and easily (*ibid.*). It is, however, energetically expensive and although flexible, is ephemeral. Timing, spacing and other characteristics of song will therefore be critical if it is to be a cost-effective signal.

Birds generally use song to communicate two fairly simple messages:

- Ownership of territory
- Readiness to mate

Despite the simplicity of these messages, extreme variability in songs exists both between and within species and populations (Krebs & Davies, 1993). At a broad level, ecological constraints will

impose limits on the design of songs. For example, numerous studies have shown that many bird species that are living below the canopy in tropical forests use a lower frequency, a larger proportion of pure tones and a narrower range of frequencies in their songs than songs of grasslands birds, in order to limit the effects of attenuation and degradation of the song before it reaches the intended receiver(s) (Krebs & Davies, 1993). A further selective pressure will be in the response of reactors at whom the song is directed (ie sexual selection) (Krebs & Davies, 1993). Ellers & Slabbekoorn (2003) note that one song may contain different songtypes with different functions: the short and stereotypic phrases for male-male competition and more complex and variable song phrases for attracting females.

The little greenbul *Andropadus virens* has been the subject of a number of studies of variation and divergence in morphology (including song) in tropical rainforests (eg Slabbekoorn & Smith, 2002; Smith *et al*, 2004). Slabbekoorn & Smith (2002) recorded and analysed the temporal and spectral characteristics of the song of the little greenbul in order to investigate the ecological factors shaping song variation across a rainforest gradient (between populations). In this study we aimed to investigate variation in song on a much smaller scale, ie within a population of little greenbuls. We used other measures of song variation, namely number of songs per minute and mean length of song (per minute) to test our prediction that birds would vary the rate and duration of song in response to a number of key biotic and abiotic factors. Because of time constraints and practical considerations we chose not to undertake spectral analysis of songs and therefore our protocol did not include a comparison of birds in different habitats. We also wanted to test whether there is temporal variation in singing activity (and in song characteristics when they do sing), since little greenbuls are one of a few species that are reported as singing all day and all year (Keith *et al*, 1992).

Objectives

This project aimed to answer three research questions:

1. Does song activity, song rate and/or duration vary with varying population densities, over time and/or with varying ambient noise levels?
2. Do neighbouring birds interact in terms of song?
3. Does playback of little greenbul song elicit a territorial response?

On the basis of initial observations, we predicted that

- Although little greenbuls would be heard singing throughout the day, there would be a peak in activity in the early morning and this would decrease over the day;

- Song rate and/or duration would be greater early in the morning and decrease over the course of the day;
- Song rate and/or duration would be higher in sites with higher population densities;
- After playback of little greenbul song, the frequency of singing would increase (and duration decrease).
- There would be a correlation in the rate of singing of neighbours at the same point in time and that the song of one neighbour would be more likely to be followed by the song of the neighbour than by his own song.

METHODS

Study site

This study was carried out as part of a Tropical Biology Association course that took place in Amani Nature Reserve in September 2005. Fieldwork was undertaken between 15 and 22 September, along two transects on different sides of a swamp/pond near Amani Village. We chose the transects on the basis of preliminary observations, which indicated a lower population density in transect 2 (which ran along a road bordering the swamp).

Study species

The little greenbul is common across its range (sub-Saharan West and Central Africa, extending into parts of East Africa). It prefers thick secondary growth and forest edge habitats and is often found along riverine and waterside vegetation. It tends to be solitary and shy, remaining hidden in thick undergrowth and shrubs. Despite this, the presence of the little greenbul is easily established by its characteristic bubbling song, given all day and all year, like only three other members of the genus (Keith, et al., 1992). Territoriality in this species is recorded as being rare, except when nesting, although it moves around only locally (Keith, et al., 1992). The combination of these factors make the little greenbul an ideal species for behavioural ecology studies.

Data collection

In order to identify individuals to test, we walked each transect at a steady pace on several occasions over the course of a day and when a greenbul was heard singing or seen within 20 meters of the transect we marked the site. Once potential “territories” were identified we walked each transect three times a day: between 06.30 and 08.30am, 11.30 and 13.00 and between 15.30 and 17.30 over a period of 6 days. At each site we waited for 2 minutes before taking measurements in order to reduce the likelihood that our presence affected the results. If the bird was not singing when

we arrived (or if it stopped before we could measure song duration and rate) we waited for a further period of 5 minutes or, if it still did not sing in the vicinity, we recorded it on the way back.

We used the results from each time we walked the transect to refine our population density estimates along both transects. Our estimates are included in table 1.

We used stopwatches to measure the number of songs per minute (rate) and the duration (in milliseconds) of each song over a period of one minute. For the first 4 days we also recorded each bird with a tape recorder. We measured the sound pressure level at the beginning and end of each transect with a digital sound level meter. If additional sites along transects were identified (believed to be different individual birds to those already identified) these were marked and measurements made if birds were singing.

With a sub-sample of birds we measured rate of singing of two neighbouring birds over the same period of a minute. In order to gain data on the sequence of singing between neighbouring individuals, we recorded the time at which each of two neighbouring birds started singing within the same minute period.

We also undertook a small number of playback experiments with birds on both transects, in order to measure whether singing rate and/or duration were affected. Before playback we measured rate and duration as outlined above. We then played approximately 30 seconds of song recorded earlier (the source of the song differed each time) and then repeated the measurements.

We made a number of assumptions in project design and in analysis of data:

1. If birds were found singing at the same site, these were treated as the same bird. Over the course of the 6 days, we were able to identify some elements of the song of individual birds and differentiate them from other birds. With others this was not possible. We initially intended to listen to repeated recordings from the same site back in the laboratory in order to gain greater assurance of this. However, the time needed to transfer songs onto appropriate software (let alone to analyse them) meant that this was unfeasible.
2. The 18 birds that we identified and measured were independent of each other, both within and between the two transects. Noticeable differences in the songs of some individuals, the reliability with which birds were found singing at the same site and the fact that this species is known to move around only locally and to rarely move out of the dense shrub layer support this assumption.

Data analysis

We used parametric tests (ANOVA and unpaired t-tests) to analyse differences in rate and song duration between transects and at different times of day. We also tested for difference in sound pressure levels between transects and over time. Chi-squared analysis was used to compare singing activity (singing vs not singing) between different times of day. Differences in song rate and duration before and after playback were tested using Wilcoxon's matched pairs test. We used linear regression to establish the strength of the correlation between the singing rates of neighbouring birds.

RESULTS

Our total sample size was 18 birds, 9 at each site. We measured the duration of over 1200 songs over the course of the 6 days and therefore used means per bird or per transect for further analysis. Frequency distributions of both song rates and durations showed a normal distribution (Figure 1) and parametric tests were therefore used.

We revised our estimate of birds during the fieldwork as we identified further territories and these revised density estimates are included in table 1.

Table 1: Estimate of population densities along transects 1 (swamp path) and 2 (road)

	Number of birds	Length of transect	Population density
Transect 1 (swamp)	9	567m	*1 bird/2520m ²
Transect 2 (road)	9	725m	*1 bird/3222m ²

*At some of the sites where birds were singing we saw more than 1 bird. This will therefore mean that density estimates are understated and estimates of territory density are more appropriate.

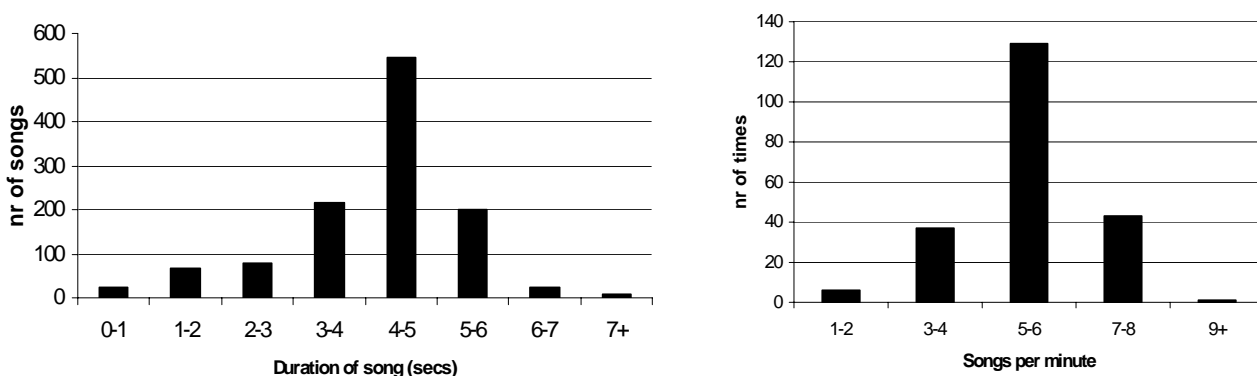


Figure 1: Histograms showing distribution of song durations (left) and song rates per minute (right) for both transects

Variation between transects

We found no difference in either rate of singing or song duration between transects at any time of day. (Song duration: $T=0.507$, $df=16$, $P=0.6187$; Song rate: $T=-0.582$, $df=16$, $P=0.5865$). We therefore pooled our data from both transects for further analysis ($n=18$).

Variation with time of day

Singing activity at different times of day was significantly different from that which would be expected if it were random, with highest singing activity in the early morning, decreasing over the day as predicted (Figure 2) ($\chi^2=8.72$, $df=2$, $p<0.05$).

Although frequencies and durations of song are slightly higher in the morning, there is no significant difference in either song rate or duration between the three times of day (Rate of song: $F=1.154$, $df=2$, $P=0.3234$; Duration: $F=1.435$, $df=2$, $P=0.2476$) (Figure 3).

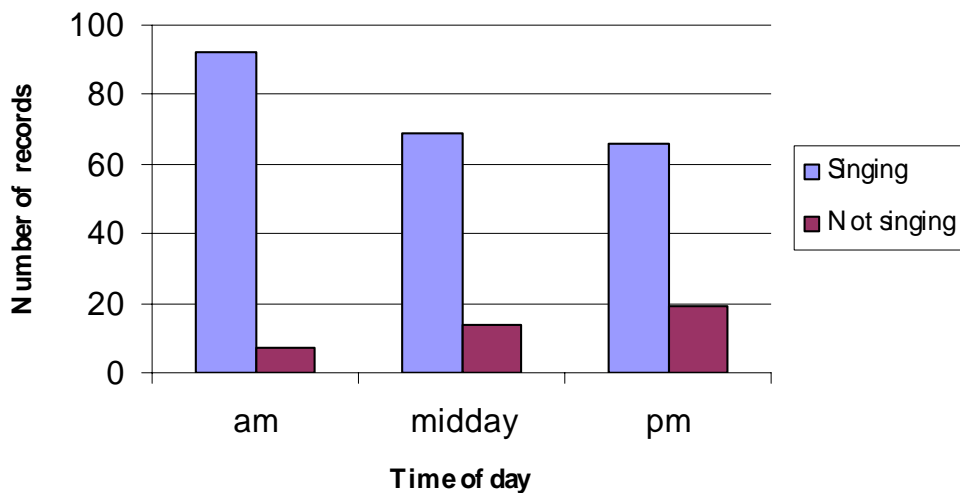


Figure 2: Difference in singing activity at different times of day

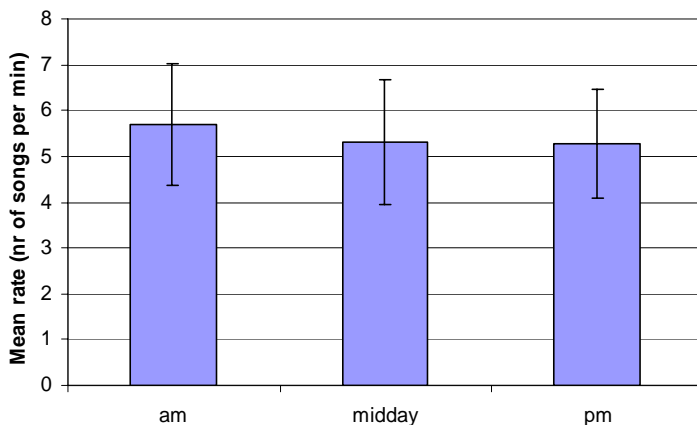


Figure 3: There is no significant difference in mean rate of singing (in both transects) at different times of day

Variation in ambient noise

Sound pressure levels varied significantly with time of day ($F=18.521$, $df=2$, $P<0.0001$) although there was no difference between transects ($T=-0.411$, $df=16$, $P=0.6827$). The trend goes counter to that seen in singing activity (Figure 4). Sound pressure levels over the 6 days followed a similar trend in both transects, which is to be expected given the relative proximity to each other (Figure 5).

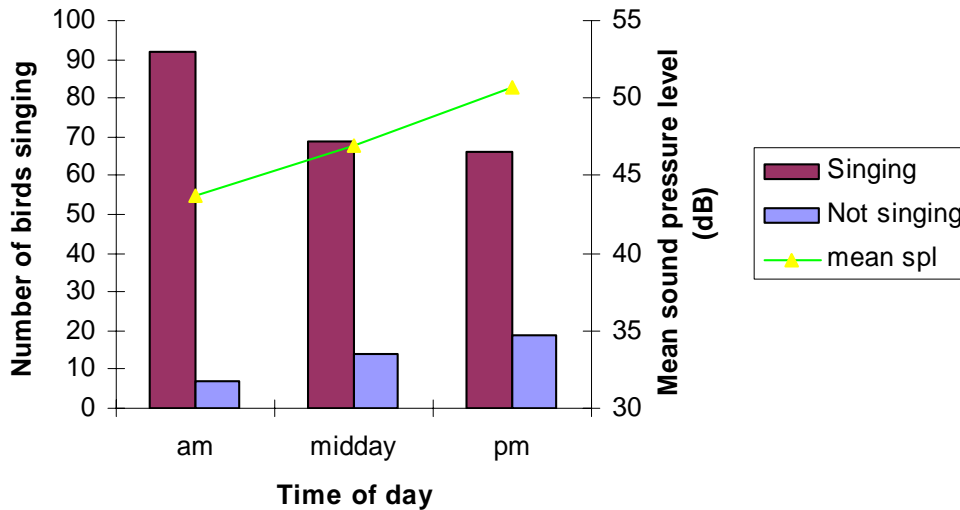


Figure 4: Variation in singing activity of little greenbuls and in mean sound pressure levels at different times of day

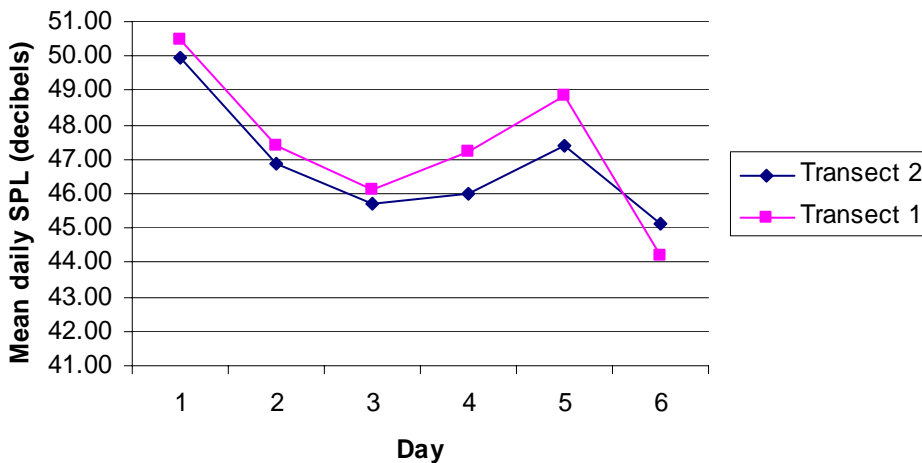


Figure 5: Changes in sound pressure level over the 6 days of fieldwork in both transects

Variation within and between individuals

Variation between birds was more evident in rate of singing than in the duration of song (Figures 6 and 7). The mean duration was between 3 and 4.5 seconds. The mean rate ranged from less than 4.5

to 6.5 times per minute. Some birds varied little in the rate of singing (eg R2) whilst others showed much greater variation (eg S6).

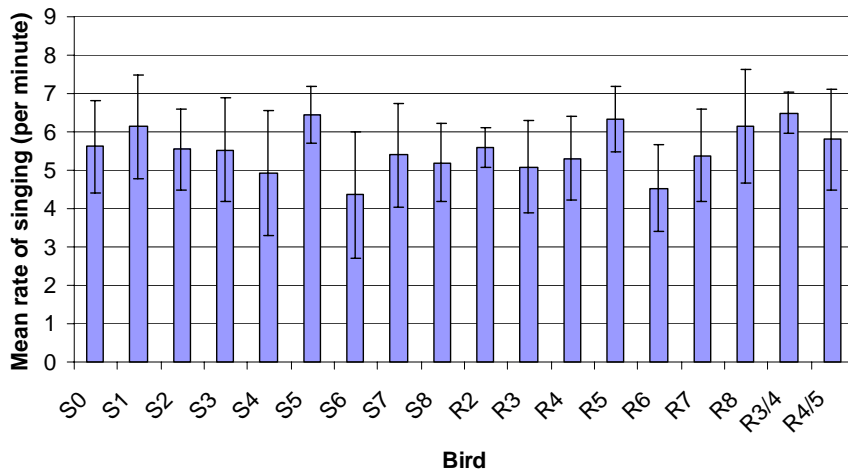


Figure 6: Variation in mean rate of singing between individual birds (error bars indicate standard deviation). Prefix S indicates birds in swamp transect 1; R the road transect 2

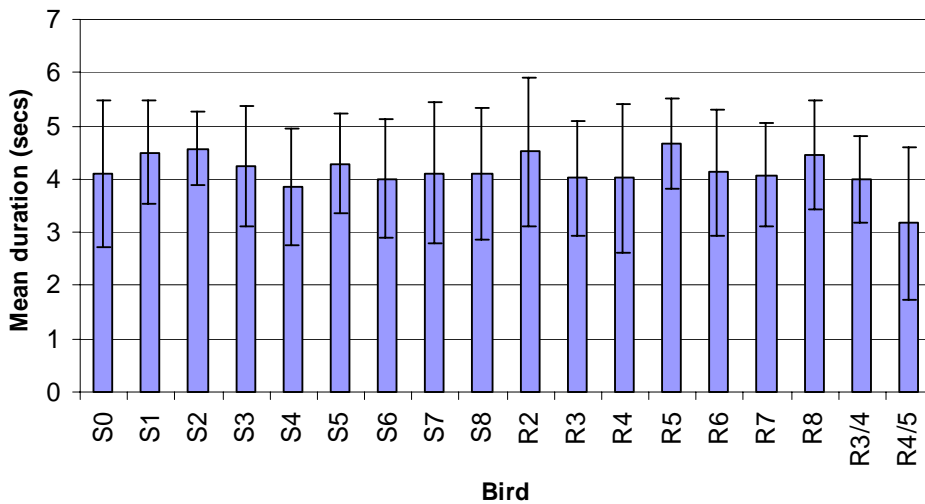


Figure 7: Variation between individuals in mean duration of songs (error bars indicate standard deviation). Prefix S indicates birds in swamp transect 1; R the road transect 2

Song interactions between neighbouring birds

We recorded rates of singing of 9 pairs of neighbouring birds and, when plotted, these indicated a weak correlation between pairs, which although not significant, may indicate an interesting trend (Figure 8) ($R^2=0.3185$, $P=0.0705$).

Our observations of timing of songs of neighbouring birds over the same 60 second period also show some interesting patterns (appendix 1): the majority of songs were followed by the song of the neighbour before the bird sang again.

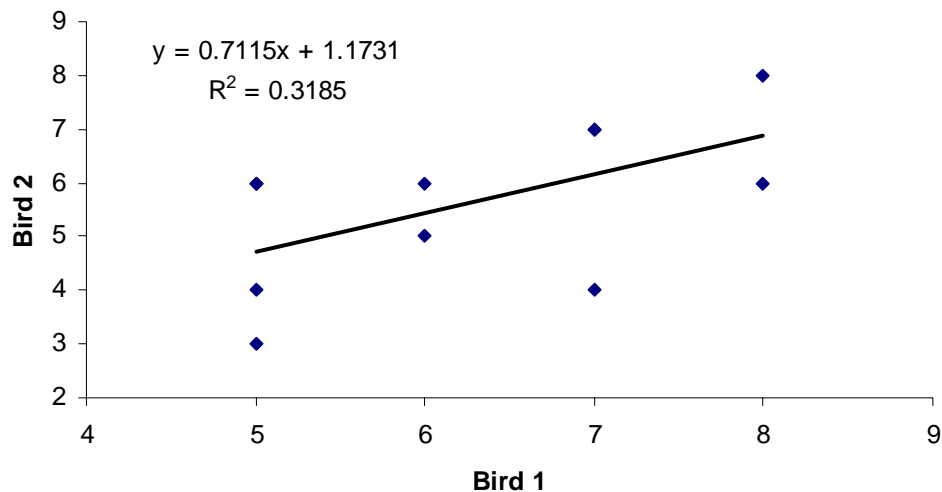


Figure 8: Relationship between rates of singing of neighbouring birds over the same period of time

Changes in song after playback

Analysis of the rate and duration of song of birds before and after playback did not show any significant differences (Rate: $Z=-0.530$, $n=6$, $P=0.5961$; duration $Z=-0.314$, $n=6$, $P=0.7552$). There was, however, considerable variation in the responses of individual birds.

DISCUSSION

Temporal variation in song

We were able to confirm that, during late September at least, little greenbuls do indeed sing throughout the day. The data also shows that there is a peak in singing early in the morning and a decrease over the course of the day, as predicted. This peak takes the form of a higher number of birds singing at any one time. However, although the data does suggest a slight trend for higher singing rates and longer songs in the early morning, the differences are not significant.

It is interesting to find that, like most other passerines, this day-long singer still exhibits the early morning singing peak. A discussion of the functional and evolutionary explanations for a greater tendency to sing early in the morning is beyond the scope of this paper. However, a number of functional explanations may be relevant:

- Advertisement to competitors that an individual has survived the night and that territory is still taken;
- Lower predation risk;
- Signal to potential mates, indicating enhanced fitness (sexual selection);
- Environmental variables make singing more cost-effective (eg lower wind, air pressure, temperatures etc);
- Lower ambient noise levels.

The slight early morning peak in the two measures (rate and duration) of song that we did observe is perhaps explained by the higher levels of inter and intraspecific 'song competition' at that time of day. The significantly lower ambient noise levels at this time of day may also be an important explanatory factor. However, the trends in mean rate and duration of song over the 6 day period do not appear to show any relationship with ambient noise levels over the same period (which was consistent across both transects).

Other measures of song may provide evidence of a more pronounced difference between times of day, in particular amplitude and frequency.

Population density and its effect on song

The absence of any significant difference in song duration and rate between the two study areas where population densities were different may indicate that resources (food, mates, nesting sites) are not limited and/or that song is not density-dependent (at least amongst this local population of little greenbuls). Alternatively it may not be a case of relative population densities between the two sites, but whether one of the sites was below some kind of threshold below which resources are insufficient (and song may be affected).

It is also possible that our density estimates were inaccurate. Indeed, we became increasingly aware that there were a number of singing birds in shrub/tree 'islands' in the swamp between our transects, and these were not picked up by our protocol. Our estimates were also based upon singing individuals and as noted above, on a number of occasions we saw more than one bird at the same site (although only one was singing at any one time).

Song duration and rate may not be the most relevant measures of variation when considering the effects of competition. An analysis of amplitude and/or frequencies of song under contrasting conditions may give more revealing results. It should also be noted that our analysis did not

consider the interactions of multiple ecological factors on song and although we chose the two sites on the basis that habitats were similar (and therefore the effects of this controlled for), this may have been an oversimplification.

Interactions between neighbouring birds

As outlined in the introduction, bird song is generally about communicating two types of signal: readiness to mate and ownership of territory. The weak (and marginally significant) correlation in rate of song between neighbouring birds may suggest that there is some level of interaction via song (particularly when combined with the limited data on sequence of singers (appendix 1)). It may be that the songs of neighbours act as prompts to each other. Whether there is an element of copying of song sequences or notes remains unclear. Regardless, the data does seem to support the theory that, at least at some periods in the day, song is communicating territorial messages to competitors.

An analysis of the sequences of notes and songtypes used during such (presumably male-male) song interactions may provide evidence to support differential functions of the different sequences within the song of the little greenbul (Ellers & Slabbekoorn, 2003).

Variation in song as a result of playback

Our playback experiments showed no significant difference in rate or duration of song, despite some very promising initial results. On one occasion, playback of the individual's own song appeared to elicit a very strong reaction (rate of singing doubled from 4 per minute to 8 and song duration reduced to below 4 seconds). This was accompanied by frantic flying around the source of the song (us) and approaches to within 2 metres.

During the period after playback we noticed the presence of a second bird (not singing). The mated status of birds is one of a number of confounding variables that may have affected the results. We were unable to use the same recording for each playback experiment and the distance between playback source and focal bird also varied considerably. The variability in responses may indicate the varied functions of the song of the little greenbul (ie not just territorial message). A larger sample size and more consistent protocol would therefore have been beneficial.

Further research

Although the results of our playback experiments show no evidence of a change in song duration and frequency, this would be an interesting area for further study. Interactions between neighbours,

in particular the use of different song sequences by individuals and their neighbours, may also bring interesting results.

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