

## Differences between the songs of rural and urban Australian magpies (*Gymnorhina tibicen*) and the potential consequences for territorial interactions

ARLIE H. McCARTHY  
DOMINIQUE A. POTVIN\*  
TEGAN ASLAM  
RACHAEL BARTLETT  
SARAH BEEBE  
JACQUI BENNETT  
DANIEL J. HITCHCOCK  
MICHELLE TEE  
Department of Zoology, University of Melbourne, VIC, Australia, 3010

**Abstract** A number of studies have found that birds in urban areas alter singing behaviour, possibly to increase signal transmission and avoid masking by high levels of anthropogenic background noise. However, few studies have focused on how these song differences might be interpreted by receivers. We investigated differences in song between populations of urban and rural Australian magpies (*Gymnorhina tibicen*), an Australian species abundant in both habitats. First, we compared urban and rural magpie songs to determine if magpies shift the frequency, duration and output of songs in response to anthropogenic noise. Unlike some songbirds, urban magpies did not shift minimum frequencies to avoid masking, however they did sing shorter songs. We then played back unfamiliar urban and rural songs to groups of both urban and rural magpies, and monitored their territorial responses. Results showed that differences in song across both habitats do not affect receiver responses, indicating that magpies from both urban and rural habitats can readily communicate with each other. Interestingly, rural magpies responded with more aggression to rural songs than to either urban songs or to control songs. We propose that the flexibility of Australian magpie songs aids this species in its ability to adapt successfully to urban environments.

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### INTRODUCTION

Urban habitats present new challenges and selective pressures to many species. Anthropogenic noise is one such selective pressure, often acting upon acoustic signals (Brumm & Slabbekoorn 2005). In

cities, noise is characteristically loud (high energy) and constant, with most of the energy concentrated at low frequencies (1-4 kHz; Skiba 2000). This creates the potential to mask low-frequency communication signals, and thus reduce the efficacy and transmission of low-frequency signals (Brumm & Slabbekoorn 2005). The acoustic adaptation hypothesis (AAH) predicts that animals should adjust their acoustic signals to increase signal perceptibility in noisy habitats, so long as these

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\*Correspondence: dpotvin@museum.vic.gov.au

\*Current address: Sciences Department, Museum Victoria, Melbourne, VIC, Australia, 3001

adjustments are adaptive (Morton 1975; Hansen 1979). The hypothesis was originally proposed to account for how birds adapt to noise from other species and abiotic factors (*e.g.*, wind), but has been also applied to explain changes in bird song in response to noise in human environments.

Passerines are an ideal group to study the effects of urban noise on acoustic communication. Song is a flexible trait with some species responding to changes in noise conditions by altering songs over a very short time period (Halfwerk & Slabbekoorn 2009; Gross *et al.* 2010). Since song is used to defend territories, find mates and recognise conspecifics (Catchpole & Slater 2008), it is crucial to maintain signal efficacy, potentially in a variety of habitat types. The presence of some species of birds in urban environments may indicate a capacity to adapt acoustically or the possession of pre-adapted traits such as high-frequency song that are not affected by anthropogenic noise (Hu & Cardoso 2009).

Studies of urban noise effects on avian communication have increased in recent years and reveal widespread changes in behaviour (Slabbekoorn & Ripmeester 2008). For example, European robins (*Erithacus rubecula*) are more likely to sing at night to avoid traffic noise (Fuller *et al.* 2007), while great tits (*Parus major*) sing higher minimum frequencies in urban areas to avoid the low frequencies that are often masked by anthropogenic noise (Slabbekoorn & den Boer-Visser 2006). Changes in song duration (Marler & Slabbekoorn 2004) and syllable use (Nemeth & Brumm 2009) have also been observed. In Australia, the silvereye (*Zosterops lateralis*) and grey shrike-thrush (*Colluricincla harmonica*) have been found to raise their minimum frequencies and decrease syllable rate in response to urban noise (Parris & Schneider 2009; Potvin *et al.* 2011). These changes indicate a level of urban-rural divergence in song, with potential consequences for effective communication across populations. Habitat-dependent song divergence may affect interactions between birds within or across habitat gradients if such changes result in songs becoming unfamiliar or conveying unintended information (Mockford & Marshall 2009; Ripmeester *et al.* 2010).

Despite the recent interest in the effects of anthropogenic noise on bird songs, few experimental studies have investigated receiver response to urban-rural song variations. If the information of an altered signal remains intact and receivers respond equally to both urban and rural signals, then observed changes in urban song should remain ecologically inconsequential to the species. Playback studies investigating behavioural responses to habitat-dependent song have found that great tits (Mockford & Marshall 2009) and European blackbirds (*Turdus merula*; Ripmeester

*et al.* 2010) respond more strongly to songs from a similar habitat (homotypic songs) than to songs from a different habitat (heterotypic songs). However, these studies failed to control adequately for potential familiarity or individual song recognition, which may have affected their results.

The aims of this study were twofold: firstly, to determine if birds adjust singing behaviour in response to urban noise, we investigated differences between urban and rural Australian magpie (*Gymnorhina tibicen*) songs, focusing on song frequency, duration and rate. We predicted that magpies, like other bird species, would sing at higher minimum frequencies in urban environments, and that urban birds may sing longer songs at a higher rate to increase signal redundancy in a noisy environment, in concordance with results from previous studies (Brumm *et al.* 2004; Foote *et al.* 2004; Halfwerk & Slabbekoorn 2009). The second aim was to determine whether receivers might alter behaviour in response to any changes, both detected and undetected by our analysis. To do this we observed responses of urban and rural magpies to group songs (carols) originating from both an unfamiliar urban and unfamiliar rural group (2 birds). We predicted that magpies would respond most strongly to homotypic song (song originating from the same environment as the focal magpies), especially if there were discernable changes between urban and rural songs.

## MATERIALS AND METHODS

### Study species

The Australian magpie is a passerine with a complex, melodious song. Magpies are found throughout Australia and inhabit both rural and urban habitats successfully. They rely on vocalisations such as carols (group songs), to defend territories year round (Brown & Farabaugh 1991) and consequently we have focused our study on this aspect of singing behaviour. Furthermore, magpie songs are sung in low-frequency bandwidths, which are likely to be masked by traffic noise (Hu & Cardoso 2009). Magpies also display stereotypical, quantifiable territorial behaviours ideal for playback studies. Since disputes are resolved at the family-group level (Brown *et al.* 1988), magpie responses to song may be less affected by an individual receiver's 'personality', a potential confounding factor in previous experiments that focus on one individual.

### Song recording and analysis

We recorded carols of individual Australian magpies within territorial groups (2-3 individuals, identified by proximity and interactive behaviour) from Mar-Apr 2010 at 3 urban and 3 rural sites around Melbourne, Victoria. Urban sites were

Royal Park, Parkville (-37.778 S, 144.953 E), Royal Botanic Gardens, Melbourne (-37.830 S, 144.978 E) and Princes Park, Carlton (-37.782 S, 144.961 E). Rural sites were: Trumans Rd Reserve, Tootgarook (-38.378 S, 144.862 E), South Gisborne (-37.546 S, 144.614 E) and Mt. Macedon (-37.406 S, 144.577 E). At each site we recorded 10 caroling bouts by separate groups at random using Marantz Professional PMD660 Solid State recorders and Sennheiser ME67 directional microphones. Recordings were made between 0700 and 1000 AEST to coincide with peak hour traffic. We visited each site only once, with each site visited during different days (all weekdays with consistent weather) so as to avoid pseudoreplication. Carols were recorded for 10 minutes, with constant observation to ensure that the same birds were recorded for the entire period, and not recorded twice at the same site. We tallied the number of songs each individual sang within the 10 minute period and the total number of songs sung by the group over a 1-hour period to obtain a measure of song output at both an individual and group scale.

We created a spectrograph for each recording for analysis using Syrinx 2.6h software (John Burt, <http://www.syrinxpc.com/>). We then visually identified each song within the recording, and the minimum (lowest) frequency, maximum (highest) frequency, average (mean) frequency (Hz), and the duration of each song(s) were automatically calculated by Syrinx. These values were then averaged for each individual bird.

To measure ambient noise levels we used a Lutron SL-4001 Sound Level Meter 190 set to a slow response measurement with 'A' weighting. We took 5 sequential sound level measurements of ambient noise covering all directions (north, south, east and west) and averaged these to determine average ambient noise levels for the site.

We used Student's *t*-tests in R version 2.13.0 to compare each song variable (lowest frequency, highest frequency, average frequency, song duration, individual song rate, and group song rate) between urban and rural habitats. Where unequal variances were identified, we used a Welch's *t*-test. Regression analyses were also performed to determine whether any variation from the song variables was correlated with ambient noise in each site.

### Playback experiment

We conducted playback experiments during Apr 2011 at 5 urban and 5 rural sites around Melbourne and rural areas of Victoria between 1500 and 1700 AEST. We conducted playback at each of the following urban sites: King's Domain (-37.829 S, 144.973 E), Carlton Gardens (-37.806 S, 144.971 E), Yarra Park (-37.817 S, 144.985 E), Royal Park (-37.792 S, 144.954 E) and the University of

Melbourne (-37.798 S, 144.960 E); and the following rural sites: Woodend (-37.353 S, 144.590 E), Mount Worth (-38.283 S, 145.997 E), Portarlington (-38.114 S, 144.642 E), Anakie (-37.916 S, 144.252 E) and Arthur's Seat (-38.358 S, 144.947 E). We specifically chose sites at least 10 km from the recording sites to avoid playing songs that may have been familiar territorial songs to the focal birds.

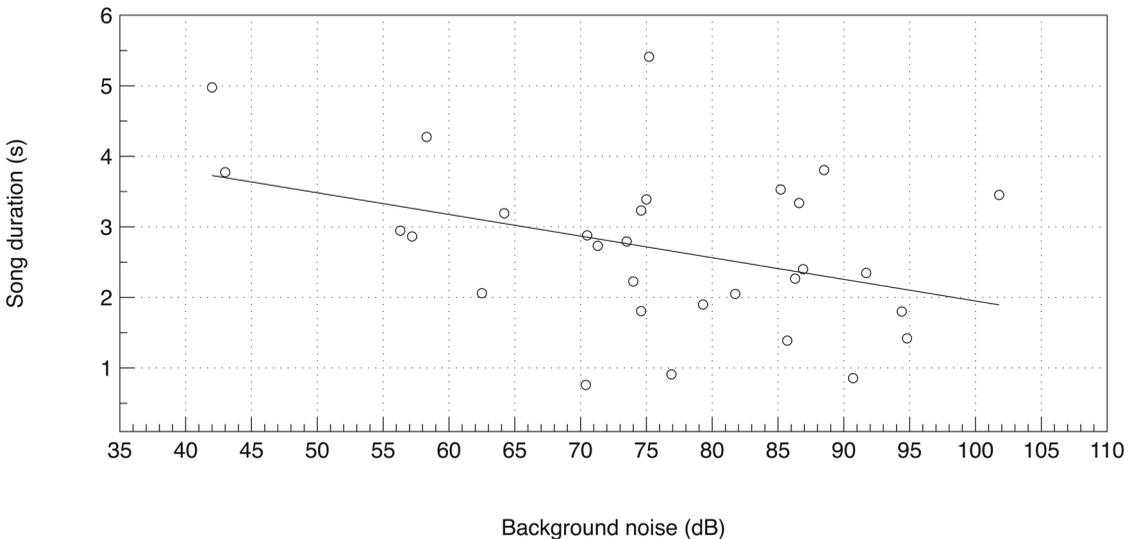
We played 5 unfamiliar carols each from urban and rural birds that we recorded in the first part of this study along with 1 recording of an Australian raven (*Corvus coronoides*) as a control at amplitudes typical of a singing bird (80 dB from a distance of 1 m). We used Audacity version 1.2.6 (D. Mazzoni & R. Dannenberg, Carnegie Mellon University, U.S.A) to prepare 5 minute playback tracks with a carol sung by 2 birds every 20 seconds. Background noise in the recordings was reduced using a high pass filter.

Playback experiments were conducted once at each site, where we played 1 unfamiliar urban song track, 1 unfamiliar rural song track, and the control track (using a Moshi Bass Burger portable speaker) in a random order to a territorial magpie group (*i.e.*, 2 or more birds) at each site. We placed the speaker 15-30 m from the group in an open area on the ground, and retreated 15-30 m in the opposite direction from target magpies where we remained hidden for observations. There was no noticeable disturbance of the nearby group at our approach or in the placement of the speaker and we waited for 10 minutes after setting up before we began the first trial, as well as between trials, to ensure the magpies were unaffected by our presence. We observed the number of birds displaying every 20 seconds during the pre-trial period of 2 minutes (*i.e.*, no playback), the trial period of 5 minutes (*i.e.*, playback of either magpie song or control song), and the post-trial period of 2 minutes (*i.e.*, no playback). At each 20 second interval, we recorded the following behaviours: vigilance, approach (within 5 m of speaker), carol (multi-syllabic song by 2 or more birds), warble (multi-syllabic song by 1 bird), call (short, 1-syllable vocalisation by 1 bird), foraging, mobbing (group displays of aggression, *e.g.*, co-ordinated swooping of speaker), flyover (low pass or swoop over speaker by an individual), physical aggression (aggressive behaviour where physical contact with the speaker was made, *e.g.*, pecking it), aggressive display (puffing up feathers, bill snaps), and retreat (moving away from speaker). Behavioural classes were determined based on descriptions by Kaplan (2004) and our own observations.

ANOVAs were conducted in R version 2.13.0 to analyse the effect of the following factors on the observed level of response for each behaviour (number of behaviours divided by the number

**Table 1.** Mean  $\pm$  standard deviation of minimum (lowest) and maximum (highest) frequencies, frequency range (maximum–minimum frequency), song duration and song rate of urban and rural Australian magpie song.

	Minimum (Hz)	Maximum (Hz)	Range (Hz)	Song duration (s)	Song rate (songs/min)
Urban	872.48 $\pm$ 116.43	1951.53 $\pm$ 201.23	1089.49 $\pm$ 198.92	2.62 $\pm$ 1.12	2.18 $\pm$ 2.42
Rural	844.78 $\pm$ 108.70	1843.40 $\pm$ 159.74	993.24 $\pm$ 229.33	2.93 $\pm$ 1.23	1.39 $\pm$ 1.00

**Fig. 1.** Relationship between song duration (s) of individuals and background noise (dB). Regression line is for illustration purposes only.

of magpies in the group, excluding carol and mobbing, which are group behaviours): magpie type (urban or rural), playback type (urban, rural or control), and the relative playback type (homotypic, heterotypic or control, similar to testing for interaction effects).

## RESULTS

### Song analysis

The ambient noise levels at rural sites were significantly lower than at urban sites ( $t = -2.72$ ,  $df = 30$ ,  $P = 0.02$ ).

There were no significant differences between urban and rural magpies in the minimum frequency ( $t = 0.82$ ,  $df = 43$ ,  $P = 0.41$ ) or frequency bandwidth ( $t = -1.506$ ,  $df = 43$ ,  $P = 0.14$ ) of their songs. However, urban magpies did sing higher maximum frequencies than rural magpies ( $t = -1.99$ ,  $df = 43$ ,  $P = 0.05$ ). There was no significant correlation between ambient noise and frequency values, at either maximum frequency ( $F = 1.1$ ,  $df = 1,28$ ,  $r = 0.03$ ,  $P = 0.30$ ), minimum frequency ( $F = 1.4$ ,  $df = 1,28$ ,  $r = 0.04$ ,  $P = 0.25$ ) or frequency bandwidth ( $F = 0.04$ ,  $df = 1,28$ ,

$r = 0.002$ ,  $P = 0.80$ ). Descriptive statistics of the mean frequencies of song are presented in Table 1.

Although individual song duration did not differ between urban and rural habitats ( $t = 0.91$ ,  $df = 43$ ,  $P = 0.37$ ), songs became shorter with increasing background noise ( $F = 5.201$ ,  $r = 0.157$ ,  $P = 0.030$ ; Fig. 1). Song rate did not differ between urban and rural individuals ( $t = -1.525$ ,  $df = 30$ ,  $P = 0.128$ ). Individual song rate was also not correlated with ambient noise ( $F = 0.15$ ,  $r = 0.005$ ,  $P = 0.7$ ). As urban groups were significantly smaller than rural groups ( $t = 2.31$ ,  $df = 8$ ,  $P = 0.014$ ), group song rate (songs per minute for entire group over a random 10 minute period) was divided by the average group size of the relevant habitat type. There was no significant difference between the group song rate of urban and rural magpies ( $t = 2.78$ ,  $df = 4$ ,  $P = 0.25$ ).

### Playback experiments

All magpies responded with significantly more vigilance ( $F = 5.09$ ,  $df = 1,28$ ,  $P = 0.032$ ), carols ( $F = 6.30$ ,  $df = 1,28$ ,  $P = 0.002$ ), warbles ( $F = 6.97$ ,  $df = 1,28$ ,  $P = 0.013$ ) and flyovers ( $F = 3.96$ ,  $df = 2,27$ ,  $P = 0.031$ ) to

**Table 2.** The number of incidents of each behaviour observed during the playback period, arranged to show the overall responses of both magpie types and the combined responses to each playback type and relative playback type. Values are the mean number of incidents of each behaviour  $\pm$  standard deviation per individual bird, except for mobbing and carol which were classified as group behaviours. \* indicates a significant result ( $P < 0.05$ ), † indicates results approaching significance ( $P < 0.1$ ).

Behaviour	Magpie type		Playback type			Relative playback type		
	Urban	Rural	Urban	Rural	Control	Homotypic	Heterotypic	Control
Vigilance	8.71 $\pm$ 5.42	5.43 $\pm$ 5.31	7.43 $\pm$ 6.58	9.78 $\pm$ 5.52	4.01 $\pm$ 2.45*	9.31 $\pm$ 5.88	7.90 $\pm$ 6.41	4.01 $\pm$ 2.45†
Approach	2.94 $\pm$ 4.40	5.72 $\pm$ 5.94	4.43 $\pm$ 5.00	5.14 $\pm$ 6.08	3.43 $\pm$ 5.28	5.43 $\pm$ 6.02	4.15 $\pm$ 5.01	3.43 $\pm$ 5.28
Carol	3.87 $\pm$ 5.03	2.60 $\pm$ 3.70	4.00 $\pm$ 5.37	5.00 $\pm$ 4.50	0.70 $\pm$ 1.25†	5.50 $\pm$ 5.80	3.50 $\pm$ 3.72	0.70 $\pm$ 1.25*
Warble	1.18 $\pm$ 1.37	1.14 $\pm$ 1.01	1.49 $\pm$ 1.27	1.62 $\pm$ 1.23	0.37 $\pm$ 0.58*	1.82 $\pm$ 1.32	1.29 $\pm$ 1.10	0.37 $\pm$ 0.58*
Call	0.14 $\pm$ 0.29	0.34 $\pm$ 0.75	0.48 $\pm$ 0.95	0.14 $\pm$ 0.15	0.12 $\pm$ 0.19	0.25 $\pm$ 0.31	0.36 $\pm$ 0.94	0.12 $\pm$ 0.19
Mobbing	0.87 $\pm$ 1.41	1.93 $\pm$ 3.58	1.10 $\pm$ 1.52	2.70 $\pm$ 4.24	0.40 $\pm$ 0.70	2.90 $\pm$ 4.25	0.90 $\pm$ 1.20	0.40 $\pm$ 0.70
Flyover	1.13 $\pm$ 2.33	0.85 $\pm$ 0.95	2.13 $\pm$ 2.62	0.68 $\pm$ 0.72	0.17 $\pm$ 0.42*	1.78 $\pm$ 2.64	1.03 $\pm$ 1.14	0.17 $\pm$ 0.42†
Physical Aggression	0.00 $\pm$ 0.00	0.29 $\pm$ 0.63†	0.05 $\pm$ 0.16	0.39 $\pm$ 0.76	0.00 $\pm$ 0.00	0.39 $\pm$ 0.76	0.05 $\pm$ 0.16	0.00 $\pm$ 0.00
Non-physical Aggression	1.02 $\pm$ 1.38	1.71 $\pm$ 3.17	1.76 $\pm$ 2.40	2.11 $\pm$ 3.27	0.30 $\pm$ 0.95	2.79 $\pm$ 3.35	1.18 $\pm$ 2.12	0.30 $\pm$ 0.95
Foraging	1.86 $\pm$ 3.53	0.97 $\pm$ 1.93	0.60 $\pm$ 1.45	0.56 $\pm$ 0.98	3.08 $\pm$ 4.26	0.13 $\pm$ 0.32	1.03 $\pm$ 1.54	3.08 $\pm$ 4.26

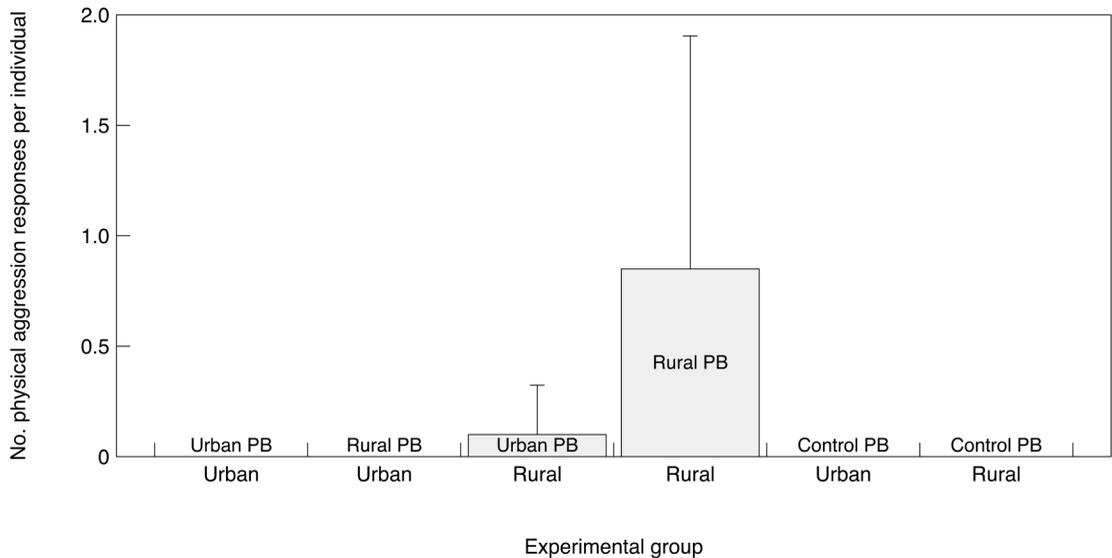
the magpie playback tracks compared to the control. They also spent significantly more time foraging ( $F = 6.08$ ,  $df = 1, 28$ ,  $P = 0.020$ ) during the control playback. Playback order had no effect on behavioural response. Overall, urban magpies showed no differences in response levels to rural magpies in any behaviour class (all  $P > 0.05$ ). No effect of playback type (urban or rural), or relative playback type (heterotypic or homotypic) was found on response behaviour (all  $P > 0.05$ ; Table 2). The treatment of playing rural song to rural magpies elicited significantly more physical aggression ( $F = 3.00$ ,  $df = 5, 24$ ,  $P = 0.03$ ) than any other playback treatment (Fig. 2). There were no further significant behavioural response results (all  $P > 0.05$ ) for any other playback treatment combinations.

## DISCUSSION

Despite significantly louder ambient noise levels at urban sites compared to rural sites, we found only minor differences in the song of urban and rural magpies, namely that song duration was negatively correlated with background noise. There were no differences in minimum frequencies, frequency bandwidth or song rate between urban and rural magpies. Subsequently, we found that magpies from both habitats responded similarly to both kinds of magpie song, although rural birds showed a higher level of physical aggression to the rural (homotypic) playback.

Our results contrast with other studies that have routinely identified shifts in minimum frequency between rural and urban birds (e.g., Slabbekoorn & Ripmeester 2008; Halfwerk & Slabbekoorn 2009; Mockford & Marshall 2009; Nemeth & Brumm 2009; Potvin *et al.* 2011). The minimum frequency of magpie song is well within the masking range of anthropogenic background noise (Hu & Cardoso 2009), however we were unable to identify any shift in the minimum frequency of urban magpie song, consistent with other studies (Hu & Cardoso 2010). The trend towards higher maximum frequencies in urban song may indicate a tendency to use more notes in the higher range in urban areas, possibly as an attempt to increase transmission. Without further evidence this hypothesis is speculative, however it may indicate that magpies are physically or physiologically unable to alter their low-frequency notes. Alternatively, it may not be adaptive to do so: if low frequencies contain evolutionary significant information then shifting these lowest frequencies upwards may be maladaptive. Unfortunately, the function of frequency in magpie song is still unknown.

There is some evidence that increased pitch might be less effective in improving signal transmission than increased amplitude (Nemeth & Brumm 2010) – a quality of song that is very difficult to quantify in the field. In addition, independent manipulation of frequency and amplitude has been



**Fig. 2.** The average number of physically aggressive responses per individual per minute as observed during the playback period for each experimental group. Labels inside the bars represent the playback type, while the x-axis indicates the focal group habitat type.

identified in a number of songbirds (Suthers *et al.* 1999; Cardoso & Atwell 2011). With this in mind, it is possible that the urban magpies we recorded have altered the amplitude of their song rather than raising their song frequency. This ability might also contribute to their apparent success in colonising urban environments.

Some changes to singing behaviour may be adaptive responses to the acoustic environment, however singing behaviours can be affected by other variables such as energetic costs. If acoustic alterations to overcome urban noise (such as raising amplitude or frequency) are energetically costly, there may be an advantage to singing shorter songs. Although we originally predicted that urban birds may sing longer or may repeat more songs in order to increase signal redundancy in noisy areas, we found no support for this. In our study, high levels of background noise predicted shorter song duration but not song rate. Shorter song duration has also been observed in great tits (Halfwerk & Slabbekoorn 2009), and may be indicative of an unwillingness to communicate and expend energy in areas with high levels of noise where the effort may be futile.

### Playback experiments

We found no effect of song type *per se*, nor did we find any significant evidence that urban magpies responded more strongly to homotypic songs. The first part of this study indicated that there are no significant observable differences in the characteristics of the song and it is possible that song

divergence of magpies is not as great as that found in other species (see Slabbekoorn & Ripmeester 2008). Alternatively, urban and rural magpies may simply be unable to detect minute differences between songs from different habitats. However, this hypothesis is unlikely considering that birds are often able to detect small differences that might contain information regarding individual quality or identity (Catchpole & Slater 2008). Sensitivity to small variations in song is of particular importance to magpies given their social structure. Urban and rural magpies appear to respond equally to conspecific song regardless of background and habitat.

Magpies show vocal plasticity, demonstrated by imitation and improvisation (Brown *et al.* 1988) such that even within a territorial group there are syllables unique to individuals. This adaptation may allow magpies to recognise unfamiliar syllables as magpie song if they occur within the context of a known song structure, such as a carol. Conversely, greater syllable sharing between neighbouring groups than unfamiliar groups (Brown & Farabaugh 1991) might result in a muted response to any songs that differ from the familiar vocalisations of neighbours. Great tits and magpies both thrive in noisy urban environments and both show plasticity in singing behaviour. Noise-dependent song switching in great tits has been shown to occur within a very short timeframe (Franco & Slabbekoorn 2008; Halfwerk & Slabbekoorn 2009) and is related to their flexibility in post-dispersal singing behaviour (McGregor & Krebs 1989). Magpies are able to continue learning

and changing their song through adulthood (Brown *et al.* 1988). This suggests that singing plasticity may be one mechanism by which both senders and receivers cope with novel acoustic environments.

The greater aggressive response of rural birds in comparison to their urban conspecifics may indicate that urbanisation has promoted greater passivity in magpies. Urban birds that have acclimatised to noisy, disruptive environments may have adapted to avoid wasting energy on responding with high levels of aggression to common disruptive stimuli (Lowry *et al.* 2011). Alternatively, rural magpies may be less accustomed to encountering intruding groups of birds at close proximity. Generally, birds that thrive in cities are more densely populated in urban areas (Marzluff 2001) in which case disputes in rural habitats would usually be mediated at greater distances. Unfortunately, we do not have sufficient data on the density of urban magpies to make definitive conclusions, and we propose that further investigation into the density of urban populations and the implication for territorial interactions would be useful.

Playback studies are crucial when investigating potential song differences between populations of the same species. If receivers do not respond differently to heterotypic and homotypic song, then any differences we observed (or indeed any differences that we may not have detected or considered) are not likely to affect the ecology of the species. Despite the evidence for frequency shifts in song between birds in urban and rural habitats in other studies, such modifications may not necessarily be adaptive nor universal, and it is therefore equally as important to consider both the species that demonstrate urban song shifts and those that do not, and investigate potential consequences. Magpies may be able to adapt to noisy anthropogenic environments, just as they are able to adapt to noisy natural environments through other means. The magpie is a species that has thrived in both urban and rural areas, despite possessing a song that would appear maladapted to urban environments based on frequency alone.

In conclusion, the Australian magpie does not show a minimum frequency shift in song in urban habitats, although it does shorten the duration of its song and may modify maximum frequency. These could be adaptations to avoid masking by urban noise through selective timing and upper note use. Minimum frequency may be an important characteristic of magpie carolling, making urban shifts non-adaptive. Alternatively, it may be more effective to alter other song characteristics such as amplitude. In addition, rural and urban birds appear not to respond differently to heterotypic songs, suggesting that despite changes in song, communication is still effective between individuals originating from

different habitat types. The finding that rural birds respond with high levels of aggression in some situations may be evidence for decreased sensitivity in urban magpies, and we suggest future research focus on personality, aggressiveness, overstimulation and acclimatization in rural and urban birds.

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