Vocal duets in a nonpasserine: An examination of territory defence and neighbour-stranger discrimination in a neighbourhood of barred owls

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Vocal duets in a nonpasserine: an examination of territory defence and neighbour–stranger discrimination in a neighbourhood of barred owls

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Summary

Mated pairs of animals in many taxa coordinate their vocalizations into duets, yet most research on duetting has focused on songbirds. Here we examine the duetting behaviour of barred owls (*Strix varia*) by addressing three questions: (1) Do owl duets play a role in territorial interactions? (2) Do owls discriminate between duets of neighbours versus strangers? (3) Do duets play a role in extended communication among a neighbourhood of owls? We simulated territorial encounters by broadcasting duets of adjacent, territory-holding owls (neighbours) and distant owls (strangers). We assessed responses to playback using a 3.5-km transect of automated recording devices. We compared vocal activity during a pre-playback period and following both playback treatments for the focal pair, their neighbours, and more distant owls within the neighbourhood. After playback, focal owls gave significantly more duets, vocalized for a longer duration, and emphasized different call types compared to the pre-playback period, demonstrating that barred owls use duets in territory defence. Focal owls did not respond significantly differently to neighbours versus strangers. At the neighbourhood level, owls did not behave differently during silent pre-playback periods or post-playback periods. Our results suggest barred owl duets function primarily in immediate confrontations during territorial conflicts.

Keywords: communication, vocal duet, neighbour–stranger discrimination, *Strix varia*.

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Introduction

Coordinated vocalizations between male and female breeding partners, known as duets, have evolved independently in many different animals (e.g., Emerson & Boyd, 1999; Geissmann, 2002; Bailey, 2003; Hall, 2004; Mann et al., 2009). Hypotheses for the primary functions of duets include pair bond maintenance, acoustic contact, mate guarding, joint territory defence and breeding synchrony (reviewed in Hall, 2004). Proposed secondary functions of duets, which have received considerably less attention, include sex recognition, individual recognition, maintaining reproductive isolation, and ritualized appeasement (Hall, 2004). For the primary and secondary functions of duets, duetting is often distinguished as being cooperative or conflict-based (Logue, 2005; Mennill & Vehrencamp, 2008; Seddon & Tobias, 2009). Males and females may cooperatively combine their vocalizations to jointly defend a territory or maintain a pair-bond (Thorpe, 1972), or each individual could join its partner's song to competitively guard their mate or their paternity (Sonnenschein & Reyer, 1983; Hall, 2004). Because duets may signal both cooperation or conflict between a pair, they may relay information about the duetting pair to eavesdropping conspecific individuals in the neighbourhood around them (Hall, 2004; Hall & Magrath, 2007). We explored one primary and one secondary function of duets, as well as the influence of duets on nearby conspecifics, by examining territory defence and neighbour–stranger discrimination of duets within a neighbourhood of barred owls (*Strix varia*).

Many duet studies have focused on primary functions of duetting, particularly territory defence (Thorpe, 1972; e.g., Hall, 2006; Mennill, 2006). Many investigations support a territory defence function of duetting by demonstrating aggressive responses to duet playback, including increased calling, duetting, or approach to the playback speaker (e.g., Rogers et al., 2004; Seddon & Tobias, 2005; Mennill, 2006; Molles & Waas, 2006). Previous studies, however, involve a relatively small number of study species, all of them passerine birds. Given the diversity of oscine passerine, suboscine passerine, and non-passerine birds that are known to duet (Farabaugh, 1982), more extensive research on duet function across a broader taxonomic spectrum is needed. Owls, Order Strigiformes, offer a particularly interesting system for addressing duet function because duetting is common in owls, but few studies have examined the combined role of male and female vocalizations (exception: Appleby et al., 1999).

The secondary functions of duetting, such as conspecific discrimination and individual recognition, have received relatively little attention (however, see Wiley & Wiley, 1977; Mitani, 1985; Brown & Farabaugh, 1991; Hall, 2000; Grafe & Bitz, 2004; Klenova et al., 2008). Many studies support the idea that songbirds can distinguish between the voices of different individuals and much research supports the idea that individually distinctive vocalizations facilitate territorial interactions (reviewed in Stoddard, 1996). Recent research indicates that the fairly stereotyped vocalizations of non-song-learning species, as well as complex signals such as duets, can also carry individually-distinctive information (Lovell & Lein, 2004; Radford, 2005; Fitzsimmons et al. 2008a; Lein, 2008). Two owl species have been shown to discriminate between neighbours and strangers based on playback experiments of solo calls (Galeotti & Pavan, 1993; Hardouin et al., 2006) and many other Strigiformes exhibit individually distinctive vocalizations (Cavanaugh & Ritchison, 1987; Fitton, 1991; Galeotti & Pavan, 1991; Freeman, 2000; Lengagne, 2001; Holschuh & Otter, 2005). Beyond owls, three studies have demonstrated neighbour stranger discrimination on the basis of duets, including two passerine species (*Campylorhynchus nuchalis*: Wiley & Wiley, 1977; *Laniarius aethiopicus*: Grafe & Bitz, 2004) and one gibbon species (*Hylobates muelleri*: Mitani, 1985). However, no experiments have tested a non-passerine bird's ability to discriminate between conspecifics based on duets. Conspecific discrimination is classically studied in the form of a neighbour–stranger experiment and requires that animals can distinguish between familiar and unfamiliar vocalizations (Brooks & Falls, 1975; reviewed in Stoddard 1996; in contrast to individual recognition, which requires that animals distinguish between vocalizations in the correct context or location). The results are typically assessed in the context of the 'dear-enemy' hypothesis (*sensu* Fisher, 1954), which posits that an animal should respond more aggressively to an unfamiliar stranger than to a known neighbour (Brooks & Falls, 1975; reviewed in Temeles, 1994).

Another challenge in understanding duet function is determining which individuals within a population are listening to and responding to duets. The idea that duetting animals may signal to receivers other than their partner is fairly recent (Hall, 2004) and has developed alongside the communication network perspective of animal communication (reviewed in McGregor, 2005). The communication network model accounts for individuals exchanging signals with multiple receivers simultaneously, either intentionally or unintentionally (McGregor, 2005). Not only might animals communicate with individuals other than their mate when they contribute to a duet, but outside individuals may be able to gain information from listening to the duets of other nearby individuals. To date, no one has explored duet function within an extended communication network. Communication network research has focused on the response of nearby individuals to song contests and territory intrusions (e.g., McGregor & Peake, 2000). Research on communication networks has demonstrated that interactions observed by eavesdropping individuals can influence the immediate vocal behaviour (e.g., Mennill & Ratcliffe 2004; Fitzsimmons et al., 2008b) or the future mating and territorial decisions of eavesdroppers (e.g., Peake et al., 2001; Mennill et al., 2002). Vocal duets are a prime candidate for imparting information to eavesdroppers because they may impart information about multiple individuals (i.e., the two duetting animals) to the neighbours around them.

In this study we evaluate the responses of barred owls to playback of duets of familiar and unfamiliar individuals. We employed a neighbour–stranger experimental design, playing duets of familiar, adjacent territory-holding owls (neighbours) and unfamiliar, distant owls (strangers) to territorial, mated pairs of barred owls. We evaluate the vocal response of focal pairs of owls to playback within their territory. We simultaneously evaluate the responses of owls in neighbouring territories. Our investigation has three goals. (1) We test the idea that barred owl duets play a role in territory defence. (2) We evaluate whether individuals can discriminate between the duets of familiar versus unfamiliar pairs. (3) We examine the influence of duets broadcast at one location on the vocal behaviour of the surrounding neighbourhood of birds. If barred owl duets are used in territory defence, we expected pairs would respond aggressively to duet playback, particularly by increasing their own duet output. If barred owl duets are used in neighbour–stranger discrimination, we expected an increased response to playback of stranger duets compared to neighbour duets. Lastly, based on the communication network model, we predicted that a simulated territory encounter would lead to heightened vocal behaviour among neighbours and possibly other nearby owls in the population.

Methods

We studied barred owls at three sites within Holmes and Washington counties along the Choctawhatchee River in northwest Florida. Playback trials took place during the pre-breeding season of barred owls in January and February 2008. We simulated duets through a single loudspeaker positioned at the territory boundary of focal pairs of owls. We recorded the responses of playback subjects and adjacent owls using a 3.5-km transect of automated recording devices. Preliminary observations indicated that each automated recording device was capable of detecting a far-carrying signal up to 250 m, so we spaced devices 500 m apart for continuous recording across the 3.5-km transect. We replicated this design at each of the three recording locations, which were separated by distances of 1.0 to 10.0 km.

Study species

Vocal signalling plays a large role in the communication behaviour of owls, which are largely nocturnal (Galeotti & Pavan, 1991). Barred owls are highly vocal and perform long, far-carrying duets (Mazur & James, 2000). Surveys and observations in our study site and other southeastern populations suggest barred owls maintain contiguous territories averaging 250–500 m in diameter in bottomland forests (Odom, unpublished data; R. Bierregaard, Jr., personal communication). We often heard two to three pairs of barred owls from a single location, demonstrating that communication network effects are possible. Freeman (2000) showed that barred owls possess spectrographically individually-distinctive vocalizations, an important precursor for individual discrimination (Stoddard, 1996). Pair bonds are maintained across multiple years, mated pairs defend territories year-round, and territory boundaries are stable over several years (Mazur & James, 2000). Barred owl duets are continuous bouts of polyphonal calling between a mated male and female (Mazur & James, 2000). Duets usually begin with a male call, and duets are easily distinguished from solo vocalizations by repeated boisterous gurgle vocalizations that do not typically occur outside of duets (Odom, 2009; Odom & Mennill, data not shown).

Recording and playback equipment

Each of the seven automated recording devices consisted of a Sennheiser ME-62 omni-directional microphone with K6 power module and Marantz PMD-670 solid-state digital recorder powered by a sealed lead-acid battery. Microphones were mounted on shelf brackets attached to 3 m wooden posts and were attached to small trees within the study site. Recordings were collected as MP3 files on a Hitachi 3GB microdrive at a sampling rate of 44.1 kHz, 16 bit, 160 kb/s. Full details of the automated recording devices can be found in Hill et al. (2006). Focal recordings were made with a Marantz PMD 670 and a Sennhieser ME67 shotgun microphone. Focal recordings were collected as WAV files with the same sampling rate as above. Playback was broadcast through an Anchor-Audio loudspeaker (model PB-25; frequency response 0.1–12 kHz; power output 15 W).

Playback design

We used playback to simulate the vocalizations of a duetting pair of owls at the boundary of a focal pair's territory. We simulated duets of both a familiar, neighbouring pair of owls, and an unfamiliar, stranger pair of owls. Neighbour vocalizations were recorded in a territory adjacent to the focal pair and played at the shared territory boundary. Stranger vocalizations were recorded from territories at least 4 km from the focal pair, but usually 10–20 km from the focal pair. We assessed territory positions by evaluating positions of vocalizing pairs of owls in the vicinity of each playback location several nights in a row prior to playback. Duets used to create playback stimuli were elicited using a standardized playback of four tracks of a male and female owl performing two common solos: one track of eight two-phrased hoots and three identical tracks of three minutes of ascending hoots (Mazur & James, 2000). We ceased playback once the target pair began to vocalize and we recorded the pair until several clear duets were obtained at close range (10–30 m). Stimuli for the experiment were taken from recordings of the owls within thirty minutes from the broadcast of this playback.

Stimuli for the experiment were prepared using Audition (Adobe Systems, San Jose, CA, USA). All stimuli were created by isolating one natural duet bout per pair lasting 35 ± 5 s. The duet stimulus was repeated four times with 30 s of silence between each repetition. Duets chosen for the stimuli consisted of several male-initiated two-phrased or ascending hoots joined by the female and escalating into the main caterwaul bout (Mazur & James, 2000). Duets finished with a few soft, short ascending hoots. This arrangement was typical of duets in our study population (Odom & Mennill, unpublished data). Twelve stimuli were made and used in different combinations to create unique neighbour–stranger paired stimuli for each experimental trial. Each stimulus was used once to simulate a neighbour and once to simulate a stranger in different parts of the study population. Stimulus amplitude was standardized to -1 dB using the normalize feature of Audition, and then burned onto CD as uncompressed WAV files for playback in the field.

Stimuli were broadcast at the same volume across all trials, based on an amplitude which we assessed to be a natural volume by comparing sounds from our playback device to owl duets in the field. Playback trials consisted of an initial 20 min of silent observation, the broadcast of the first playback stimulus (either neighbour or stranger stimulus), 20 min of observation to assess responses to playback, 20 min of silence, the broadcast of the second (opposite) playback stimulus, and a final 20 min of observation to assess responses to the second stimulus. We alternated the order of neighbour and stranger playback stimulus so that half the trials began with neighbour playback and half began with stranger playback. Playback response was recorded with a directional microphone near the site of playback and also with the 3.5-km transect of seven automated recording devices. We conducted eleven paired neighbour–stranger playback trials in total, in three to four territories in each of three transects. No owls responded to either stimulus in one trial. Several of the automated recorders failed in another trial, preventing analysis of neighbourhood-level responses for that trial. In total, we assessed responses of the focal pair across $n = 10$ trials and responses of the surrounding neighbourhood across $n = 9$ trials. Trials were conducted between 0300 h and 0530 h.

Sound analysis

We visualized recordings as spectrograms in Syrinx-PC (J. Burt, Seattle, WA, USA). We annotated all owl vocalizations that occurred in each of three 20-min periods: (I) the silent period 20 min prior to the first playback, (II) the post-neighbour playback period starting at the beginning of the neighbour stimulus and (III) the post-stranger playback period starting at the beginning of the stranger stimulus. We calculated five parameters within each period: (i) duration of response, (ii) number of solo calls, (iii) number of duets, (iv) latency from start of the playback to the first solo and (v) latency to the first duet. We defined duration of response as the period of time between an owl's first vocalization after playback and the start of a five minute period of silence (based on our observation that owls were unlikely to resume vocalizing after 5 min of silence). We counted duets as bouts of overlapping male and female vocalizations. A silent gap greater than 1 s was used to differentiate between duet bouts and distinct solo calls (owls usually transitioned to solo calls by one sex or ceased vocalizing after a gap of more than 1 s; pers. obs.). We calculated the number of calls as the number of solo vocalizations that occurred outside of duet bouts. Both latency parameters were calculated from the start of each observation period until the first call or duet, respectively. We also calculated the number of each of two common calls given by barred owls (Odom, 2009): inspection calls (a contact call) and ascending hoots (presumed to be a territorial call).

We compared owl behaviour at three levels: the response of the focal pair receiving the playback, the response of neighbours in immediately adjacent territories, and the neighbourhood response of all owls except the focal pair across the entire 3.5-km recording transect (approximately 8 territories of mated pairs). The focal pair's response was calculated from focal recordings taken at the playback location. The immediate neighbours' and the neighbourhood response were calculated from passive recordings taken by the automated recording devices. Immediate neighbours were defined as owls recorded at the two automated recording devices adjacent to the recording device at the location of the playback, and each parameter was calculated as the sum of vocal activity at both of these devices. The neighbourhood response was calculated as the sum of vocal activity of all owl vocalizations detected at all the automated recording devices minus the activity at the device nearest to the playback location.

Statistical analysis

We addressed each of our three main goals using separate statistical comparisons. For parametric tests, the five parameters of response were transformed to achieve normal distributions, with log transformations applied to all continuous variables (both latency measures and duration of response) and square root transformations applied to counts (number of calls and duets).

To examine duet function in territory defence (goal 1), we used data from the focal pair's response. We used linear mixed-models to conduct repeated measures ANOVA with restricted maximum likelihood method, type III sum of squares, and treatment as the independent variable. We examined all five main parameters for differences between the pre-playback period and neighbour and stranger stimuli. To understand how inspection calls and ascending hoots contributed to the overall number of calls and territory defence, we also compared the occurrence of each of these call types between the three treatments using Kruskal–Wallis tests on untransformed data. We used planned post hoc comparisons to evaluate differences between treatments for both sets of tests.

To examine neighbour–stranger discrimination based on duets (goal 2), we used data from the focal pair's response. We used the results of the post hoc tests from the territory defence analysis for the five main parameters to evaluate differences in response between the neighbour and stranger treatments. This approach was equivalent to conducting paired t-tests between neighbour–stranger response on the five parameters.

To test the role of duets in a communication network (goal 3), we used the linear mixed-model design used to examine territory defence to conduct repeated-measures ANOVA. Comparisons were between the pre-playback period and neighbour and stranger treatments for both immediate neighbours and the wider neighbourhood (i.e., all birds recorded at all automated recording devices minus the device nearest the site of playback). In order to minimize the number of statistical tests performed, only those parameters for which the focal pair showed a significant response to playback were examined for the immediate neighbours and neighbourhood.

To determine if our design was sufficient to detect an effect for any non-significant results, we calculated effect sizes for our data using Cohen's d (Cohen, 1988; Nakagawa & Cuthill, 2007). We also calculated effect sizes for three published studies with similar designs to our three primary goals (see Introduction; goal 1: Brooks & Falls, 1975; goal 2: Hardouin et al., 2006; goal 3: Fitzsimmons et al., 2008b). As suggested by Thomas & Juanes (1996), we used these previous studies' effect sizes as standardized values for comparison to our effect sizes. We corrected for multiple comparisons within each of our main goals by accepting an alpha level of 0.007 for the territory defence analysis (seven comparisons) and 0.01 for communication network analysis (four comparisons). Linear mixed-models and post hoc analyses were conducted in SPSS (SPSS, Chicago, IL, USA). Kruskal–Wallis tests were conducted in JMP 5.0.1 (SAS Systems, Cary, NC, USA).

Results

Territory defence

Barred owls responded strongly to duets simulated through playback. Focal owls at the site of playback vocalized for a significantly longer duration (repeated measures ANOVA: $F_{2,27} = 6.3$, $p < 0.006$; Figure 1a) and performed significantly more duets ($F_{2,27} = 6.0$, $p = 0.007$, Figure 1b) in response to playback of neighbour or stranger stimuli than during the pre-playback period. The number of solo calls by focal owls did not differ between the playback and pre-playback periods when all solo call types were combined ($F_{2,27} = 1.3$, $p = 0.30$; Figure 1c). Neither latency to first solo call ($F_{2,27} = 0.5$, $p = 0.63$) nor latency to first duet ($F_{2,27} = 0.1$, $p = 0.94$) were significantly different between the pre-playback period or the two playback treatments (Figure 1d and 1e). There were, however, significant differences in numbers of particular types of calls before and after playback. Inspection calls decreased significantly following playback (Kruskal–Wallis: $H = 11.5, N = 10, p = 0.003$; Figure 2a), while ascending hoots increased significantly between the pre-playback period and stranger playback ($H = 9.8$, $N = 10$, $p = 0.007$; Figure 2b).

Neighbour–stranger discrimination

There were no significant differences in response to neighbour and stranger stimuli by the focal pair (Table 1, Figure 1). Although differences were not significant, stranger stimuli elicited an increased response compared to neighbour stimuli from the focal pair: focal owls vocalized for a longer duration (Table 1, Figure 1a) and responded more quickly with solos (Figure 1d) in response to strangers than neighbours. The effect sizes from both these values were comparable to those calculated from the results of a previous neighbour–stranger study (Table 1).

Neighbourhood-level communication

Looking beyond the level of the focal pair, we found that neither immediate neighbours nor the entire recorded neighbourhood performed significantly different numbers of duets (repeated measures ANOVA: $F_{2,24} = 1.5$, $p = 0.24$ and $F_{2,24} = 1.8$, $p = 0.18$) or for significantly different durations ($F_{2,24} < 0.1$, $p = 0.96$ and $F_{2,24} = 1.0$, $p = 0.40$) across all treatments

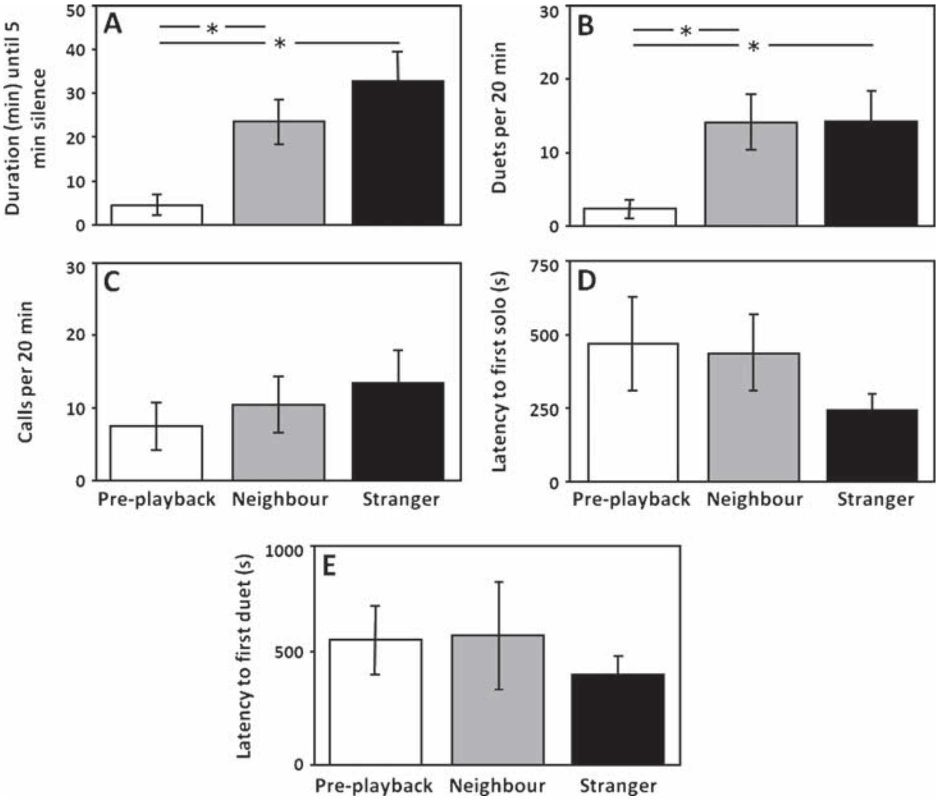

Figure 1. Vocal behaviour of focal barred owls during a pre-playback silent period and in response to playback of duets of a neighbour and stranger pair of owls. Duration of vocal behaviour (A) and number of duets (B) increased significantly after playback when compared to a silent pre-playback period. Number of calls (C), latency to first solo (D), and latency to first duet (E) did not vary significantly across the three periods. Asterisk shows significant differences based on Tukey's test of honestly significant differences.

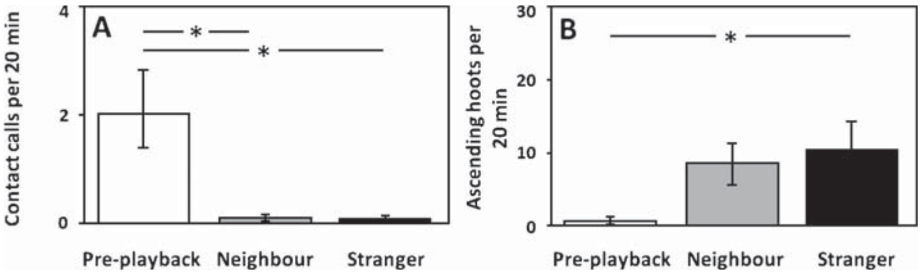

Figure 2. The number of contact calls (A) decreased significantly after playback, whereas the number of ascending hoots (B) increased significantly after playback when compared to a silent pre-playback period for the focal pair. Asterisk shows significant differences based on Tukey's test of honestly significant differences.

Table 1. Effect sizes for the current study compared to standard effect sizes calculated from previous studies examining each of the hypotheses examined: (A) territory defence, (B) neighbour–stranger discrimination and (C) neighbourhood-level communication.

Group	Parameter	*N*	$\overline{x}_{\text{control}}$	$\overline{x}_{\text{neighbour}}$	$\overline{x}_{\text{stranger}}$	SE	*p*	*d*
A. Territory defence								
Focal pair	No. of calls	10	7.3	10.5	13.3	3.3	0.30	0.31
Focal pair	No. of duets	10	2.3	14.5	14.7	3.4	<0.01	1.13
Focal pair	Duration (min)	10	4.5	23.8	33.2	4.7	<0.01	1.31
Focal pair	Latency to first solo (min)	10	7.9	7.4	4.1	2.0	0.63	−0.08
Focal pair	Latency to first duet (min)	10	9.4	9.8	6.8	2.9	0.94	0.03
Comparison[1]	No. of songs	18	0.8	2.0	4.1	0.1	<0.01	2.71
B. Neighbour–stranger discrimination								
Focal pair	No. of calls	10		10.5	13.3	3.3	0.37	0.26
Focal pair	No. of duets	10		14.5	14.7	3.8	0.91	0.02
Focal pair	Duration (min)	10		23.8	33.2	5.1	0.41	0.54
Focal pair	Latency to first solo (min)	10		7.4	4.1	2.2	0.42	−0.62
Focal pair	Latency to first duet (min)	10		9.8	6.8	4.1	0.79	−0.30
Comparison[2]	Hoots/min	21		10.0	13.6	1.0	0.0001	0.56
Comparison[2]	Duration of response	21		135.0	210.0	16.1	0.0001	0.72
Comparison[2]	Latency to first response	21		105.0	40.0	16.9	0.0001	−0.59
C. Neighbourhood-level communication								
Immediate neighbour	No. of duets	9	2.6	6.2	7.4	2.6	0.24	0.16
Immediate neighbour	Duration (min)	9	6.8	11.5	13.7	3.9	0.96	0.19
Neighbourhood	No. of duets	9	8.4	15.2	24.8	6.2	0.18	0.54
Neighbourhood	Duration (min)	9	24.1	42.4	45.0	11.6	0.40	0.08
Comparison[3]	Song output–neighbourhood	10	12.5	9.0	17.5	2.2	0.04	1.16
Comparison[3]	Song output–individuals	10	3.3	2.6	4.0	0.9	0.06	1.48

Cohen's *d* for territory defence were calculated from means and mean square error with pre-playback as the comparison group, for neighbour–stranger discrimination from means and standard deviations and for neighbourhood-level communication from means and mean square error with stranger as the comparison group.

[1] From Brooks & Falls (1975).

[2] From Hardouin et al. (2006).

[3] From Fitzsimmons et al. (2008b); treatments were 'submissive' vs 'aggressive' rather than 'neighbour' vs 'stranger'.

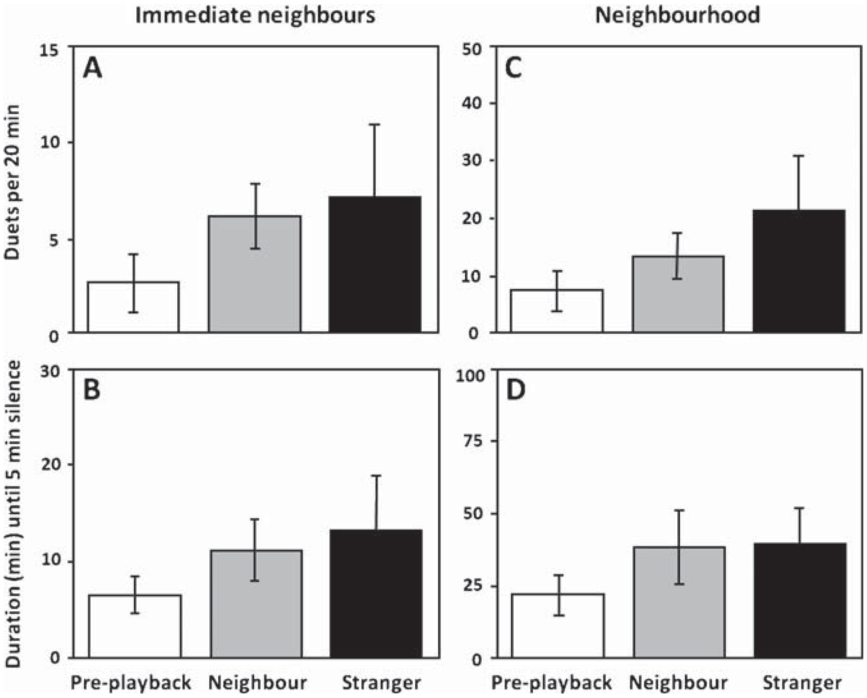

Figure 3. Vocal behaviour of territorial owl pairs adjacent to the site of playback (A and B) and of the entire neighbourhood of owls (C and D) recorded with a 3.5-km transect of microphones. No significant differences were detected outside of focal pairs' territories for number of duets and duration of vocalizing.

(Figure 3). We compared immediate neighbour and neighbourhood response based only on numbers of duets and duration because these were the only two of the five calculated parameters that showed a significant difference within the focal pair analysis. Although non-significant, all four comparisons (Figure 3) were in the predicted direction, with higher responses to neighbour and stranger playback than control periods. Effect sizes for communication network analyses were small compared to results of another communication network study (Table 1).

Discussion

Barred owl responses to playback indicate that pairs perform vocal duets during encounters with rival pairs. We found that only the barred owls within the territory experiencing the simulated encounter responded strongly to duets. We did not find compelling evidence that duets are signals of conspecific discrimination or signals that transmit information within a communication network, although owls showed non-significant increases in their response to strangers versus neighbours and non-significantly higher levels of vocal output following interactions taking place beyond their territory boundaries. Our findings are in agreement with previous studies of songbird duets, showing that duets are important in territorial interactions. However our results stand in contrast to previous studies of both conspecific discrimination and communication networks, given that we failed to find statistical support for the idea that owls respond differently to neighbour versus stranger playback or that playback induces communication network-level effects.

Territory defence

Barred owls demonstrated a territorial response to playback of duets by increasing their calling and duetting rates, and by vocalizing for extended periods compared to the silent pre-playback period. The increased number of duets, in particular, points to the fact that barred owls use their duets when confronting a rival pair performing duets at their territory boundary. Our findings agree with the majority of studies that have examined the territory defence hypothesis for the function of vocal duetting (e.g., Hall, 2004; Rogers et al., 2004; Molles & Waas, 2006; Mennill & Vehrencamp, 2008). Previous studies show increased duetting and calling in response to duets in several oscine passerine and one suboscine passerine species (Rogers et al., 2004; Seddon & Tobias, 2005; Mennill, 2006; Molles & Waas, 2006). To our knowledge, this is the first direct, empirical study to provide support for the territory defence hypothesis of duetting in a nonpasserine bird.

Our results do not exclude the possibility that barred owl duets have additional functions (such as acoustic contact or mate guarding), nor do they provide information on the conflicting versus cooperative nature of duets. However, we did not find an increase in solo calling in response to playback treatments, as we might expect if owls show sex-specific responses to duets. More information on sex-specific response is needed to address other potential duet functions in this species. The increase in duetting we observed, without an increase in solo calling, provides initial support for the idea that mated pairs combined their vocalizations to defend their territory.

Neighbour–stranger discrimination

Barred owls did not show significant differences in response to playback of neighbours' versus strangers' duets, although we found a non-significant pattern of heightened responses toward strangers. There are several explanations for barred owls' similar responses to neighbours versus strangers. First, the heavy degree of overlap within the duets of barred owls may encumber neighbour–stranger discrimination within their complex duets. We consider this explanation unlikely. Although their complex duets have a high degree of overlap, the beginning and end of each duet typically features several calls given by the male or female independently, which might facilitate individual discrimination. Since barred owls have individually distinct solos (Freeman, 2000), it is possible that they are also able to discriminate between duets based on vocal recognition of individuals within sections of little overlap. In addition, Radford (2005) provides evidence for neighbour–stranger discrimination in green woodhoopoes (*Phoeniculus purpureus*) based on a group signature within their choruses, even though the individual contributions within these choruses are highly overlapping. We did not directly test whether owls might distinguish between entire duets or the calls of the individuals within duets; a playback experiment that compares owls' responses to duets versus the solo calls that comprise duets would help to elucidate the importance of each duet component.

A second explanation for the similar responses observed for neighbour versus stranger playback is that barred owls may not have been selected to discriminate neighbours from strangers. The current literature on neighbour–stranger discrimination and recognition among suboscine and nonpasserine birds has found mixed results. The spotted antbird (*Hylophylax naevioides*: Bard et al., 2002), a suboscine passerine, has individually distinct vocalizations, but does not exhibit conspecific discrimination in playback experiments. The suboscine alder flycatcher (*Empidonax alnorum*), on the other hand, exhibits both individually distinct vocalizations and neighbour–stranger discrimination (Lovell & Lein, 2004). Many owl species, including barred owls, possess the important prerequisite of individually distinctive vocalizations (Cavanaugh & Ritchison, 1987; Fitton, 1991; Galeotti & Pavan, 1991; Freeman, 2000; Lengagne, 2001; Holschuh & Otter, 2005), but there is mixed evidence for neighbour–stranger discrimination in owls. Galeotti & Pavan (1993; $N = 20$) and Hardouin et al. (2006; $N = 21$) found neighbour–stranger discrimination in two owl species (tawny owl, *Strix aluco*, and little owl, *Athene noctua*, respectively), whereas Waldo (2002; $N = 13$) did not find evidence for neighbour–stranger discrimination in the spotted owl (*Strix* *occidentalis*), the closest relative of the barred owl. Barred owl pairs maintain stable year-round territories and territory boundaries (Mazur & James, 2000), suggesting that neighbours should be perceived as a lower risk than unfamiliar non-neighbouring individuals, consistent with conditions of the ‘dear-enemy’ hypothesis (Fisher, 1954). Nevertheless, the strong territorial responses exhibited in response to all duet stimuli may have masked subtle differences in response to neighbours versus strangers.

A third alternative is that our sample size was too small to allow us to detect neighbour–stranger discrimination. Although we failed to find neighbour–stranger discrimination in barred owls, trends and effect sizes of our results indicate that barred owls may discriminate between the duets of neighbours and strangers. For nearly all parameters, the reaction to the stranger stimulus was in the direction predicted by the ‘dear-enemy’ hypothesis (Temeles, 1994). Also, effect sizes for neighbours versus strangers were comparable to those from other published studies (Table 1), indicating the trends toward neighbour–stranger discrimination in barred owls were meaningful. These trends, in combination with comparable effect sizes to published studies, suggests that neighbour–stranger discrimination may occur in barred owls, but a larger sample size is needed before firm conclusions are made.

Neighbourhood-level communication

Our playback study with barred owls did not provide evidence for communication taking place within a network that extends beyond birds’ territory boundaries. This result was contrary to our expectations; given that barred owls produce far-carrying acoustic signals and closely-spaced territories, they seem to be an ideal candidate for information being transferred in a network-like fashion (McGregor, 2005). Again, there are several explanations for the absence of pronounced network-level communication. First, our sample size may have been too small to detect an effect. Second, our methods may not have been appropriate for detecting communication networks in this species. Third, extended neighbourhood-level communication may not exist among barred owls. In contrast to Fitzsimmons et al. (2008b), we did not find immediate response to an observed territorial interaction within a neighbourhood of birds. However, sample sizes of both experiments were similar. Our sample size did allow us to detect a distinct response of focal owls to playback when compared to a pre-playback period. Thus, it is possible we would have detected a difference between at least the pre-playback period and playback trials within the neighbourhood had such a relationship existed. Effect sizes for immediate neighbour and neighbourhood responses were small in comparison to standardized effect sizes (Table 1). These results do not allow us to conclude that communication networks do not exist among barred owls, however, the disparity with published research indicates a much greater sample size would be needed to detect an effect if one exists. Trends for the communication network analysis were in the predicted direction, but non-significant and weak in comparison to studies that did see a significant difference.

Another possibility is that communication networks exist within barred owl populations, but they function in other ways. For example, Schmidt et al. (2007) found that song contests observed by eavesdropping nightingales (*Luscinia megarhynchos*) influenced how they responded to the observed nightingales the next day. Nightingales that lost song contests were more likely to be approached and challenged in future song contests (Schmidt et al., 2007). A barred owl's decisions and future interactions may be influenced by listening to duet bouts and territorial encounters in adjacent territories, but our experiment evaluated neighbourhood-level responses only in the twenty minutes following playback. Alternatively, communication network-level responses may occur for variables that we did not measure in our study, such as non-vocal or sex-specific vocal responses of neighbours. Other owl species do use their vocalizations for between-pair communication (Appleby et al., 1999; Delgado & Penteriani, 2006), suggesting owl vocalizations could function in a communication network and the need for additional research.

Owls (Strigiformes) and songbirds (Passeriformes) show many differences in life histories, and these differences may help to explain why we did not find support for the communication network model. Most birds of prey are fairly solitary with large home ranges determined by their prey abundance (Mazur et al., 1998). In northern populations of barred owls, individuals maintain territories averaging 1.18–2.28 km^2, depending on the season (Elody & Sloan, 1985), 2–4-times the size of the territories in our study population. Such distances between pairs likely inhibit network-level communication, while duets may still be useful for within-pair or direct territorial interactions. Complex communication networks may, therefore, be reduced among birds of prey and other animals that typically have large, spaced-out territories, even though the potential for communication networks is present in some populations were individuals are present at higher densities.

Conclusions

In summary, barred owl responses to playback demonstrate that duets play a role in territory defence, but do not provide support for the idea that barred owl duets function in neighbour–stranger discrimination or communication networks. Barred owls used duets during confrontations with simulated rivals, vocalizing for extended periods of time and giving more ascending hoots and fewer contact calls in response to playback. Barred owls gave more calls and responded sooner to strangers than neighbours, but this difference was not statistically significant. Distant barred owls did not vocalize more after neighbour or stranger playback than during a pre-playback silent period, indicating immediate neighbours and nearby owls do not strongly respond vocally to duets, although barred owl duets might function within a communication network in non-vocal or sex-specific ways. An important direction for future research on barred owl duets is playback experiments that evaluate sex-specific response to male and female solos and duets through a dual-speaker design (e.g., Douglas & Mennill, in press). Such research would further our knowledge of whether the territory defence function of barred owl duets is a cooperative or conflict-based behaviour. Investigating non-vocal and delayed responses in a communication network is also an important direction for future research in this system, although such research is challenging in nocturnal animals. We encourage continued research on multiple functions of duets, including conspecific discrimination and communication networks, in a diversity of oscine and suboscine passerines and nonpasserines with a variety of life histories.

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