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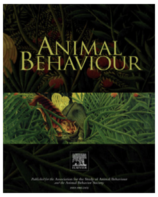

Large vocal repertoires do not constrain the dear enemy effect: a playback experiment and comparative study of songbirds

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A R T I C L E I N F O

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Many territorial animals are less aggressive towards neighbours than they are towards strangers. This phenomenon is known as the ‘dear enemy’ effect and it occurs because strangers represent a considerably higher threat to territory take-over compared to neighbours. Some evidence has suggested that large repertoires may constrain neighbour–stranger discrimination. We tested whether songbirds with large repertoires exhibit neighbour–stranger discrimination, conducting a playback study on a songbird with a large vocal repertoire, and a comparative analysis of the dear enemy effect across all published studies of songbirds. In our playback study, we broadcast neighbour and stranger songs within the breeding territories of red-eyed vireos, *Vireo olivaceus*, a songbird species with a large song repertoire (ca. 50 songs per individual). Vireos responded significantly more aggressively to playback of stranger versus neighbour songs; subjects approached closer to the loudspeaker, had a lower latency to approach the loudspeaker, spent more time near the loudspeaker and sang more soft songs during stranger trials than during neighbour trials. We examined song sharing between red-eyed vireos and found low levels of song sharing between neighbours, suggesting that red-eyed vireos may discriminate among conspecifics based on individually distinctive song types. We then conducted a comparative analysis of neighbour–stranger discrimination across the published literature on songbirds, using a phylogenetically controlled analysis to explore whether species with large repertoires are less likely to discriminate between neighbours and strangers. Across 34 species, we found no evidence that songbirds with large repertoires are constrained in their ability to distinguish between neighbours and strangers. We conclude that large song repertoires do not inhibit neighbour–stranger discrimination in red-eyed vireos specifically, or songbirds generally.

The sexual signals of animals play a central role in mate attraction and resource defence (Bradbury & Vehrencamp, 2011). Many animals produce individually distinctive signals (reviewed in Tibbetts & Dale, 2007) that facilitate individual identification of conspecific animals (e.g. Müller & Manser, 2007). During signalling interactions, any time an animal identifies a signaller it must decide whether the signaller is threatening or nonthreatening and respond appropriately. In territorial animals, unfamiliar ‘strangers’ are often considered a greater threat than familiar ‘neighbours’ because strangers may be prospecting for a breeding territory whereas neighbours should be encountered routinely and already possess a territory (Getty, 1987). This phenomenon of decreased aggression towards neighbours is known as the ‘dear enemy effect’ (Fisher, 1954) and has been found in a wide variety of taxa including reptiles (Ibáñez, Marzal, López, & Martín, 2013), birds (Linhart, Slabbekoorn, & Fuchs, 2012), mammals (Monclús, Saavedra, & de Miguel, 2014), insects (Langen, Tripet, & Nonacs, 2000), fish (McGregor &Westby, 1992), amphibians (Bee & Gerhardt, 2002) and crustaceans (Booksmythe, Jennions, & Backwell, 2010) (reviewed in Temeles, 1994).

Many animals rely on vocal signals for territorial signalling (Bradbury & Vehrencamp, 2011). Acoustic signals are often individually distinctive, usually based on fine structural differences in the vocalizations of conspecific individuals (e.g. Arnold & Wilkinson, 2011; Bee, Kozich, Blackwell, & Gerhardt, 2001; Kennedy, Evans, & McDonald, 2009). A compelling body of evidence supports the idea that animals differentiate among individually distinctive vocalizations, including operant conditioning or habituation–discrimination studies (e.g. Trefry & Hik, 2009; Weary & Krebs, 1992) and field-based studies of free-living animals (e.g.

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Osiejuk, 2014; Price, Boutin, & Ydenberg, 1990; Wilson & Mennill, 2010). This acoustic discrimination ability allows animals to identify conspecific individuals and respond appropriately.

Birds show extensive variation in song repertoire sizes, ranging from 1 to over 2000 song types (MacDougall-Shackleton, 1997). Several studies have suggested that birds with large song repertoires display weaker discrimination abilities than birds with small song repertoires (Falls & D'Agincourt, 1981; Godard, 1993a; Hoelzel, 1986; Kroodsma, 1976; McGregor & Avery, 1986). There are at least three reasons why large song repertoires may impose a constraint on individual recognition: (1) birds must learn more songs to facilitate discrimination; (2) each song type will be heard less frequently, creating less opportunity to learn each song; and (3) song sharing may be higher, making identity assignment more difficult (Stoddard, 1996). In contrast, other studies have found that some bird species capably discriminate between conspecific individuals despite their large repertoires (Botero, Riveros, & Vehrencamp, 2007; Hyman, 2005; Weary, Lemon, & Perreault, 1992). Additionally, two decades ago, a comparative analysis suggested that there was no relationship between repertoire size and neighbour–stranger discrimination ability across 20 species of passerines of the suborder Passeri (Weary et al., 1992). It is clear that evidence exists both to support and contradict the hypothesis that large repertoires constrain individual discrimination, and more research is needed to fully understand the effect repertoire size has on individual discrimination.

Red-eyed vireos, *Vireo olivaceus*, are songbirds that have large vocal repertoires, with repertoire size estimates ranging from a median of 28.5 song types (Borror, 1981) to 51 song types (Godard, 1993a). Previous research suggested that red-eyed vireos are unable to discriminate between individual neighbours due to their large repertoire size (Godard, 1993a). The distinction between individual neighbours is more difficult than the distinction between a neighbour and a stranger, because neighbours belong to the same class of conspecific individuals (i.e. familiar) whereas neighbours and strangers belong to different classes of conspecific individuals (i.e. familiar and unfamiliar) (Stoddard, 1996). Red-eyed vireos present an interesting animal in which to study neighbour–-stranger discrimination because of this previous work that has called their discrimination ability into question.

In this study we had two goals. (1) Employing the classic neighbour–stranger discrimination paradigm, we used a playback experiment to test the ability of red-eyed vireos to discriminate between neighbours and strangers. To complement this, we quantified repertoire size and song sharing at our study site. (2) Although many studies have discussed the negative effects that a large repertoire may have on an individual's capability to discriminate neighbours from strangers (Falls & D'Agincourt, 1981; Godard, 1993a; Kroodsma, 1976), only one study (Weary et al., 1992) has examined this across multiple species. We sought to update this study with a comparative analysis of neighbour–stranger discrimination literature across the songbirds (i.e. birds in the order Passeriformes, suborder Passeri), using a phylogenetically controlled analysis to ask whether songbirds with large repertoires are less likely to discriminate between neighbours and strangers.

FIELD STUDY

Methods

General field methods

We conducted a playback study with red-eyed vireos at the Queen's University Biological Station (44°34′N, 76°19′W) north of Kingston, Ontario, Canada. We conducted playback experiments from 24 May to 4 July 2015, a time when all red-eyed vireos at our site had established their breeding territories and when most subjects were incubating eggs or in the early stages of chick rearing. We studied 28 males occupying breeding territories in eight different woodlots at our study site (average ± SE distance between woodlots: 593.5 ± 92.9 m). The birds were not banded, and instead we relied on location information and features of acoustic recordings to distinguish between different males (sex was identified by song, because only males sing in this species; Cimprich, Moore, & Guilfoyle, 2000). We identified individuals by following birds on their breeding territory, paying careful attention to the movement patterns of each of our subjects, monitoring the song posts and perches they used and the parts of the forest they occupied. We verified the identities of individuals by comparing recordings of the songs they sang during playback trials to songs we collected in previous focal recordings collected during observation sessions. We based our analyses of repertoire size and song sharing on 21 males where we had recorded at least 250 songs from each bird. We based our analysis of playback responses on 21 males (14 of these males were the same males used for repertoire and song-sharing analyses) after excluding three males due to uncertainty regarding identity (no shared songs were detected during playback trials when compared to previous recording sessions), two males due to neighbour interference during playback and two additional males due to a lack of response to our playback stimuli.

All methods involving animals were approved by the University of Windsor Animal Care Committee (AUPP number 13-15).

Song collection and playback stimuli

To quantify repertoire size and song sharing, and to gather sounds for playback stimuli, we recorded spontaneous bouts of song from male red-eyed vireos. We collected recordings with an omni-directional microphone (model: Sennheiser ME62/K6, Sennheiser, Wedemark, Germany) mounted in a parabolic reflector (model: Telinga MK2, Telinga Microphones, Uppsala, Sweden) connected to a digital solid-state recorder (model: Marantz PMD660, 44.1 kHz sampling rate, 16-bit encoding, Wave format). Before recording a bird, we followed it around its breeding territory for at least 30 min, paying careful attention to the bird's song posts and the locations of its neighbours, in order to be certain that we were recording the correct bird. We then collected at least 10 min of continuous song from each red-eyed vireo. After song collection, we hung flagging tape to mark the territory boundaries we had observed during the observation session.

We created playback stimuli using Audition 3.0 software (Adobe, San Jose, CA, U.S.A.). Playback stimuli were composed of 1 min of continuous red-eyed vireo song repeated three times for a total of 3 min. From our field recordings, we selected the 1 min portion with the lowest level of background noise, based on visual assessment of sound spectrograms. We applied a 1000 Hz high-pass filter to filter out low-frequency background noise, below the range of red-eyed vireo songs. We then trimmed or added small sections of silence between songs, so that all songs were separated by intersong intervals of 0.6–0.8 s. Our preliminary analyses demonstrated that this was a natural song rate in our population. We normalized playback stimuli to −1 dB in Audition. In the field, we standardized the sound output from the loudspeakers using a sound level meter (Casella CEL-240; C-weighting, fast response) so that the peak amplitude of each stimulus was 80 dB at a distance of 1 m from the loudspeaker, a natural song amplitude for this species.

For each subject, ‘neighbour stimuli’ were songs recorded from a male that occupied a territory adjacent to the focal bird, and ‘stranger stimuli’ were songs recorded from birds that occupied a territory at least 1.5 km away from the focal bird. We chose this distance because red-eyed vireos do not move far from their territories after establishment, and therefore it is unlikely that a bird would hear the song of another conspecific 1.5 km away. In total, we created 32 stimuli for our 42 trials; 10 stimuli were used twice (five were used twice as strangers, four were used twice as neighbours and one was used once as a neighbour and once as a stranger).

Playback experiment

We carried out playback experiments between 0700 and 1100 hours, a time when song rate is high for red-eyed vireos (C. Moser-Purdy, personal observation). Trials consisted of a 3 min playback period followed by a 10 min postplayback observation period. We flipped a coin before the first playback trial, to determine whether neighbour or stranger stimuli would be presented first; for all subsequent trials we alternated which stimuli was presented first. Across all 28 subjects, we played both neighbour and stranger playback first an equal number of times; however, out of the 21 subjects included in our final analysis, eight received neighbour playback first and 13 received stranger playback first. Neighbour and stranger playback trials took place on consecutive days except for three trials that took place 2 days apart and one trial that took place 3 days apart due to inclement weather.

We placed the loudspeaker (model: Scorpion TX200, FOXPRO, Inc., Lewistown, PA, U.S.A.) in a tree between 1.5 m and 2 m above the ground, roughly 10 m into the focal bird's territory, nearest to the boundary with its neighbour (as in Godard, 1993a). We set up flagging tape at 2 m and 5 m in four equally spaced directions from the loudspeaker to facilitate estimates of the distance of the focal bird from the loudspeaker. We began playback trials when the focal bird was singing at least 15 m away from the loudspeaker and the neighbour used to create the neighbour stimulus was silent. We placed the loudspeaker in the same location within the focal bird's territory for each playback trial. An observer (C.M.-P.) dictated the behaviour of the focal male and recorded the vocalizations of the focal male using a shotgun microphone (Sennheiser ME67/K6) connected to a solid-state digital recorder (Marantz PMD660, New York, NY, U.S.A.). The same observer (C.M.-P.) then scanned through the recordings of the trial in Syrinx-PC (John Burt, Seattle, WA, U.S.A.) and annotated the spoken commentary of the bird's activities and the songs of the subject to create a time-stamped record of the bird's behaviour.

From the time-stamped record of the subjects' behaviour, we extracted the following response measures: distance of closest approach to the loudspeaker (in metres), latency to approach within 5 m of the loudspeaker (in seconds), duration of time spent within 5 m of the loudspeaker during the playback trial (in seconds), duration of time spent within 5 m of the loudspeaker in the post-playback observation period (in seconds), number of songs sung and number of soft songs sung. Soft songs were of unusually low amplitude and fairly easy to identify in the field after spending time observing red-eyed vireos throughout the 2014–2015 field seasons. Soft songs have received recent attention because they may be associated with aggressive intent in several songbird species (Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015). There are no previous reports of soft song in red-eyed vireos; however, our preliminary observations suggested that they occur in this species, just as they appear to be common among many other songbirds (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998; Reichard & Welklin, 2015).

Repertoire size and song sharing

To quantify repertoire size, we used Syrinx-PC to visualize spectrograms of the recordings we collected of spontaneously singing males. We calculated repertoire size for all birds where we had recordings of 250 or more songs ($N = 21$). In most cases, we were able to collect all required songs during a single recording session. In cases where this was not possible, we combined song types recorded on multiple days and compared song types between these days to ensure that the same bird was recorded. If the majority of song types were similar between the two recording sessions, we assumed that it was the same individual singing. Following Borror (1981), we considered syllables to be part of the same song when they were separated by less than 0.3 s of silence. Borror (1981) studied red-eyed vireo songs across the species' range in the United States and found that red-eyed vireos sing with immediate variety and that their song types are highly stereotyped across renditions. The songs in our recordings matched this pattern, and we found that new song types were simple to detect because songs were either notably different from each previous song type, or a perfect match with a previous song type. We developed a library of song types for each individual. For every song encountered in our recordings, we visualized it as a sound spectrogram in Syrinx-PC and compared it to all of the previous songs sung by that bird. If there was no match with a song in that bird's accumulated library, we added the new song to the library. We calculated repertoire size as the total number of song types sung over the recordings we had for each bird. To determine whether our recordings were adequate to estimate the full repertoire size of each bird, we plotted the number of new songs sung over the total number of songs sung (Fig. 1). If this graph approached a horizontal asymptote, we assumed that we had recorded a complete or near-complete recording of the bird's full repertoire (as in Godard, 1993a).

Using the song libraries we developed for each of the 21 males, we measured song sharing between red-eyed vireos. For this analysis, we focused on 10 neighbouring pairs and 7 non-neighbouring pairs. We defined non-neighbours as birds that occupied the same woodlot but did not share a territory boundary. We compared a bird's repertoire to all possible neighbours and non-neighbours for which we had recordings. We compared each song from each male's song library to the songs in the second male's song library, and assigned each song a status of ‘shared song’ or ‘unshared song’. We considered a song to be shared when songs had nearly identical fine structural features including bandwidth, length and shape features (see Fig. 2). We calculated the degree of pairwise song sharing using the standard song-sharing index: 2 × (number of songs shared between two individuals)/(repertoire size of individual 1 + repertoire size of individual 2) (Harris & Lemon, 1972).

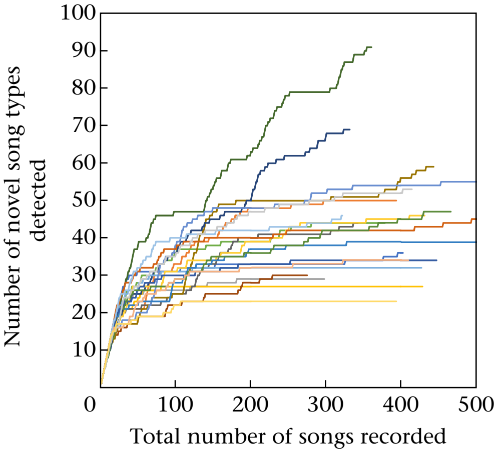

Figure 1. Repertoire size accumulation curves for 21 red-eyed vireos, each coded by a different colour. When a curve approaches an asymptote, such as the lowest curve in the figure, repertoire sampling can be assumed to be complete, given that no new song types are sung as the bird continues to cycle through its repertoire. In our data set, repertoire sampling was complete for nine individuals and incomplete for 12 individuals.

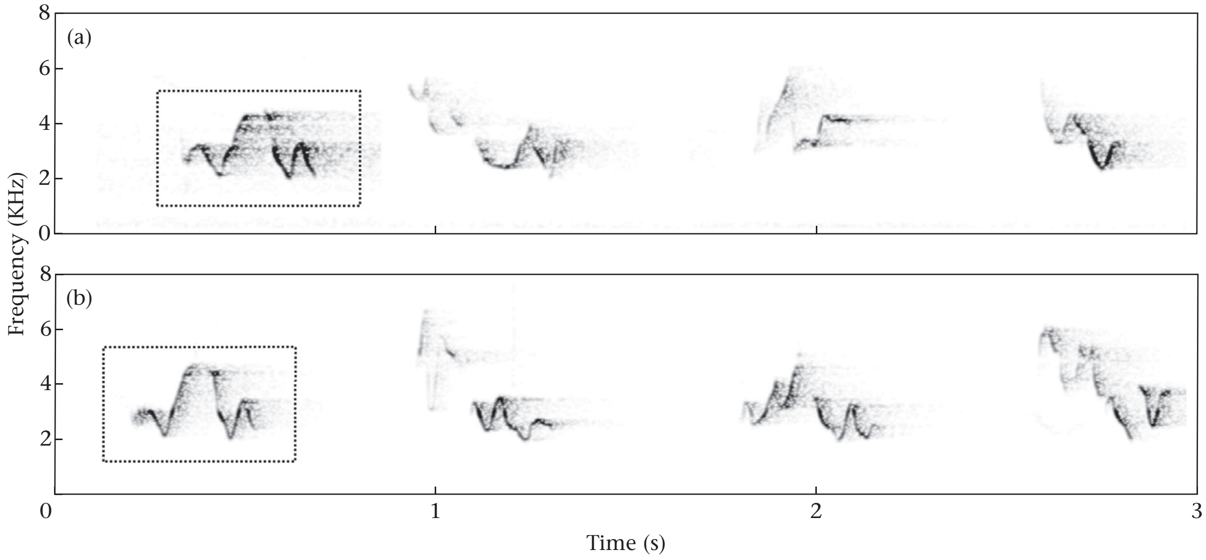

Figure 2. Two spectrograms (a, b) from neighbouring red-eyed vireos. Boxes denote a shared song type.

Statistical analysis

We conducted statistical analyses using R (v.3.2.3, R Development Core Team, 2015). Our song-sharing data and playback response data both showed a non-normal distribution (Shapiro–Wilk tests: song sharing: $W = 0.86$, $N = 20$, $P = 0.008$; closest approach to the loudspeaker: $W = 0.78$, $P < 0.0001$; latency to approach within 5 m of the loudspeaker: $W = 0.70$, $P < 0.0001$; time spent within 5 m of the loudspeaker during playback: $W = 0.84$, $P < 0.0001$; time spent within 5 m of the loudspeaker after playback: $W = 0.80$, $P < 0.0001$; number of songs sung: $W = 0.94$, $P = 0.02$; number of soft songs sung: $W = 0.56$, $P < 0.0001$; all $N = 21$) likely due to a preponderance of minimum and maximum values. For our playback response data, we used an exact Wilcoxon signed-ranks test using the package exactRankTests (Hothorn & Hornik, 2015). To correct for multiple comparisons given the six response variables analysed, we applied a Bonferroni correction. Tests were considered significant if they had a P value of less than 0.008. To determine difference in song sharing between neighbours and non-neighbours occupying the same woodlots, we used an exact Wilcoxon two-sample test using the package exactRankTests.

Results

Playback experiment

Red-eyed vireos showed a more intense response to strangers than to neighbours for four of six response variables: closest approach to the loudspeaker, time spent within 5 m of the loudspeaker during playback, latency to approach the loudspeaker and number of soft songs sung (Fig. 3a–c, f, Table 1). Red-eyed vireos showed an equal response to neighbours and strangers for the remaining two variables: total number of songs sung over the entire trial and the time spent within 5 m of the loudspeaker during the postplayback observation period (Fig. 3d, e, Table 1).

Repertoire size and song sharing

Red-eyed vireos in our study population had large song repertoires (median ± interquartile range male repertoire size = 44 ± 16 song types, range 23–91; Fig. 1), consistent with three previous studies of this species (Borror, 1981; Godard, 1993a; Lemon, 1971). For nine birds where repertoire size approached an obvious horizontal asymptote, median repertoire size was 34 ± 1.5 song types (range 23–55).

Red-eyed vireos showed very low levels of song sharing. The median ± interquartile range song-sharing index was 6.5 ± 2.2% (range 2.5–7.8%) for neighbours and 2.2 ± 0.4% (range 0–2.8%) for non-neighbours. Song sharing was significantly higher between neighbours than between non-neighbours (exact Wilcoxon two-sample test: $W = 3$, $N = 17$, $P = 0.0004$).

COMPARATIVE ANALYSIS

Methods

Data collection

To better understand the effect of repertoire size on neighbour–stranger discrimination at a broader scale, we conducted a comparative analysis across the published literature on songbirds. We compiled repertoire sizes for all neighbour–stranger discrimination studies, to our knowledge, that have been conducted on male songbirds (i.e. birds in the suborder Passeri within the order Passeriformes) using song playback and without other experimental manipulations (e.g. experimentally varying plumage colour in blue tits, *Cyanistes caeruleus*; Poesel, Dabelsteen, Darden, Delhey, & Peters, 2007). We excluded studies that used altered song types of neighbours to imitate strangers (e.g. Aubin, Mathevon, Da Silva, Vielliard, & Sebe, 2004; Osiejuk, 2014) because these experiments do not directly test neighbour–stranger discrimination but rather what elements of a song are used for individual discrimination. We chose to focus on songbirds because they have received extensive study, because song repertoires are common (MacDougall-Shackleton, 1997), and because there have been numerous experiments on neighbour–stranger discrimination in these animals (Stoddard, 1996). We compiled repertoire sizes preferably based on empirical studies. When this was not possible, we used rough estimates of repertoire size found in the literature (preferably the same paper with the neighbour–stranger discrimination experiment). Note: skylark, *Alauda arvensis*, repertoire size was given as syllable repertoire size since skylarks sing long continuous songs and syllable repertoire is more indicative of the complexity of their repertoire (Briefer, Rybak, & Aubin, 2008), and stripe-backed wren, *Campylorhynchus nuchalis*, repertoire size was given as the duet

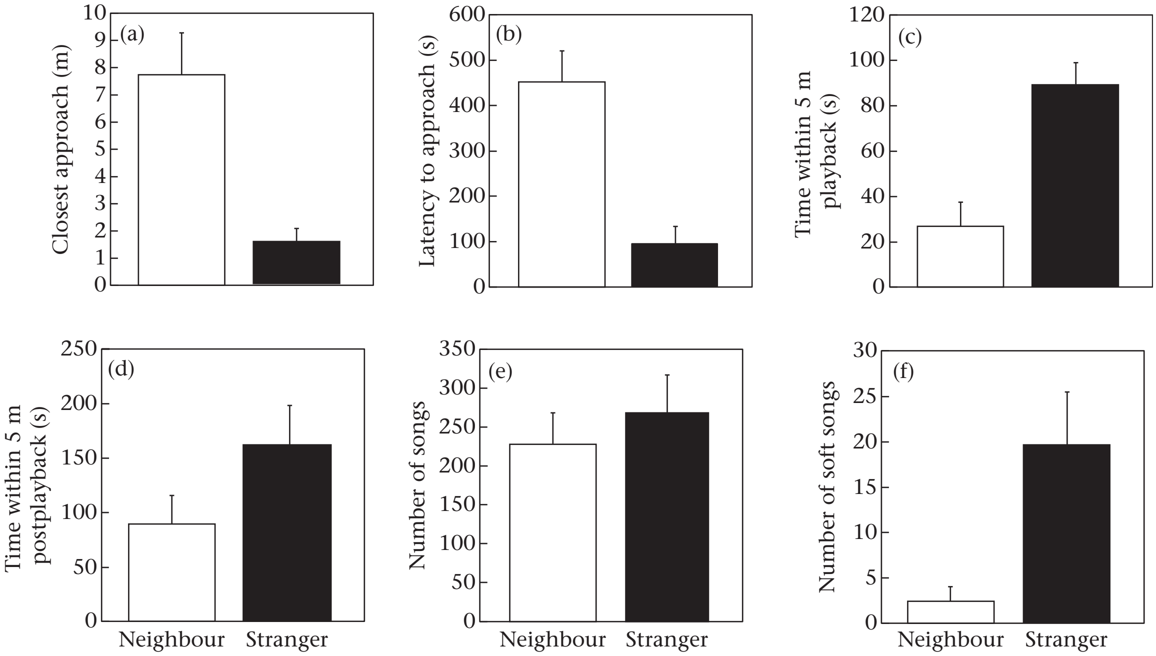

Figure 3. Red-eyed vireos' responses to stranger and neighbour stimuli for each of the six variables (a-f) examined.

repertoire size because duets were used as the playback stimuli in this study (Wiley & Wiley, 1977).

We were interested in investigating whether the strength of neighbour—stranger discrimination could be influenced by repertoire size. We calculated effect sizes of responses between neighbours and strangers as our metric for strength using Cohen's *d*. Our analysis focuses on 34 species where the playback study reported information that allowed us to calculate effect size, Cohen's *d*, for the strength of the difference in response to strangers versus neighbours. We calculated Cohen's *d* using means and standard errors or deviations as reported in the original studies, but when these were not provided, we used the test statistics given in the original studies. We used the response measure that gave the highest Cohen's *d* for our analysis. For articles that did not present their means and standard deviations or errors in text form, but presented these values in graphs, we manually measured the graphs using a ruler with the graph zoomed to fill the screen.

Statistical analysis

We used a phylogenetic generalized least squares analysis (PGLS) to analyse our comparative data, to test for an effect of repertoire size on the effect size of the difference in response to neighbours versus strangers, while controlling for phylogeny. We downloaded 1000 phylogenetic trees using the Hackett sequence-based data set (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; www.birdtree.org). Using TreeAnnotator (v.1.8.2; Drummond, Suchard, Xie, & Rambaut, 2012), we calculated a maximum clade credibility tree with burn-in value set to 0, posterior probability limit set to 0, and node heights as median heights. We used the package 'caper' (Orme, 2013) implemented in R. Our data overlapped with 17 of the 20 studies that Weary et al. (1992) used in their comparative analysis (we excluded two studies due to lack of sufficient information for calculating Cohen's *d*, and a third study because we did not agree that it tested neighbour—stranger discrimination; Godard, 1991); our data add 17 more species to this comparative analysis.

Results

We found 38 species of songbirds that have been the subject of an investigation of neighbour—stranger discrimination studies, representing a broad spectrum of families of songbirds. Across these 38 species, 33 showed discrimination between neighbours and strangers and five did not (Table 2). For 34 of these species, we found information on species-typical repertoire sizes and sufficient data to calculate effect size (Cohen's *d*) of the strength of their response to neighbours versus strangers. We found no significant relationship between repertoire size and the strength of the response to strangers versus neighbours (PGLS: $R^2 < 0.0001$, $N = 34$, $P > 0.99$; Fig. 4).

Table 1
Red-eyed vireos responded more strongly to neighbours than to strangers in four out of six response measures

Response measure	Mean+SE		*W*	*P*
	Neighbour	Stranger		
Closest approach to loudspeaker (m)	7.9±1.6	1.6±0.5	179.5	**0.0002**
Latency to approach within 5 m of loudspeaker (s)	462.9±71.7	95.6±35.2	204	**0.00003**
Time (s) within 5 m of loudspeaker during playback	26.9±10.6	87.8±8.6	12	**0.0001**
Time (s) within 5 m of loudspeaker after playback	86.0±25.4	157.5±36.4	48	0.06
Total number of songs sung	225.3±39.9	270±46.4	84	0.29
Total number of soft songs sung	2.1±1.4	19.4±6.2	9.5	**0.002**

We used an exact Wilcoxon signed-ranks test to determine significance. Significant outcomes ($P < 0.008$) are shown in bold.

Table 2
Comparative analysis of neighbour–stranger discrimination in 38 songbird species

Species	Repertoire size	Source	
		Neighbour–stranger discrimination	Repertoire size
Neighbour–stranger discrimination			
Agelaius phoeniceus	4.3	Yasukawa, Bick, Wagman, and Marler (1982)	Yasukawa (1981)
Alauda arvensis	70.7	Briefer et al. (2008)	Briefer, Rybak, and Aubin (2011)
Baeolophus bicolor[1]	12.3	Schroeder and Wiley (1983)	Duguay and Ritchison (1998)
Campylorhynchus nuchalis	5	Wiley and Wiley (1977)	Wiley and Wiley (1977)
Catharus fuscescens	3	Weary, Lemon, and Date (1987)	Weary et al. (1987)
Cettia diphone	4	Momose (2000)	Hamao and Ueda (2000)
Emberiza citrinella	2.2	Hansen (1984)	Caro, Keulen, and Poncin (2009)
Emberiza elegans	59	Hwang and Park (1996)	Zeng et al. (2007)
Emberiza fucata	2	Hwang and Park (1996)	Kim and Park (1993)
Emberiza hortulana	4.2	Skierczynski, Czarnecka, and Osiejuk (2007)	Osiejuk, Ratyńska, Cygan, and Dale (2003)
Erithacus rubecula	175	Brindley (1991)	Brindley (1991)
Fringilla coelebs	2.9	Pickstock and Krebs (1980)	Slater (1981)
Geothlypis trichas	1	Wunderle (1978)	Wunderle (1978)
Icteria virens[2]	62.2	Ritchison (1988)	Dussourd and Ritchison (2003)
Liocichla steerii[2]	Unknown	Weng et al. (2012)	
Melospiza georgiana	3.5	Searcy, McArthur, Peters, and Marler (1981)	Searcy et al. (1981)
Melospiza melodia	9.6	Harris and Lemon (1976), Kroodsma (1976), Stoddard, Beecher, Horning, and Willis (1990)	Wilson, Towner, and Vehrencamp (2000)
Parus major	3	Järvi, Radestäter, and Jakobsson (1977), Krebs (1971)	McGregor, Krebs, and Perrins (1981)
Parus venustulus	5	Wei, Lloyd, and Zhang (2011)	Wei et al. (2011)
Passerina cyanea	1	Belcher and Thompson (1969), Emlen (1971)	Payne (1982)
Phoenicurus ochruros	2.4	Draganoiu, Ravaux, Moreau, Mathevon, and Bonckaert (2014)	Draganoiu et al. (2014)
Seiurus aurocapilla	1	Weeden and Falls (1959)	Lein (1981)
Setophaga petechia	11.8	Weary et al. (1992)	Beebee (2002)
Setophaga ruticilla	4.4	Weary et al. (1992)	Lemon, Cotter, MacNally, and Monette (1985)
Spizella pusilla[2]	2	Goldman (1973)	Nelson and Croner (1991)
Sturnella neglecta	7.1	Falls and D'Agincourt (1981)	Falls and D'Agincourt (1981)
Thryophilus pleurostictus	19.7	Molles and Vehrencamp (2001)	Molles and Vehrencamp (1999)
Thryothorus ludovicianus	32.4	Hyman (2005), Shy and Morton (1986)	Morton (1987)
Troglodytes troglodytes[1]	6	Courvoisier, Camacho-Schlenker, and Aubin (2014)	Camacho-Schlenker, Courvoisier, and Aubin (2011)
Vermivora celata	1	Yoon, Sillett, Morrison, and Ghalambor (2012)	Yoon et al. (2012)
Vireo olivaceus	44	Present study	Present study
Zonotrichia albicollis[2]	1	Brooks and Falls (1975a, 1975b)	Wasserman (1979)
Zonotrichia leucophrys	1	Baker, Thompson, and Sherman (1981), Falls (1969)	Nelson and Poesel (2010)
No neighbour–stranger discrimination			
Mimus gilvus[3]	130	Botero et al. (2007)	Botero et al. (2007)
Phylloscopus trochilloides	8.5	Katti (2001)	Irwin (2000)
Spizella passerina	1	Albrecht and Oring (1995)	Albrecht and Oring (1995)
Sturnella magna	61.3	Falls and D'Agincourt (1981)	Falls and D'Agincourt (1981)
Thryophilus rufalbus	10.8	Battiston, Wilson, Graham, Kovach, and Mennill (2015)	Mennill and Vehrencamp (2005)

[1] Shows stronger response to neighbours than to strangers.
[2] Excluded from our calculation of effect size of the intensity of the difference in response to neighbours versus strangers because of insufficient data.
[3] Shows recognition of other classes of conspecific individuals.

GENERAL DISCUSSION

Red-eyed vireos readily discriminated between neighbours and strangers in four out of six variables. For each of these four variables, red-eyed vireos responded more intensely to stranger playback than to neighbour playback, thus exhibiting the dear enemy effect. Red-eyed vireos at our study site had large repertoires and displayed low levels of song sharing, with greater song sharing between neighbouring birds than between non-neighbouring birds occupying the same woodlot. We found no effect of repertoire size on the strength of discrimination in our comparative analysis. Our evidence shows that large repertoires do not inhibit neighbour–-stranger discrimination in red-eyed vireos or songbirds as a whole.

Neighbour–Stranger Discrimination

Our results indicate that red-eyed vireos are capable of acoustically differentiating between neighbours and strangers, even though they have large vocal repertoires. Red-eyed vireos approached closer to the loudspeaker, spent more time within 5 m of the loudspeaker during playback, had a lower latency to approach the loudspeaker within 5 m and sang more soft songs during stranger trials than during neighbour trials. These physical response variables are all indicative of an aggressive response to an intruding individual. An increased number of soft songs is also indicative of an aggressive response, in line with previous studies

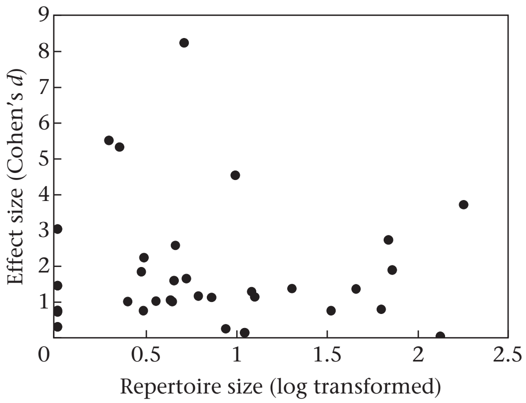

Figure 4. Results of a comparative analysis of 34 songbird species' log repertoire sizes with their effect sizes in response to neighbours and strangers ($R^2 < 0.0001$, $P > 0.99$).

that have found similar results (e.g. Akçay, Tom, Holmes, Campbell, & Beecher, 2011). Soft songs have received substantial attention recently, but little is known about why birds use them to indicate aggressive intent and how these signals remain reliable (Akçay et al., 2015). Despite this, a wide array of animals, including birds (Akçay et al., 2015) and some mammals (Gustison & Townsend, 2015), are known to use soft vocalizations in aggressive contexts, and red-eyed vireos now join these animals.

Two measures of red-eyed vireos' playback responses showed no differences in response to neighbours versus strangers. During the postplayback observation period, there was no significant effect of treatment on the amount of time spent 5 m from the loudspeaker. Shortly after the playback ended, we often observed subjects vacate the area near the loudspeaker and sing from various locations in their territory, which may explain the lack of significance in this result. Red-eyed vireos did not differ in the number of songs they sang during neighbour and stranger playback trials. Red-eyed vireos have a high singing rate (Borror, 1981), so this result is likely due to red-eyed vireos spontaneously singing their territorial songs during neighbour playback trials rather than singing their territorial songs as an aggressive response to the playback. Indeed, this is what we observed in the field. Furthermore, outside of soft songs, there is little evidence in other bird species that singing behaviour is a signal of aggressive intent and physical responses may be more reliable indicators of aggression than vocal behaviours (Searcy & Beecher, 2009; Searcy, Anderson, & Nowicki, 2006).

Our results suggest that red-eyed vireos perceive strangers as a greater threat than neighbours during the breeding season. Since neighbours represent a lesser threat than strangers (Temeles, 1994), territorial individuals benefit from expending energy on tasks such as foraging when hearing neighbour song instead of engaging in territory defence, a behaviour more appropriate when hearing nearby stranger song. The dear enemy effect, and more broadly neighbour–stranger discrimination, appears to be a common phenomenon across a wide array of territorial taxa (Temeles, 1994). In territorial animals, it may be wise to assume neighbour–stranger discrimination is present a priori due to the taxonomic breadth of this phenomenon.

A previous study by Godard (1993a) found no difference between the responses of red-eyed vireos to neighbour playback near their shared boundary and neighbour playback near an unshared boundary. It is possible that Godard's result was due to the inability of red-eyed vireos to differentiate between the more difficult distinction of two familiar individuals (i.e. two neighbours) compared to our study where we investigated the ability of red-eyed vireos to make the simpler distinction between a familiar and unfamiliar individual (i.e. a neighbour versus a stranger). However, due to the low amount of song sharing between neighbours, and thus the high amount of individually unique songs each red-eyed vireo sings, it seems unlikely that red-eyed vireos would be incapable of differentiating between individual neighbours. One alternative explanation for these results may be that red-eyed vireos perceive neighbours as an equal threat regardless of location, warranting an equal response to playback of all neighbour stimuli. Godard (1993a) did not give the breeding stage of her study subjects, and her playback may have been conducted during the fertile period when neighbours may represent an increased threat due to extrapair paternity. Red-eyed vireos have high levels of extrapair paternity (58% of nestlings; 57% of broods; Morton, Stutchbury, Hewlett, & Pipef, 1998), and neighbours are the most common sires of extrapair offspring (Griffith, Owens, & Thuman, 2002; Hill, Akçay, Campbell, & Beecher, 2011; Mennill, Ramsay, Boag, & Ratcliffe, 2004), suggesting that neighbours may be an increased threat during fertile periods. We conducted our study during the incubation and chick-rearing stages, when neighbours are no longer a threat to extrapair paternity and territory borders are well established. Further research exploring seasonal variation in neighbour–stranger discrimination, across different stages of female fertility, is a worthy area of future study.

Future work examining the neighbour–neighbour discrimination ability of red-eyed vireos may benefit from using a design similar to that of Godard (1993b) or Akçay et al. (2009), wherein researchers simulated the intrusion of a neighbour and then observed whether the subjects responded more aggressively to this ‘uncooperative’ neighbour after the intrusion. This would provide a more rigorous test of red-eyed vireos' abilities to discriminate between familiar conspecifics by increasing their motivation to respond more aggressively to an intruding bird.

Repertoire Size and Song Sharing

Red-eyed vireos in our study population had large repertoires (median of 44 song types), in line with previous studies that have found similar results (median: 28.5 song types, $N = 38$, range 12–73, Borror, 1981; median: 51 song types, $N = 5$, range 31–95, Godard, 1993a). Our results should be interpreted as conservative estimates of repertoire sizes, however, because many of our birds had not approached a repertoire asymptote (Fig. 1). Interestingly, repertoire size seems to be highly variable in this species, with a wide range of 23–91 song types in this study, 12–117 song types found by Borror (1981) and 31–95 song types found by Godard (1993a). Large repertoires may be indicative of male quality (Catchpole & Slater, 2008). Evidence for this hypothesis exists in several bird species where larger song repertoires are correlated with male fitness indicators such as body size, territory tenure and reproductive success (e.g. Hesler et al., 2012; Hiebert, Stoddard, & Arcese, 1989; Kipper, Mundry, Sommer, Hultsch, & Todt, 2006; Reid et al., 2005; but see; Beecher, Campbell, & Nordby, 2000). Because of the large individual variation in red-eyed vireo song repertoires, it may represent an ideal species in which to further test this hypothesis.

Red-eyed vireos appear to have considerably low song sharing between individuals, with slightly higher sharing with neighbours than with non-neighbours from the same site. This pattern is commonly found across many bird species (e.g. Foote & Barber, 2007; Griessmann & Naguib, 2002; Mennill & Vehrencamp, 2005; Price & Yuan, 2011), although in many of these species, song sharing is considerably higher than what we report in red-eyed vireos. However, despite the low song sharing in red-eyed vireos, they still follow this pattern of higher song sharing between neighbours than between non-neighbours (but see Borror, 1981). Because of the low song sharing that we found, it is likely that red-eyed vireos can distinguish among different individuals based on songs that are unique to each individual, with what are sometimes called ‘signature songs’ (Weary, Norris, & Falls, 1990). Since each red-eyed vireo in this study sang many songs that their neighbours did not sing, individuals of this species should not have difficulty differentiating between conspecific individuals. Note, however, that in most cases, we did not record repertoires of each individual's neighbours to determine song sharing between all neighbours and likely did not record full repertoires for all individuals; thus, some shared songs may have been missed (see Fig. 1). Still, given the low song sharing observed in this study, even for the animals whose repertoires reached an asymptote, it is unlikely that the individuals in this large-repertoire species would share all of their songs with their neighbours. O'Lochlen and Beecher (1999) found that female song sparrows are capable of discriminating between males based on unshared song types, and there is evidence that great tits, *Parus major*, may discriminate more strongly based upon unshared songs of neighbours than on shared songs of neighbours (McGregor & Avery, 1986). Alternatively, red-eyed vireos may discriminate between individuals based on individually distinctive vocal characteristics; Weary and Krebs (1992) found that great tits were capable of classifying unheard songs to the correct bird after being trained with other songs from the same bird's repertoire, suggesting that their songs have unique vocal characteristics. Red-eyed vireos may also discriminate between neighbours based on fine structural differences between shared vocalizations as found in many other animals (Digweed, Rendall, & Imbeau, 2012; Osiejuk, 2014). Our results suggest that red-eyed vireos are capable of discriminating conspecific individuals based on songs, but more research is needed to elucidate song features that facilitate this discrimination.

Comparative Analysis

Repertoire size did not have a significant effect on a bird's ability to discriminate between neighbours and strangers. This is unsurprising as many large-repertoire birds such as the European robin, *Erithacus rubecula* (Brindley, 1991), and now the red-eyed vireo, discriminate between neighbours and strangers, whereas some birds with small repertoires do not exhibit behavioural discrimination between neighbours and strangers, like the chipping sparrow, *Spizella passerina* (Albrecht & Oring, 1995). A previous study examined the effect of repertoire size on the strength of response to neighbours and strangers and found no evidence to support the hypothesis that repertoire size constrains discrimination (Weary et al., 1992), and our updated analysis with 17 additional species confirms this position. The idea that repertoire size may constrain neighbour–stranger discrimination and conspecific discrimination has received little recent support despite early findings that supported this hypothesis (e.g. Falls & D'Agincourt, 1981; Kroodsma, 1976). Given the results of the current study and those of various previous studies on recognition abilities of large-repertoire birds (e.g. Briefer et al., 2008; Jaška, Linhart, & Fuchs, 2015; Ritchison, 1988), it is abundantly clear that large repertoires do not constrain conspecific discrimination abilities.

Large repertoires may be positively correlated with male quality, allowing females to select the best males based on repertoire size (Catchpole & Slater, 2008). Future studies may benefit from an examination of dominance and variation in male response to conspecific individuals with large and small repertoires. Some work has been done on this topic. For example, Yasukawa (1981) found that red-winged blackbirds, *Agelaius phoeniceus*, were less likely to intrude on a territory when multiple song types were broadcast than when only one song type was broadcast. However, other studies have found that repertoire size had no effect on response to playback (Balsby & Dabelsteen, 2001; Hesler, Mundry, & Dabelsteen, 2011). Red-eyed vireos may be an ideal species in which to study the effect of repertoire size on male–male interactions due to the wide range of repertoire sizes reported here and in other studies (Borror, 1981; Godard, 1993a).

Conclusions

Large repertoires do not constrain neighbour–stranger discrimination. The red-eyed vireo, a large-repertoire songbird, capably discriminated between neighbours and strangers. Furthermore, we found no relation between repertoire size and neighbour–stranger discrimination in a comparative analysis across 34 passerines of the suborder Passeri. Future studies involving repertoire sizes may benefit from a focus on male response to varying repertoire sizes.

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