Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics

Jessica L. Yorzinski and Gail L. Patricelli

References	This article cites 26 articles, 4 of which can be accessed free http://rspb.royalsocietypublishing.org/content/277/1683/923.full.html#ref-list-1
Subject collections	Articles on similar topics can be found in the following collections behaviour (1041 articles) evolution (1417 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Proc. R. Soc. B* go to: **http://rspb.royalsocietypublishing.org/subscriptions**

Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics

Jessica L. Yorzinski* and Gail L. Patricelli

Department of Evolution and Ecology and Animal Behavior Graduate Group, University of California, Davis, CA 95616, USA

Animals in many vertebrate species vocalize in response to predators, but it is often unclear whether these antipredator calls function to communicate with predators, conspecifics or both. We evaluated the function of antipredator calls in 10 species of passerines by measuring the acoustic directionality of these calls in response to experimental presentations of a model predator. Acoustic directionality quantifies the radiation pattern of vocalizations and may provide evidence about the receiver of these calls. We predicted that antipredator calls would have a lower directionality if they function to communicate with surrounding conspecifics, and a higher directionality and aimed at the receiver if they function to communicate with the predator. Our results support both of these functions. Overall, the birds produce antipredator calls that have a relatively low directionality, suggesting that the calls radiate in many directions to alert conspecifics. However, birds in some species increase the directionality of their calls when facing the predator. They can even direct their calls towards the predator when facing lateral to it—effectively vocalizing sideways towards the predator. These results suggest that antipredator calls in some species are used to communicate both to conspecifics and to predators, and that birds adjust the directionality of their calls with remarkable sophistication according to the context in which they are used.

Keywords: acoustic directionality; antipredator calls; dark-eyed juncos; communication; house finches; yellow-rumped warblers

1. INTRODUCTION

Animals that produce antipredator calls take potentially deadly risks by attracting the attention of predators (Taylor *et al*. 1990; Caro 2005). Despite these risks, many animals emit antipredator calls and presumably benefit by doing so. There are several hypotheses that explain the function of antipredator calls. One hypothesis is that these calls function to alert conspecifics to the presence of a predator (either to warn them of the danger or to recruit them to mob the predator). A second hypothesis is that these calls function as signals to predators, communicating to predators that they have been detected and should leave the area (Sherman 1977; Curio 1978). These hypotheses are not mutually exclusive, and antipredator calls could function to both alert conspecifics and signal to predators. Even though many studies have investigated the different functions of antipredator calls (e.g. Curio 1978; Flasskamp 1994), fewer studies have systematically tried to discriminate among these functions. It is often difficult to make this discrimination because we cannot determine whether these calls are directed towards conspecifics, predators or both (but see Zuberbühler *et al*. 1997).

Acoustic directionality may provide evidence about the receivers of antipredator calls. Acoustic directionality describes the sound radiation pattern of vocalizations (Witkin 1977), and when combined with information about the orientation of animals relative to receivers, may allow us to determine where the energy of the vocalization is directed. Vocalizations can range from omnidirectional (radiating with equal amplitude in all directions; e.g. crickets, Forrest 1991) to highly directional (e.g. bats, Henze & O'Neill 1991; sage grouse, Dantzker *et al*. 1999). More omnidirectional vocalizations may allow animals to communicate with surrounding conspecifics, whereas more directional signals may allow animals to beam their signals to intended receivers (such as predators; Witkin 1977; Hunter *et al*. 1986; Larsen & Dabelsteen 1990; Dabelsteen 2005). In red-winged blackbirds, Patricelli *et al*. (2007) found that calls directed to multiple surrounding conspecifics (e.g. alarm calls) are more omnidirectional than calls used in direct interactions with specific individuals (e.g. courtship calls), supporting the hypothesis that directionality may be adapted to the function of the vocalization.

In order to investigate the function of antipredator calls, we analysed the acoustic directionality of antipredator calls emitted by 10 species of passerines: Bewick's wren (*Thryomanes bewickii*), bushtit (*Psaltiparus minimus*), black phoebe (*Sayornis nigricans*), dark-eyed junco (*Junco hyemalis*), fox sparrow (*Passerella iliaca*), house finch (*Carpodacus mexicanus*), northern mockingbird (*Mimus polyglottos*), orange-crowned warbler (*Vermivora celata*), white-breasted nuthatch (*Sitta carolinensis*) and yellow-rumped warbler (*Dendroica coronata*). All of these species are probably targeted by avian and mammalian predators (Derrickson & Breitwisch 1992; Hill 1993; Sogge *et al*. 1994; Kennedy & White 1997; Wolf 1997; Hunt & Flaspohler 1998; Sloane 2001; Nolan *et al*. 2002;

* Author for correspondence (jyorzinski@ucdavis.edu).

Weckstein *et al.* 2002; Grubb & Pravosudov 2008). We analysed the antipredator calls of all 10 species, and performed detailed analyses on three of them (dark-eyed juncos, house finches and yellow-rumped warblers). In response to predators, dark-eyed juncos emit 'chack' calls (Nolan *et al.* 2002), house finches emit 'chirp' calls (Hill 1993) and yellow-rumped warblers emit 'chip' calls (Hunt & Flaspohler 1998). Dark-eyed juncos and house finches emit these calls while mobbing a taxidermic great horned owl (J. L. Yorzinski 2007–2008, personal observation), but no information is available on the behavioural responses of yellow-rumped warblers (without nestlings present) to predators (Hunt & Flaspohler 1998).

To test predictions about the receivers of antipredator calls, we measured the acoustic directionality of antipredator calls and the orientation of calling birds before and after the experimental presentation of a taxidermic great horned owl. If antipredator calls function primarily to alert surrounding conspecifics (in unknown locations), then we predicted that the calls would be less directional (i.e. relatively omnidirectional) and radiate broadly to surrounding conspecifics. If antipredator calls function mainly to signal to predators, we predicted that the calls would be more directional and aimed towards the predator. And if the calls function to both alert conspecifics and signal to the predator, we would expect a compromise, where calls are broadcast widely but also aimed towards the predator. Birds may accomplish this by shifting the directionality of the calls depending on the receiver.

2. MATERIAL AND METHODS

(a) *Subjects and location*
We examined the acoustic directionality of antipredator calls of 10 species of passerines: Bewick's wren (BEWR), bushtit (BUSH), black phoebe (BLPH), dark-eyed junco (DEJU), fox sparrow (FOSP), house finch (HOFI), northern mockingbird (NOMO), orange-crowned warbler (OCWA), white-breasted nuthatch (WBNU) and yellow-rumped warbler (YRWA; table 1). Between July and December 2007, the birds were captured with Potter traps or mist nets at the Animal Communication Laboratory in Davis, California (38.55° N, 121.74° W). They were transported approximately 0.3 km away to the TB-1 building and tested within 24 h of being captured. After being tested, they were transported back to the Animal Communication Laboratory and were banded with an individually unique metal band. They were then released back into the wild.

(b) *Experimental set-up*
Each bird was only tested in one trial and was tested individually within an outdoor aviary (5.5 × 4.6 × 2 m) between 06.30 and 19.30. Within the aviary, the bird was enclosed within a smaller metal cage (0.18 × 0.25 × 0.24 m) that was mounted atop a metal pole (1.52 m tall); this smaller metal cage was in the centre of an eight-microphone array (described below). A taxidermic great horned owl (*Bubo virginianus*) was mounted atop a black pole (1.32 m tall) located 3.3 m away from the small metal cage but still within the aviary. The recording equipment was stored in a hunting blind located 8.32 m from the small metal cage and was outside the aviary.

The microphone array consisted of eight omnidirectional microphones (Sennheiser K6 microphones with ME62

Table 1. Descriptive statistics of the antipredator calls (only those emitted after the owl was revealed) of each species.

species[a]	DEJU	HOFI	YRWA	BEWR	BUSH[b]	BUSH[c]	BLPH[d]	BLPH[e]	FOSP	NOMO	OCWA	WBNU
no. of individuals tested	10	17	12	1	2	2	2	1	1	1	1	1
no. of antipredator calls[f]	0 and 932	76 and 562	125 and 606	0 and 2	0 and 224	1 and 186	0 and 68	0 and 19	0 and 95	0 and 4	0 and 48	0 and 4
DI mean (s.e.)	2.23 (0.014)	1.71 (0.021)	1.89 (0.019)	2.13 (0.068)	1.95 (0.035)	2.09 (0.038)	2.25 (0.069)	1.72 (0.08)	2.49 (0.047)	1.87 (0.23)	2.29 (0.078)	1.43 (0.21)
max–min difference (dB SPL) mean (s.e.)	5.65 (0.036)	3.63 (0.039)	4.60 (0.049)	4.40 (0.13)	5.11 (0.09)	5.37 (0.092)	5.72 (0.20)	4.00 (0.18)	6.85 (0.13)	4.56 (0.63)	5.57 (0.21)	2.50 (0.41)
max amplitude (dB SPL) mean (s.e.)	68.13 (0.076)	67.57 (0.13)	70.94 (0.13)	59.82 (0.63)	68.17 (0.14)	66.55 (0.18)	76.64 (0.38)	75.59 (0.57)	75.11 (0.23)	77.57 (3.36)	76.71 (0.21)	67.03 (0.64)
peak frequency (Hz) mean (s.e.)	6651.1 (35.8)	4561.1 (25.3)	5928.7 (20.6)	7149.0 (0)	8121.5 (40.1)	5729.7 (18.0)	5221.2 (24.2)	5589.6 (66.8)	6305.8 (52.4)	5383 (260)	7215.4 (71.2)	3014.6 (35.2)
duration (s) mean (s.e.)	0.014 (0.0001)	0.19 (0.002)	0.024 (0.0002)	0.80 (0.045)	0.059 (0.0007)	0.052 (0.0004)	0.043 (0.0023)	0.21 (0.013)	0.017 (0.0003)	0.042 (0.0017)	0.012 (0.0004)	0.14 (0.002)

[a]DEJU, dark-eyed junco; HOFI, house finch; YRWA, yellow-rumped warbler; WBNU, white-breasted nuthatch. [b]Call type shown in figure 2d. [c]Call type shown in figure 2e. [d]Call type shown in figure 2f. [e]Call type shown in figure 2f. [f]Antipredator calls emitted before and after the owl was revealed, respectively. BEWR, Bewick's wren; BUSH, bushtit; BLPH, black phoebe; FOSP, fox sparrow; NOMO, northern mockingbird; OCWA, orange-crowned warbler.
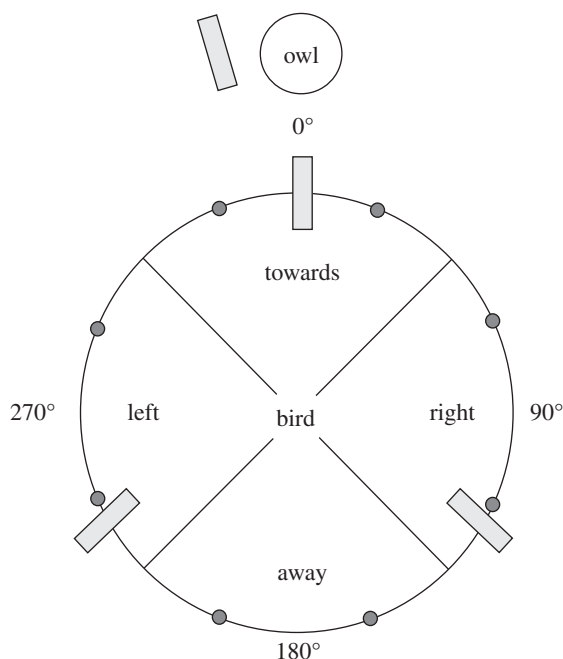
Figure 1. The experimental set-up. Each bird was placed inside a small cage in the middle of an 8-microphone array. When the beak of the bird was directed in the 'towards', 'away', 'left' and 'right' quadrants, the bird was facing towards, away, to the left and to the right of the owl, respectively. The circles represent the microphones and the rectangles represent the video camcorders.

omnidirectional capsules and MZW64 windscreens), and three closed-circuit video cameras that were separated along a 2 m diameter metal ring (1.55 m from the tips of the microphones to the ground). A detailed description of the array recording methods are given in Patricelli *et al.* (2007); only differences between those methods and ours are noted here. A fourth closed-circuit video camera was positioned near the owl; all four cameras were directed towards the small metal cage at the centre of the ring where the focal bird was kept (figure 1). We used an Everfocus EDSR400H DVR to multiplex all four camcorder images. We recorded digital audio (44.1 kHz, 16 bits, WAV format) with a Mark of the Unicorn (MOTU) Audio 896HD, which digitized and recorded audio directly to hard disk on a Macintosh Powerbook G4 laptop running MOTU DIGITAL PERFORMER and CLOCKWORKS.

For each trial, the experimenter (J.L.Y.) placed a bird inside the small metal cage, recorded the ambient temperature and entered the blind. During the first 20 min of the trial, the owl was fully concealed underneath a cloth. The experimenter (while inside the blind) then removed the cloth by pulling on clear fishing line that was attached to the cloth. The owl was exposed for 20 min. The vocalizations and movements of the bird were continuously recorded with the 8 microphones and 4 video camcorders, respectively. At the end of the trial, the experimenter emerged from the blind and removed the bird from the small metal cage. If the bird did not emit vocalizations within 5 min of the owl being exposed, the trial was aborted and excluded from the analyses; the mean latency to vocalize was 38 ± 8 s (s.e.).

(c) Measurements

We used SYRINX (John Burt, Univ. of Washington) to display our 8-channel audio recordings and choose vocalizations for analysis. Most of the antipredator calls (figure 2) emitted 5 min before the owl was exposed and 5 min after the owl was exposed were analysed; only antipredator calls with high background noise were excluded from the analysis. For each vocalization at each microphone, we calculated the sound pressure level in decibels (dB SPL re 20 uPa) at 1 m from the sound source using a MATLAB routine. This routine first used ArrayBatchGui (John Burt, University of Washington) to measure the path length between the sound source and each microphone using acoustic localization (Spiesberger & Fristrup 1990). Recordings were normalized to a path length of 1 m using the assumption of spherical spreading (path lengths varied slightly—approx. ± 0.15 m— because of the geometry of the recording perch and the position of the bird while singing). We assume that environmental transmission effects between the microphone and the bird are negligible at this short distance and equal along all paths (groundcover was uniform bare dirt). Second, we measured amplitude from sound files in the frequency domain (FFT size 512, overlap 0.7, Hann window). We filtered below the minimum frequency of vocalizations for each species (high-pass filter cutoffs (Hz): BEWR, 1340; BUSH, 2000; BLPH, 2600; DEJU, 1500; FOSP, 1200; HOFI, 950; NOMO, 750; OCWA, 3700; WBN, 500; YRWA, 1500) to eliminate the effects of background noise. Patricelli *et al.* (2007) provide details on calibration and the measurement of amplitude; here we converted these measures to dB SPL and corrected for variation in recording gain and system sensitivity by normalizing amplitude measurements to a 94 dB SPL calibration tone recorded on each microphone from a Larson Davis CAL200 precision calibrator. We measured acoustic radiation patterns of these calls using the directivity index (DI; see appendix 3 in Dantzker *et al.* 1999). The DI compares the intensity of the maximum lobe of a two-dimensional beam pattern with the intensity of a uniform source radiating the same total power output (Dantzker *et al.* 1999). For comparison, an omnidirectional vocalization would have a DI of 0; red-winged blackbirds produced alarm calls with a relatively low directionality of 2.7 (7.2 dB min–max difference in amplitude; Patricelli *et al.* 2007) and greater sage grouse produced strut vocalizations with a relatively high directionality of 6.7 (22.9 dB min–max difference; Dantzker *et al.* 1999). Peak frequency was measured as described in Patricelli *et al.* (2007).

We also measured the mean amplitude in the front, back, right and left of the bird by taking the average amplitude in dB SPL of 32 interpolated points within 271–89, 91–269, 1–179 and 181–364°, respectively (with 0° defined as directly anterior to the bird's beak; Patricelli *et al.* 2007). By using a mean of interpolated measures, we minimized artefacts caused by differences in the location of the microphones relative to the bird's head among recordings. We calculated a left-to-right ratio by dividing the mean amplitude of the left by the mean amplitude of the right; we then took this ratio and subtracted one so that the value was centred around zero. We also calculated a front-to-back ratio by dividing the mean amplitude of the front by the mean amplitude of the back; we also subtracted one from this ratio. Therefore, a positive left-to-right ratio indicates that the sound is skewed towards the left of the bird while a negative ratio indicates that the sound is skewed to the right of the bird; likewise, a positive front-to-back ratio indicates that the sound is skewed towards the front and a negative ratio indicates that the sound is skewed to the back.
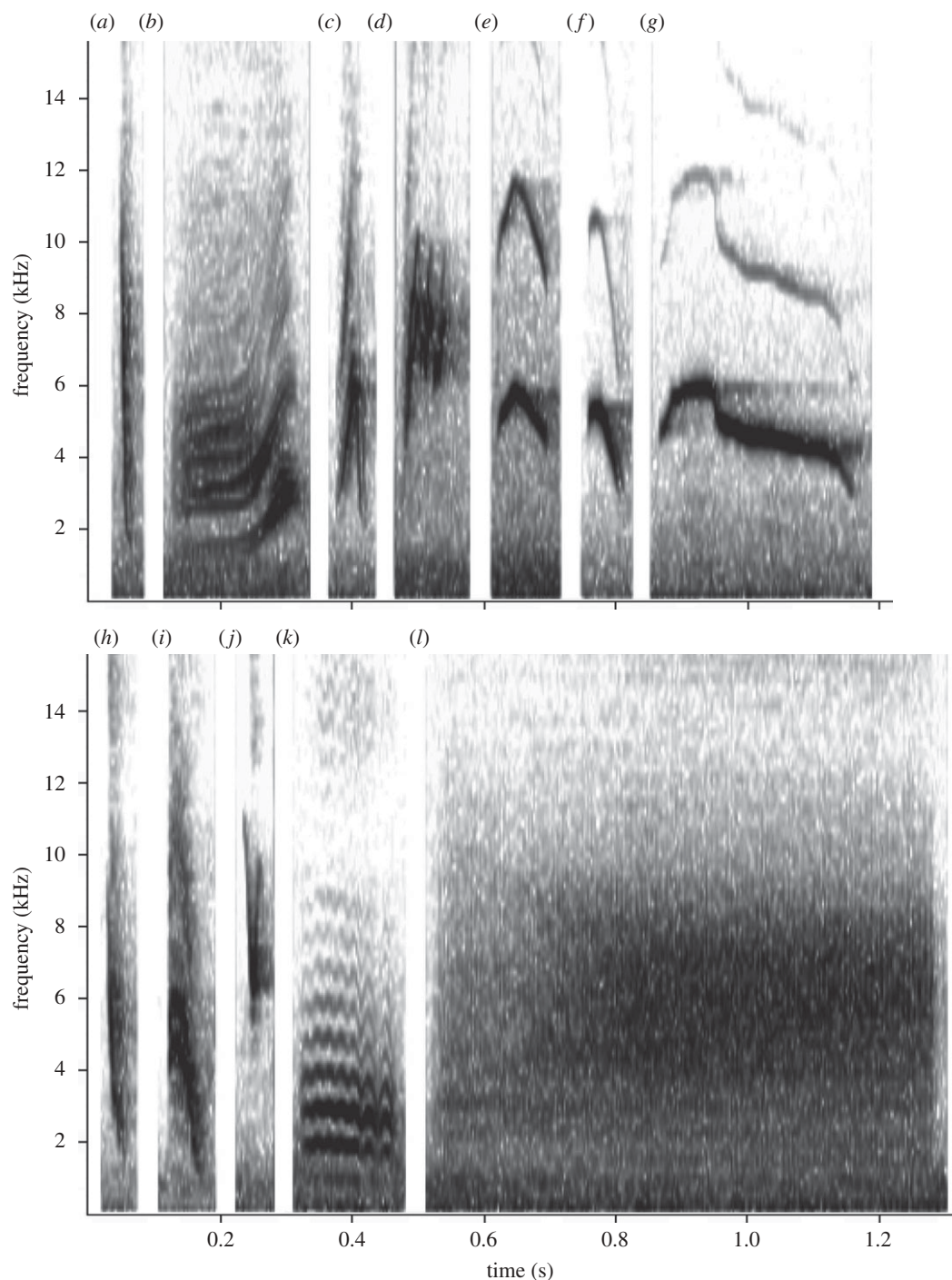
Figure 2. The antipredator calls of the (*a*) dark-eyed junco, (*b*) house finch, (*c*) yellow-rumped warbler, (*d,e*) bushtit, (*f,g*) black phoebe, (*h*) fox sparrow, (*i*) northern mockingbird, (*j*) orange-crowned warbler, (*k*) white-breasted nuthatch and (*l*) Bewick's wren.

We determined the bird's head orientation (but not body orientation) for each vocalization by comparing the multiplexed video images with video images of a model bird rotated in 15° increments (Patricelli *et al*. 2007). If the bird moved while it was vocalizing, the head orientation it exhibited at the start of its vocalization was used.

The bird dirrectly faced the owl at 0° and faced away from the owl at 180°. Head orientations were lumped into four broad groups relative to the location of the owl: towards (315–45°), right (46–135°), away (136–225°) and left (226–314°; figure 1). The videos were analysed frame-by-frame with Windows MOVIE MAKER; the experimenters did

not know the acoustic measurements associated with the calls as they were scoring the videos.

During one house finch trial, another house finch landed atop the aviary and began mobbing the predator. Because we were unable to track the position of this wild bird relative to the experimental bird, we excluded this trial from the analysis. Wild birds sometimes produced antipredator calls from nearby trees (because of foliage density, we were not always able to identify these birds and observe their behaviours). We did not exclude these trials because the experimental and wild birds were not directly interacting with each other.

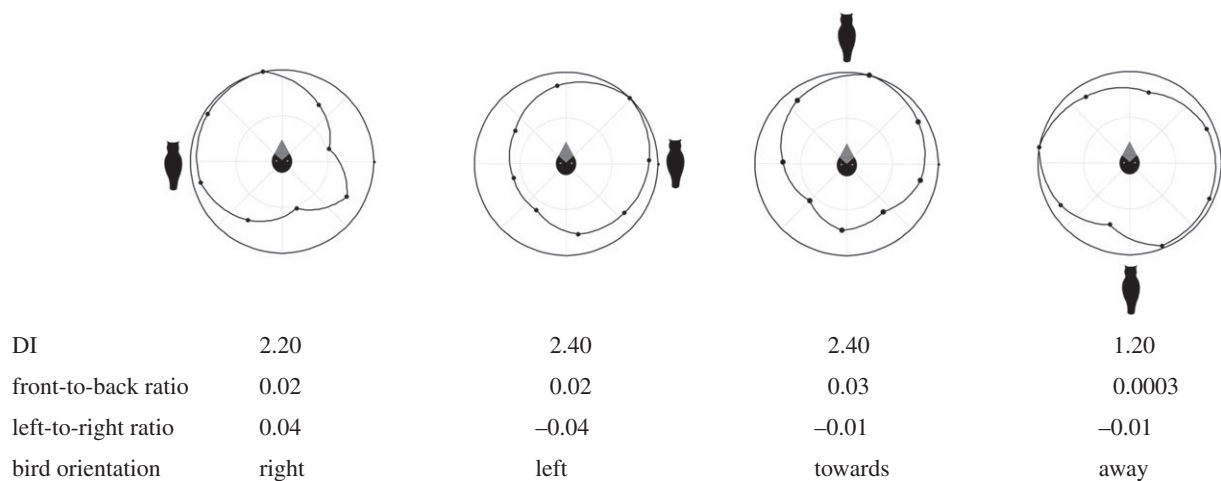|				
DI	2.20	2.40	2.40	1.20
front-to-back ratio	0.02	0.02	0.03	0.0003
left-to-right ratio	0.04	–0.04	–0.01	–0.01
bird orientation	right	left	towards	away

Figure 3. Sample polar plots of acoustic radiation of yellow-rumped warbler antipredator calls. Points on each plot represent the amplitude as measured at each of the eight microphones, connected by linear interpolation. All polar plots are in decibels, with the loudest value normalized to 0 dB (outermost circle on the plot) and an origin at −12 dB. All plots are oriented so that the bird's head is facing upward; the relative position of the owl is indicated by an owl icon.

Because the location of the owl could not be randomized owing to constraints imposed by the animal enclosure, the owl position was confounded with possible sound reflectors in the environment. To test whether reflected sounds biased the acoustic measurements, we reanalysed only the first portion of each call, before sounds from the closest reflector could reach the microphones. The closest reflectors were vehicles parked outside the aviary, 6.7 metres from the closest microphones. The minimum reflection time was therefore approximately 0.036 s from the bird to the vehicles and back to the closest microphone; because of differences in temperature, calculated times varied slightly among trials. The antipredator calls of dark-eyed juncos were all shorter than the minimum reflection times, so it was unnecessary to reanalyse their calls. The mean difference in the directionality of house finch calls (full minus shortened duration) was -0.10 ± 0.01 (s.e.) and the mean difference in the directionality of yellow-rumped warbler calls was only $-2 \times 10^{-5} \pm 5 \times 10^{-5}$. Using the shortened calls, the directionality of house finch calls in relation to their orientation, their left-to-right ratio, and their front-to-back ratio showed the same patterns as when the entire call was analysed (figure 3). Because the results were not qualitatively different, we used the entire duration of calls for all analyses.

(d) Statistical analysis

We used a repeated-measures mixed model ANOVA to test for differences in directivity using PROC MIXED in SAS v. 9.1 with the identity of the bird included as a random block effect. For dark-eyed juncos, house finches and yellow-rumped warblers, we ran three repeated mixed models to compare three measures of the antipredator calls emitted before and after the owl was revealed (DI, front-to-back ratio and left-to-right ratio). We could not analyse the calls emitted before the owl was revealed in the dark-eyed junco trials because the birds did not emit any antipredator calls during this period.

We used least-squares means estimates to determine whether birds that were oriented towards the predator emitted calls with front-to-back ratios that were greater than zero (skewed towards the front) and birds that were oriented away from the predator emitted calls with front-to-back ratios that were less than zero (skewed towards the back). We also used these estimates to assess whether birds that were oriented towards the right of the predator emitted calls with left-to-right ratios greater than zero (skewed to the left) and whether birds that were oriented towards the left of the predator emitted calls with left-to-right ratios less than zero (skewed to the right). All models were initially run with the movement variable (whether the bird moved while it was calling or not), but this variable was dropped from the final models because it was not significant (p always greater than 0.15). In the left-to-right ratio mixed model, we included whether the birds' heads moved towards or away from the predator while calling (or did not move); we did not include this direction of movement variable in the other models because the birds were already facing towards or away from the predator.

We used paired t-tests to assess whether birds emitted more calls before the owl was revealed compared with after it was revealed, and whether the birds called from specific orientations relative to the predator. Because the birds did not preferentially orient themselves to the right or the left side of the predator (DEJU: $t_{1,9}=0.74$, $p=0.48$; HOFI: $t_{1,16}=1.15$, $p=0.27$; YRWA: $t_{1,11}=0.65$, $p=0.53$), the frequencies of orientation in these positions were averaged; we averaged these frequencies (rather than adding them) so that the probability that the bird was within each of the three sections (side, towards and away) was the same.

Lastly, we ran three additional mixed-model ANOVAs to assess the relationship between acoustic features and bird orientation. Because the birds can direct their vocalizations towards the predator when facing laterally to it (see §3), we lumped together calls that could be directed towards the predator (when the birds were directly facing the predator and facing lateral to the predator). We evaluated whether birds emitted calls with different maximum amplitudes, peak frequencies or durations depending on whether the birds were facing towards or away from the predator. All p-values are two-tailed; means are presented $\pm$ s.e.

3. RESULTS

We analysed the acoustic directionality of more than 2900 antipredator calls from 10 species of passerines (table 1; figure 2). We conducted at least 10 trials with dark-eyed juncos, house finches and yellow-rumped warblers; because only one or two trials were conducted with each of the remaining seven species (owing to difficulty in capturing these birds), we did not include these species in subsequent statistical analyses. For these three focal species, significantly more antipredator calls were emitted after the owl was revealed compared with before it was revealed (DEJU: $t_{1,9} = 3.58$, $p = 0.006$; HOFI: $t_{1,16} = 3.36$, $p = 0.004$; YRWA: $t_{1,11} = 3.17$, $p = 0.0089$), suggesting that the predator model elicits antipredator calls.

(a) Antipredator calls have a relatively low directionality

The antipredator calls of the three focal species were significantly directional, with DI values greater than zero (DEJU: $t_{1,9} = 164.17$; HOFI: $t_{1,16} = 82.28$; YRWA: $t_{1,11} = 99.44$; all with $p < 0.0001$; table 1). There was a significant difference in the DI of antipredator calls among these three species ($F_{2,36} = 250$, $p < 0.0001$), with the highest DI in the dark-eyed junco and lowest in the house finch (table 1). The antipredator calls of the seven other passerine species had similar directionality (table 1).

All three focal species radiated their sound broadly in many directions by changing their orientations while calling. On average, each bird emitted 12.3 ± 3.3 calls when facing away from the predator, 5.6 ± 1.3 calls when facing towards the predator and 17.9 ± 3.1 calls when facing each side of the predator when the owl was exposed. House finches and yellow-rumped warblers gave significantly more calls while facing lateral to the predator than towards the predator; dark-eyed juncos showed a non-significant tendency to do the same (figure 4). House finches and dark-eyed juncos did not differ in the number of calls they emitted when they faced towards and away from the predator but yellow-rumped warblers emitted more calls when they faced away from the predator (figure 4).

(b) Antipredator calls are aimed at the predator

We found that when dark-eyed juncos and yellow-rumped warblers face towards the predator, they emit significantly more directional calls than when they face away from the predator; however, house finches do not alter the overall directionality of their calls based on their orientation relative to the predator (figure 5). Before the owl was revealed, the house finch and yellow-rumped warbler calls were unrelated to the birds' orientation (HOFI: $F_{1,1} = 2.85$, $p = 0.34$; YRWA: $F_{1,1} = 20.17$, $p = 0.14$; dark-eyed juncos did not call before the predator was revealed). Because the experimenter exited the aviary from the same direction that the owl was positioned and the blind was located in this same direction, the birds may have perceived a threat in the direction of the owl before the owl was revealed; this could explain why the calls emitted before the owl was revealed had a non-significant tendency to be directed towards that same direction.
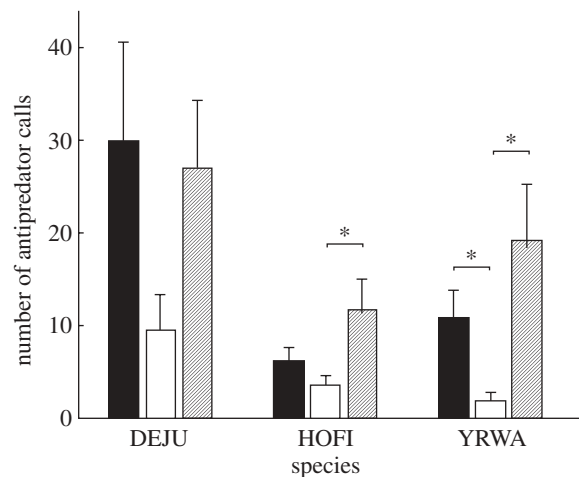

Figure 4. House finches and yellow-rumped warblers gave significantly more calls while facing lateral to the predator than towards the predator (HOFI: $t_{1,16} = 3.14$, adjusted p-value 0.013; YRWA: $t_{1,11} = 3.06$, adjusted p-value 0.022); dark-eyed juncos showed a non-significant tendency to do the same ($t_{1,9} = 2.52$, adjusted p-value 0.065). House finches and dark-eyed juncos did not differ in the number of calls they emitted when they faced towards and away from the predator (HOFI: $t_{1,16} = 1.53$, adjusted p-value 0.29; DEJU: $t_{1,9} = 1.86$, adjusted p-value 0.19), but yellow-rumped warblers emitted more calls when facing away from the predator ($t_{1,11} = 3.02$, adjusted p-value 0.023). Asterisks indicate whether the mean number of calls differed among bird orientations. Bird orientation: black bar, away; white bar, towards; hatched bar, side.

House finches, dark-eyed juncos and yellow-rumped warblers produce antipredator calls with higher front-to-back ratios (i.e. louder in front of the bird's body than behind) when facing towards the predator, compared with when they are facing away from the predator (figure 6a). Before the owl was revealed, the front-to-back ratio of house finch and yellow-rumped warbler calls was not different depending on the orientation of the bird (HOFI: $F_{1,1} = 2.80$, $p = 0.34$; YRWA: $F_{1,1} = 3.64$, $p = 0.31$).

We found that house finches and yellow-rumped warblers that are oriented lateral to the predator emit calls with asymmetric radiation patterns that are directed towards the predator. Both species emit calls that are significantly skewed towards the left or right (i.e. positive or negative left-to-right ratio, respectively) depending on whether the bird is facing to the right or left of the predator, respectively (figure 6b). Dark-eyed juncos also significantly direct their calls towards the predator when they are to the right side of the predator, but do not do so when they are on the left side of the predator (figure 6b). Before the owl was revealed, the left-to-right ratio of house finch and yellow-rumped warbler calls was not significantly different depending on the orientation of the birds (HOFI: $F_{1,3} = 8.06$, $p = 0.07$; YRWA: $t_{1,3} = 5.59$, $p = 0.10$).

The asymmetry in the left-to-right ratio of the birds' antipredator calls is greater when the birds move towards the predator while they are calling than when they remain still or move away from the predator (DEJU: $F_{4,23} = 24.99$, $p < 0.0001$; HOFI: $F_{4,35} = 24.44$, $p < 0.0001$; YRWA: $F_{4,24} = 22.74$, $p < 0.0001$), suggesting that
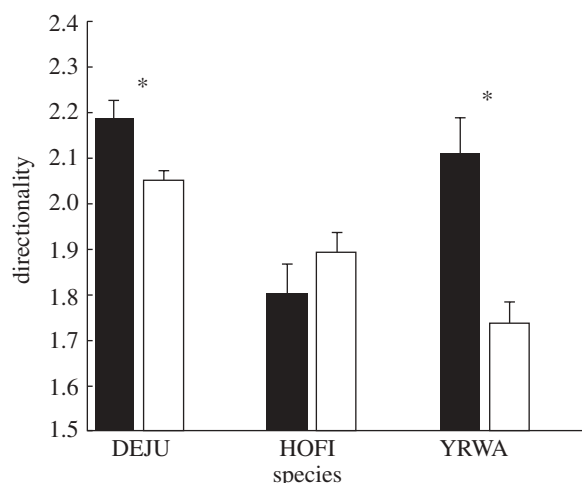
Figure 5. Dark-eyed juncos and yellow-rumped warblers emitted more-directional calls when they faced towards the predator (DEJU: $F_{1,6} = 9.02$, $p = 0.024$; YRWA: $F_{1,3} = 9.67$, $p = 0.05$). House finches did not alter the overall directionality of their calls based on their orientation relative to the predator ($F_{1,8} = 1.37$, $p = 0.28$). Asterisks indicate whether the DI was significantly different depending on bird orientation. Bird orientation: black bar, towards; white bar, away.

movement may be one mechanism of this effect. However, the results for the left-to-right ratio and bird orientation are similar even when we analyse only calls during which the bird remained still (test of the null hypothesis that the left-to-right ratio is equal to zero: DEJU: $t_{1,7} = 9.39$, adjusted p-value < 0.0001 facing right; $t_{1,7} = 2.99$, adjusted p-value 0.04 facing left; HOFI: $t_{1,7} = 5.59$, adjusted p-value 0.0016 facing right; $t_{1,7} = 9.08$, adjusted p-value < 0.0001 facing left; YRWA: $t_{1,3} = 3.06$, adjusted p-value 0.11 facing right; $t_{1,3} = 1.82$, adjusted p-value 0.33 facing left), suggesting that movement alone does not explain this phenomenon.

(c) *Other acoustic variables and bird orientations*

The maximum amplitude of dark-eyed junco and yellow-rumped warbler calls was greater when the birds faced towards the predator rather than away from the predator (DEJU: $F_{1,9} = 21.65$, $p = 0.0012$; YRWA: $F_{1,8} = 6.48$, $p = 0.034$); in contrast, house finches emitted calls with higher amplitudes when they faced away from the predator rather than towards the predator ($F_{1,12} = 12.52$, $p = 0.0041$). Dark-eyed juncos emitted calls with similar peak frequencies when they faced towards and away from the predator ($F_{1,9} = 0.01$, $p = 0.93$), house finches emitted calls with higher peak frequency when they faced away from the predator ($F_{1,12} = 18.93$, $p = 0.0009$) and yellow-rumped warblers emitted calls with higher peak frequency when they faced towards the predator ($F_{1,8} = 8.55$, $p = 0.019$). Lastly, dark-eyed juncos and house finches emitted calls with longer durations when they faced the predator (DEJU: $F_{1,9} = 23.95$, $p = 0.0009$; HOFI: $F_{1,12} = 5.76$, $p = 0.034$), but yellow-rumped warblers did not alter their call duration with respect to their orientation ($F_{1,8} = 0.00$, $p = 0.99$). These acoustic variables of house finch and yellow-rumped warbler calls were unrelated to bird orientation before the owl was revealed (maximum amplitude: HOFI: $F_{1,2} = 0.02$, $p = 0.90$; YRWA: $F_{1,3} = 0.07$,
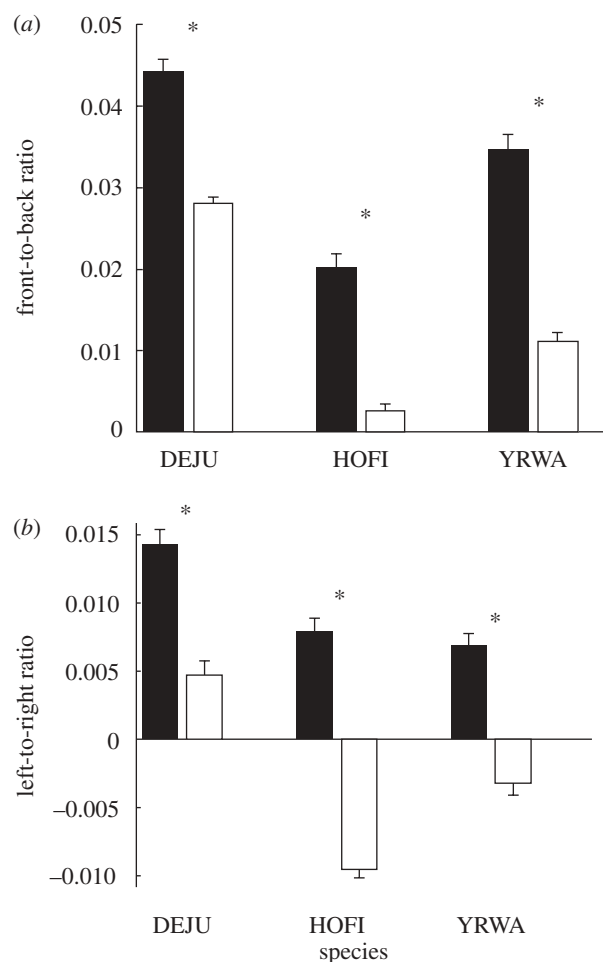
Figure 6. (a) All three species produced antipredator calls with higher front-to-back ratios (i.e. louder in front than behind the bird) when the birds were facing towards the predator, compared with facing away from the predator (DEJU: $F_{1,6} = 77.11$, $p = 0.0001$; HOFI: $F_{1,8} = 99.03$, $p < 0.0001$; YRWA: $F_{1,3} = 64.1$, $p = 0.0041$). Asterisks indicate whether the front-to-back ratio is significantly different depending on bird orientation. (b) House finches and yellow-rumped warblers emitted calls that were skewed towards the left or right depending on whether the bird was facing to the right or left of the predator, respectively (test of the null hypothesis that the left-to-right ratio is equal to zero: HOFI: $t_{1,11} = 9.81$, adjusted p-value < 0.0001 facing right; $t_{1,11} = 13.93$, adjusted p-value < 0.0001 facing left; YRWA: $t_{1,10} = 8.13$, adjusted p-value < 0.0001 facing right; $t_{1,10} = 4.26$, adjusted p-value 0.0034 facing left). Dark-eyed juncos also directed their calls towards the predator when they were facing to the right side of the predator ($t_{1,7} = 11.6$, adjusted p-value < 0.0001) but directed their calls away from the predator when they were facing to the left of the predator ($t_{1,7} = 3.09$, adjusted p-value 0.035). Asterisks indicate whether the left-to-right ratio was significantly different depending on bird orientation. (a) Bird orientation: black bar, towards; white bar, away. (b) Bird orientation: black bar, right; white bar, left.

$p = 0.81$; peak frequency: HOFI: $F_{1,2} = 0.17$, $p = 0.72$; YRWA: $F_{1,3} = 3.37$, $p = 0.16$; duration: HOFI: $F_{1,2} = 1.33$, $p = 0.37$; YRWA: $F_{1,3} = 0.89$, $p = 0.42$).

4. DISCUSSION

All 10 species of passerines emit antipredator calls with relatively low directionality. The directionality of their

calls is similar to the antipredator vocalizations of other species (e.g. blackbirds and red-winged blackbirds; Larsen & Dabelsteen 1990; Patricelli *et al.* 2007) but less directional than other species' courtship vocalizations (e.g. greater sage-grouse and red-winged blackbirds; Dantzker *et al.* 1999; Patricelli *et al.* 2007, 2008). Dark-eyed juncos, house finches and yellow-rumped warblers also rotated in many different directions as they emitted antipredator calls. The relatively low directionality of the antipredator calls together with the birds' rotation while calling ensures that the calls are radiated well in all directions; this could serve to alert conspecifics to the danger or attract widely dispersed conspecifics to mob the predator (Hunter *et al.* 1986; Larsen & Dabelsteen 1990; Dabelsteen 2005; Patricelli *et al.* 2008).

Despite being less directional than courtship vocalizations of other species, the antipredator calls are nonetheless significantly directional, and our results suggest that birds direct their calls towards predators with surprising sophistication. Dark-eyed juncos and yellow-rumped warblers emit more-directional calls when oriented towards the predator and less-directional calls when oriented away from the predator. All three species emit antipredator calls that are louder in front when they are facing the predator. In addition, house finches and yellow-rumped warblers finely skew the radiation pattern of their antipredator calls when they are facing lateral to the predator; regardless of whether these birds face towards the left or the right side of the predator, they direct their antipredator calls towards the predator.

Taken together, our results support the hypothesis that antipredator calls function both to alert conspecifics and to signal to predators. Antipredator calls have relatively low directionality (and can therefore be broadcast widely to conspecifics in unknown locations), but can also be plastically directed towards predators. Birds may benefit by producing antipredator calls that alert conspecifics (and heterospecifics) to the presence of danger. When mobbing occurs, the probability that any particular bird succumbs to predation is reduced with a larger mob (i.e. the selfish herd; Hamilton 1971). In addition, birds can share the costs of predator vigilance with other individuals and potentially resume previous activities (such as foraging) sooner (Owings & Hennessy 1984). Birds can also benefit by communicating with predators. Birds that emit antipredator calls signal to the predator that it has been detected, and this may deter the predator from attacking (Curio 1978; Sherman 1985). Moreover, these antipredator calls may signal the health and vigour of the birds to further dissuade predators (similar to stotting gazelles; FitzGibbon & Fanshawe 1988).

Directional vocalizations are typically considered beneficial when a reduction of eavesdropping is favoured (Witkin 1977; Hunter *et al.* 1986; Larsen & Dabelsteen 1990; Dabelsteen 2005); in the case of antipredator calls that we measured, however, this is unlikely to select for directional vocalizations because birds use the same calls to signal to surrounding conspecifics and predators. In contrast, birds that use antipredator calls, such as 'seet' calls, to communicate with targeted conspecifics may benefit from emitting directional calls in order to reduce eavesdropping by predators (Larsen & Dabelsteen 1990). It is possible that the increase in directionality

when dark-eyed juncos and yellow-rumped warblers face the predator may not be due to selection on directionality, but rather a side-effect of other (adaptive or non-adaptive) changes in call structure. For example, if selection favours higher-frequency calls when facing predators, then directionality would probably increase as a consequence because sound emission at higher frequencies is typically more directional (Hunter *et al.* 1986; Fletcher & Tarnopolsky 1999). Indeed we found that yellow-rumped warblers produced calls at a higher peak frequency when facing the predator; however, dark-eyed juncos did not (though other spectral properties besides peak frequency may also affect DI). Since frequency may change in response to selection on frequency *per se* or as a mechanism to achieve higher directionality, we are unable to determine which call features are under direct selection.

One way that birds might benefit from more-directional calls to predators is if this directs more sound energy towards the predator, causing a higher maximum amplitude for the same amount of energy expended. This may increase the birds' success in encouraging predators to leave (Curio 1978). We found that both yellow-rumped warblers and dark-eyed juncos produced calls at a higher maximum amplitude when facing towards the predator than when facing away, and house finches produced higher-amplitude calls while facing away. This suggests that directionality may increase maximum amplitude (or vice versa), since yellow-rumped warblers and dark-eyed juncos also produce calls with higher directionality when facing the predator. Similarly, Patricelli *et al.* (2008) found that more-directional songs had a higher maximum amplitude, and were given more often when males rotated less between songs, indicating that the males were engaged in direct interactions. However, models of sound production predict that directional patterns emerge primarily through interference effects cancelling sound energy and by the sound shadow caused by the head (Hunter *et al.* 1986; Fletcher & Tarnopolsky 1999). The models do not preclude some increased forward reflection of sound energy in more-directional calls, but further evidence would be needed to support this possibility. Alternatively (or in addition), birds may actively increase both their call amplitude and directionality while facing the predator. Playback experiments are needed to demonstrate whether more-directional antipredator calls attract conspecifics in greater numbers and deter predators more effectively compared with antipredator calls that are broadcast with different directionality patterns.

The three focal species differ slightly in their acoustic radiation patterns with respect to the predator. In contrast to dark-eyed juncos and yellow-rumped warblers, house finches emit calls with higher amplitude and greater directionality when they face away from the predator, suggesting that the calls may be functioning mainly to attract conspecifics. However, they do still direct more sound towards the front of their call when they face the predator (higher front-to-back ratio) and skew their calls towards the predator when they are facing lateral to it. Nonetheless, these results suggest that attracting conspecifics may be more important to house finches than communicating directly with the predator (compared with dark-eyed juncos and yellow-rumped warblers).

Because house finches may have a higher degree of sociality (their flocks can contain hundreds of individuals; Hill 1993) compared with dark-eyed juncos and yellow-rumped warblers (whose flocks often contain less than 20 individuals; Hunt & Flaspohler 1998; Nolan *et al.* 2002), they may rely on conspecifics to a greater extent when encountering predators (see also Roth *et al.* 2008). Comparative studies on a larger sample of species would be required to examine the relationship between flock size and sociality on the directionality of antipredator calls.

In addition to the degree of sociality influencing directionality patterns across species, the spectral and temporal structure of antipredator calls may also constrain how sounds radiate. In particular, Marler (1955) proposed that mobbing calls would have wide-frequency ranges and short durations so that they could be easily localized. Ficken & Popp (1996) found that mobbing calls can have these acoustic features but many do not. Of the 10 species of antipredator calls recorded in this study, some species have calls with wide-frequency ranges and short durations (e.g. dark-eyed juncos and fox sparrows), but others have horizontal bands (e.g. Bewick's wren), chevrons (e.g. bushtit) or more diverse structures (e.g. house finch). The peak frequencies vary from approximately 3–8 kHz, and call duration varies from about 0.01–0.80 s. Despite this diversity in acoustic structure, the mean directionality of the calls from the different species fell within a relatively narrow range. This suggests that directionality does not necessarily change tightly with these gross features of acoustic structure (see also Patricelli *et al.* 2007, 2008). Alternatively, the directionality of bird calls may be affected by these call features, but the birds overcome this by modifying the delivery of their calls to produce the favoured radiation pattern. Other factors, such as rotations while calling, changes in posture and adjustments in beak opening, could also alter directionality patterns (Hunter *et al.* 1986; Larsen & Dabelsteen 1990; Fletcher & Tarnopolsky 1999; Nelson *et al.* 2005).

Constraints imposed by the visual system could also influence call directionality by determining how birds must orient their heads to maintain visual contact with predators or conspecifics (Brumm & Todt 2003; Patricelli *et al.* 2008). Chickens, for example, use their lateral visual field to view distant conspecifics (Dawkins 1995) and are therefore unlikely to clearly see distant conspecifics while vocalizing directly towards them. Other birds may also rely on their lateral vision when viewing conspecifics and predators (Bischof 1988; Güntürkün *et al.* 1993), but we know little about the visual capabilities of the focal species used in this study (but see Fernández-Juricic *et al.* 2008). This raises the possibility that the direction birds' bills are facing may not coincide with the direction they need to beam their calls. This could favour the evolution of calls with directionality patterns that are skewed towards receivers, as we observed here when birds emitted calls that were skewed towards the predator when they were facing lateral to it.

While we do not yet understand all of the factors influencing the acoustic directionality of antipredator calls, our study suggests that birds have the flexibility to alter the radiation pattern of these vocalizations to improve the efficacy of these signals.

REFERENCES

Bischof, H. J. 1988 The visual field and visually guided behaviour in the zebra finch (*Taeniopygia guttata*). *J. Comp. Physiol. A* **163**, 329–337. (doi:10.1007/BF00604008)

Brumm, H. & Todt, D. 2003 Facing the rival: directional singing behaviour in nightingales. *Behaviour* **140**, 43–53. (doi:10.1163/156853903763999881)

Caro, T. 2005 *Antipredator defenses in birds and mammals.* Chicago, IL: University of Chicago Press.

Curio, E. 1978 The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Z. Tierpsychol.* **48**, 175–183.

Dabelsteen, T. 2005 Public, private or anonymous? Facilitating and countering eavesdropping. In *Animal communication networks* (ed. P. K. McGregor), pp. 38–62. Cambridge, UK: Cambridge University Press.

Dantzker, M. S., Deane, G. B. & Bradbury, J. W. 1999 Directional acoustic radiation in the strut display of male sage grouse *Centrocercus Urophasianus*. *J. Exp. Biol.* **202**, 2893–2909.

Dawkins, M. S. 1995 How do hens view other hens? The use of lateral and binocular visual fields in social recognition. *Behaviour* **132**, 591–606. (doi:10.1163/156853995X00225)

Derrickson, K. C. & Breitwisch, R. 1992 Northern mockingbird (*Mimus polyglottos*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Fernández-Juricic, E., Gall, M. D., Dolan, T., Tisdale, V. & Martin, G. 2008 The visual fields of two ground-foraging birds, house finches and house sparrows, allow for simultaneous foraging and anti-predator vigilance. *Ibis* **150**, 779–787. (doi:10.1111/j.1474-919X.2008.00860.x)

Ficken, M. S. & Popp, J. 1996 A comparative analysis of passerine mobbing calls. *Auk* **113**, 370–380.

FitzGibbon, C. D. & Fanshawe, J. H. 1988 Stotting in Thomson's gazelles: an honest signal of condition. *Behav. Ecol. Sociobiol.* **23**, 69–74. (doi:10.1007/BF00299889)

Flasskamp, A. 1994 The adaptive significance of avian mobbing. V: An experimental test of the 'move on' hypothesis. *Ethology* **96**, 322–333.

Fletcher, N. H. & Tarnopolsky, A. 1999 Acoustics of the avian vocal tract. *J. Acoust. Soc. Am.* **105**, 35–49. (doi:10.1121/1.424620)

Forrest, T. G. 1991 Power output and efficiency of sound production by crickets. *Behav. Ecol.* **2**, 327–338. (doi:10.1093/beheco/2.4.327)

Grubb Jr, T. C. & Pravosudov, V. V. 2008 White-breasted nuthatch (*Sitta carolinensis*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Güntürkün, O., Miceli, D. & Watanabe, M. 1993 Anatomy of the avian thalamofugal pathway. In *Vision, brain and behavior in birds* (eds H. P. Zeigler & H. J. Bischof), pp. 115–135. Cambridge, MA: MIT Press.

Hamilton, W. D. 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311. (doi:10.1016/0022-5193(71)90189-5)

Henze, D. & O'Neill, W. E. 1991 The emission pattern of vocalizations and directionality of the sonar system in the echolocating bat, *Pteronotus parnelli*. *J. Acoust. Soc. Am.* **89**, 2430–2434. (doi:10.1121/1.400975)

Hill, G. E. 1993 House finch (*Carpodacus mexicanus*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Hunt, P. D. & Flaspohler, D. J. 1998 Yellow-rumped warbler (*Dendroica coronata*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Hunter Jr, M. L., Kacelnik, A., Roberts, J. & Vuillermoz, M. 1986 Directionality of avian vocalizations: a laboratory study. *Condor* **88**, 371–375. (doi:10.2307/1368885)

Kennedy, E. D. & White, D. W. 1997 Bewick's wren (*Thryomanes bewickii*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Larsen, O. N. & Dabelsteen, T. 1990 Directionality of black-bird vocalization. Implications for vocal communication and its further study. *Ornis Scand.* **21**, 37–45. (doi:10.2307/3676376)

Marler, P. 1955 Characteristics of some animal calls. *Nature* **176**, 6–8. (doi:10.1038/176006a0)

Nelson, B. S., Beckers, G. J. L. & Suthers, R. A. 2005 Vocal tract filtering and sound radiation in a songbird. *J. Exp. Biol.* **208**, 297–308. (doi:10.1242/jeb.01378)

Nolan Jr, V., Ketterson, E. D., Cristol, D. A., Rogers, C. M., Clotfelter, E. D., Titus, R. C., Schoech, S. J. & Snajdr, E. 2002 Dark-eyed junco (*Junco hyemalis*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornthology.

Owings, D. H. & Hennessy, D. F. 1984 The importance of variation in scuirid visual and vocal communication. In *The biology of ground-dwelling squirrels* (eds J. O. Murrie & G. R. Michener). Lincoln, NB: University of Nebraska Press.

Patricelli, G. L., Dantzker, M. S. & Bradbury, J. W. 2007 Differences in acoustic directionality among vocalizations of the male red-winged blackbird (*Agelaius pheoniceus*) are related to function in communication. *Behav. Ecol. Sociobiol.* **61**, 1099–1110. (doi:10.1007/s00265-006-0343-5)

Patricelli, G. L., Dantzker, M. S. & Bradbury, J. W. 2008 Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviors. *Anim. Behav.* **76**, 1389–1401. (doi:10.1016/j.anbehav.2008.07.005)

Roth II, T. C., Cox, J. G. & Lima, S. L. 2008 The use and transfer of information about predation risk in flocks of wintering finches. *Ethology* **114**, 1218–1226.

Sherman, P. W. 1977 Nepotism and the evolution of alarm calls. *Science* **197**, 1246–1253. (doi:10.1126/science.197.4310.1246)

Sherman, P. W. 1985 Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behav. Ecol. Sociobiol.* **17**, 313–323. (doi:10.1007/BF00293209)

Sloane, S. A. 2001 Bushtit (*Psaltriparus minimus*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Sogge, M. K., Gilbert, W. M. & van Riper III, C. 1994 Orange-crowned warbler (*Vermivora celata*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Spiesberger, J. L. & Fristrup, K. M. 1990 Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography. *Am. Nat.* **135**, 107–153. (doi:10.1086/285035)

Taylor, R. J., Balph, D. F. & Balph, M. H. 1990 The evolution of alarm calling: a cost-benefit analysis. *Anim. Behav.* **39**, 860–868. (doi:10.1016/S0003-3472(05)80950-9)

Weckstein, J. D., Kroodsma, D. E. & Faucett, R. C. 2002 Fox sparrow (*Passerella iliaca*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Witkin, S. R. 1977 The importance of directional sound radiation in avian vocalization. *Condor* **79**, 490–493. (doi:10.2307/1367730)

Wolf, B. O. 1997 Black Phoebe (*Sayornis nigricans*). In *The birds of North America online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology.

Zuberbühler, K., Nöe, R. & Seyfarth, R. 1997 Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* **53**, 589–604. (doi:10.1006/anbe.1996.0334)