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SHORT COMMUNICATION

Mourning dove (*Zenaida macroura*) wing-whistles may contain threat-related information for con- and hetero-specifics

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Abstract Distinct acoustic whistles are associated with the wing-beats of many doves, and are especially noticeable when doves ascend from the ground when startled. I thus hypothesized that these sounds may be used by flock-mates as cues of potential danger. To test this hypothesis, I compared the responses of mourning doves (*Zenaida macroura*), northern cardinals (*Cardinalis cardinalis*), and house sparrows (*Passer domesticus*) to audio playbacks of dove 'startle wing-whistles', cardinal alarm calls, dove 'nonstartle wing-whistles', and sparrow 'social chatter'. Following playbacks of startle wing-whistles and alarm calls, conspecifics and heterospecifics startled and increased vigilance more than after playbacks of other sounds. Also, the latency to return to feeding was greater following playbacks of startle wing-whistles and alarm calls than following playbacks of other sounds. These results suggest that both conspecifics and heterospecifics may attend to dove wing-whistles in decisions related to antipredator behaviors. Whether the sounds of dove wing-whistles are intentionally produced signals warrants further testing.

Keywords Animal communication · Alarm calls · Anti-predator behavior · Sonation

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Introduction

In most flying birds, the movement of air across and around wing feathers during flight, and vibrations generated by feather-to-feather friction, produces sound (reviewed in Bostwick 2006). Indeed, some groups of birds are readily identifiable based solely on the sounds of their wing-beats (Ehrlich et al. 1988). Because these sounds are nearly ubiquitous among flying birds, they may provide ideal traits for evolutionary co-option for use in communication (Borgia 2006; Berglund et al. 1996; Borgia and Coleman 2000). Indeed, in some birds, wing-beat sounds have evolved into nonvocal acoustic signals, called 'sonations' (Bostwick and Prum 2003); these signals are surprisingly widespread (Bostwick 2006) but have received scant attention compared to classic avian vocal signals (e.g. Marler and Slabbekoorn 2004). In the neotropical manakins (family Pipridae), for instance, males in many species use sonations in their sexual displays (Prum 1998; Bostwick and Prum 2003). Bostwick and Prum (2005) showed that the 'tick' and 'ting' sonations of male club-winged manakins (*Machaeropterus deliciosus*) are produced through interactions among secondary wing feathers adapted for sound production. The functional significance of Piprid sonations is unclear, but they may be important in mate attraction (Prum 1998; Bostwick and Prum 2003). Sonations may also be common in the sexual displays of male hummingbirds (family Trochilidae) (Rogers 1940; Baptista and Matsui 1979; Wells and Baptista 1979; Miller and Inouye 1983; Pytte and Ficken 1994,) and grouse (family Tetraonidae) (Johnsgard 1983) but the mechanical production of these sounds is largely unclear (Bostwick 2006).

Perhaps the most common form of nonvocal feather-associated sounds are 'wing-whistles', defined by Bostwick (2006) as "a variety of pulsed and tonal sounds produced in flight...such sounds are universally attributed to vibrations caused when air is forced through flight feathers" (Bostwick 2006, p.69). Wing-whistles are widespread among distantly related species of birds (Bostwick 2006), and are particularly conspicuous in the doves and pigeons (family Columbidae). Despite widespread occurrence, wing-whistles have not been studied in the context of communication. Here I investigate one functional role that Columbid wing-whistles may play in predator avoidance.

Relative to their widespread distribution, extensive and specialized parental care (Wells and Wells 2001), elaborate courtship behavior (Partan et al. 2005), and colorful plumage (Frith 1982; Goodwin 1983; Gibbs et al. 2001), members of the Columbidae have received seemingly little scientific attention from behavioral ecologists and evolutionary biologists, with Carel ten Cate's body of work as a notable exception (see Johnson et al. 2001; de Kort et al. 2002a, b; Beckers et al. 2003; den Hartog et al. 2007). It is unclear whether Columbid wing-whistles are signals—intentionally produced by the sender to elicit a predictable response from a receiver (Bradbury and Vehrencamp 1998), in which case they would be considered sonations (Bostwick and Prum 2003)—or are simply by-products of general Columbid wing morphology not produced for the purpose of transferring information. Regardless, it is important to note that doves' wing-whistles are most conspicuous when individuals ascend from the ground, especially when individuals produce the explosive 'startle wing-whistles' in response to the sudden presence of a predator (S. W. Coleman personal observation). Here, I test the hypothesis that within single- and mixed-species foraging flocks, conspecifics and heterospecifics attend to the wing-whistle sounds of mourning doves. This hypothesis predicts that individuals respond to startle wing-whistles with antipredator behaviors, such as startling and vigilance.

Materials and methods

To test the hypothesis that individuals attend to dove wing-whistles, I conducted a series of playback experiments. Briefly, I recorded mourning dove 'startle' and 'nonstartle' wing-whistles, cardinal alarm calls, and house sparrow 'social chatter', and played these sounds to single- and mixed-species foraging flocks at feeding stations.

This study was conducted in two major phases: first, between June 4–12, 2006, at two feeding stations approximately 1-km apart, located within the city limits of Bryan, TX, USA, and second on August 15–16, 2007, on a farm located in Austin County, TX, USA; the Bryan and Austin County sites are separated by more than 100 km. At the two Bryan sites, generic birdseed (*Rich's II—Ultimate Variety*, http://wildbirdschoice.com/wildbirdfood.html) was used to attract birds to the feeding stations; at the farm site, doves were attracted to deposits of spent corn leftover from farming operations (SW Coleman personal observation). All recordings were made using an Orbiter™ listening dish/microphone (Ramphastos LLC, Olympia, WA, USA) connected to a Fujitsu Lifebook™. The dish/microphone was setup 3 m from the feeding areas, and was somewhat concealed by vegetation. Recordings were digitized using Raven™ audio software (Bioacoustics Research Program, Cornell Laboratory of Ornithology) at 16 bits with a sample rate of 22 kHz. For the tests at the Bryan sites, two separate mourning dove startle wing-whistles were recorded at 0715 and 0935, 4 June. "Bryan startle wing-whistle" samples (SWW1 and SWW2) were recorded from solitary individuals as they ascended from the ground in response to the appearance of a domestic cat (*Felis domesticus*) at the feeding station. Note: the cat was not released as part of the experiment, but based on previous observations, was expected to arrive at the feeding station. A single cardinal alarm call was recorded at 0801, 6 June. The call was recorded at the same location as the wing-whistles of the doves, and was produced in response to the appearance of the same domestic cat. The dove nonstartle wing-whistle (NSWW1) was recorded at 0743, 7 June. The recording is of an individual ascending from the ground when there were no potential threats visible to the observer. The house sparrow social chatter was recorded immediately after the dove nonstartle wing-whistle. Individuals in the group of approximately six sparrows were flitting among the branches of a large bush, the base of which was 2.90 m from the feeding site where the other recordings were made, and approximately 3 m from the microphone. On August 15 at 0738, a third startle wing-whistle (SWW3) was recorded (using the methods above) at the Austin County farm site. Like the Bryan recordings, this recording was made of a single individual ascending from the ground after startling. The source of the startle was the sudden appearance of a domestic dog, released in close proximity to the feeding area. Also on August 15, at 1119, a second nonstartle wing-whistle (NSWW2) was recorded from a single dove alighting from the feeding area with no apparent threat present.

Prior to playback experiments, playback volume was standardized at a peak amplitude of 65 dB at 1 m (CEL 314 precision impulse sound pressure level meter, C-weighting, fast response); this amplitude matches the maximum amplitude of the startle wing-whistles, but is lower than the mean amplitude of the cardinal alarm calls (81±1.39 dB).

Bryan playback trials

At the Bryan sites, playback experiments were conducted on two mornings (8 and 12 June) between 0730 and 0900, at the two feeding sites. On each morning, at approximately

0600, two Sony speakers (model SRS-A202) were concealed 1 m from the feeding station. The order of playback stimuli was randomized; individuals at Site A heard SWW1, while individuals at Site B heard SWW2. Following a stimulus, individuals were given not less than 2 min to return to feeding behavior, longer if necessary following startling stimuli. The latency between stimuli was determined by the observer. The two feeding sites were approximately 1-km apart, and the three species tested in the experiment are among the most common locally. Thus, I find it highly unlikely that the few individuals I observed were the same between the two feeding sites.

Austin County playback trials

At the Austin County farm site, playbacks were conducted between 0630 and 0900 on August 16. At this site, all flocks consisted of only mourning doves, and as such the experiments at the Austin County farm investigated the effects of the sounds on single-species mourning dove flocks. All birds at this site were presented with seven playback sounds: three startle wing-whistles (SWW1, SWW2, SWW3), two nonstartle wing-whistles (NSWW1, NSWW2), the cardinal alarm call, and the sparrow social chatter. In each trial, the order of sounds was chosen haphazardly; as a result, the order of playback sounds was different in every trial. Following each series of playbacks, the individuals at the feeding area were frightened off by my approach to the feeding area. Because of the high concentration of mourning doves at this site (SW Coleman in preparation) shortly after the focal group of doves vacated the feeding site, a new group arrived. Observers visually confirmed that the group that vacated was not the same group that subsequently arrived—at this site, small groups of doves tend to move around the farm in a highly directional pattern (SW Coleman personal observation). This reduces the likelihood that I tested the same individuals in more than one trial. Overall, five separate groups of doves, ranging from three to seven individuals were tested in playback trials.

At both the Bryan and Austin County sites, all playbacks were videotaped using a Sony miniDV Handycam™ model DCR-TRV17 with a field of view that captured all activity within approximately 3 m of the center of the feeding site. Responses to stimuli were determined using video footage. Statistical analyses were conducted using Statistica™ (StatSoft Inc.) statistical software. For each stimuli and each species, I calculated the mean proportion of individuals that (1) increased vigilance, measured as cessation of feeding behavior, and erect, head-up posture and (2) startled, jumping up with at least one wing-stroke. I also measured the latency to resumption of feeding behavior. Between the Bryan sites, there was no effect of feeding site/startle wing-whistle sample (SWW1 versus SWW2) on vigilance ($F_{1,34}$=1.30, P=0.26), startling ($F_{1,34}$=1.30, P=0.26), or the latency to resume feeding ($F_{1,34}$=1.30, P=0.26) following the startle wing-whistle playback. I thus combined data from the two feeding sites (number of individuals at each feeding site: feeding site A, *Zenaida macroura*=5, *Passer domesticus*=7, *Cardinalis cardinalis*=4; feeding site B: *Z. macroura*=3, *P. domesticus*=12, *C. cardinalis*=5). At the Austin County site, for each group (n=5) of doves I calculated the mean proportion of individuals that increased vigilance and that startled, and mean latency to return to feeding. Then, for statistical analyses, I calculated grand means across groups to compare responses to the different playback sounds. In all cases, analysis of variance(s) (ANOVA(s)) were used to evaluate (1) differences among mean responses to various stimuli and (2) species effects in responses to specific stimuli. If an ANOVA revealed significant effects, Fisher LSD tests were used to evaluate differences between specific means (Sokal and Rohlf 1987). Values reported are means±SE. To further limit the likelihood of testing the same individuals multiple times at the Bryan sites, I tested each species only once at each feeding station; that is, the five doves at feeding site A arrived together, were tested with playbacks, and I did not test any later-arriving doves at that feeding site.

Results

Within-species ANOVAs revealed significant treatment effects for doves (vigilance, $F_{3,8}$=6.55, P=0.015; startle behavior, $F_{3,8}$=7.31, P=0.011; latency to return to feeding; $F_{3,8}$=14.37, P=0.001), cardinals (vigilance, $F_{3,8}$=21.51, P<0.001; startle behavior, $F_{3,8}$=14.33, P=0.001; latency to return to feeding, $F_{3,8}$=21.02, P<0.001), and sparrows (vigilance, $F_{3,8}$=7.64, P=0.01; startle behavior, $F_{3,8}$=2.80, P=0.11; latency to return to feeding, $F_{3,8}$=7.70, P=0.01). Pairwise comparisons show that all species responded to the playbacks of dove startle wing-whistles and cardinal alarm calls with increased vigilance (Fig. 1a), startle behavior (Fig. 1b), and latency to return to feeding (Fig. 1c).

While all species responded as predicted to sounds related to potential threat (Fig. 1a–c), pairwise comparisons among-species within-treatments revealed that individuals remained vigilant longer following playbacks of conspecific sounds than following playbacks of heterospecific sounds. For instance, doves spent more time vigilant following dove wing-whistle playbacks—startle and non-startle—than did cardinals and sparrows (compare black bars to black bars, and dark grey bars to dark grey bars in Fig. 1c); cardinals spent more time vigilant following cardinal alarm call playbacks than did doves or sparrows

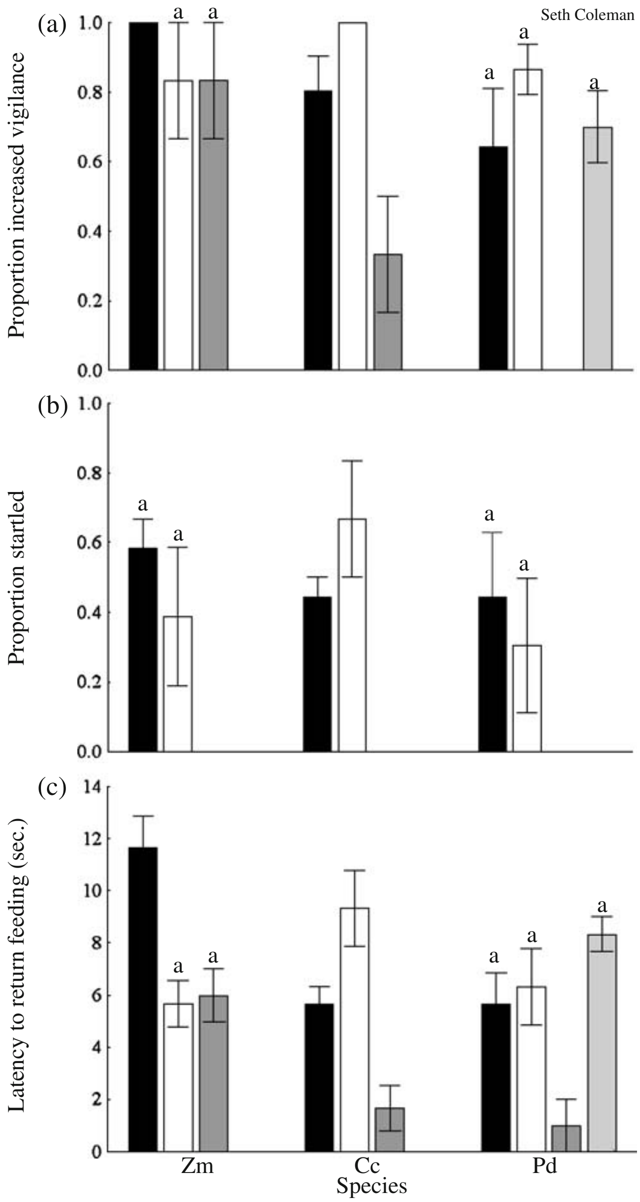

Fig. 1 At the Bryan feeding sites, effect of mourning dove startle wing-whistle (*black bars*), cardinal alarm call (*white bars*), mourning dove nonstartle wing-whistle (*dark grey bars*), and house sparrow social chatter (*light grey bars*) playbacks on dove (*Zm*), cardinal (*Cc*), and sparrow (*Pd*) vigilance (panel **a**), startling (panel **b**), and latency to return to feeding (panel **c**). *Columns* and *bars* represent means±SE. Bars that share letters above them are not significantly (P>0.05) different

(compare white bars in Fig. 1c); and sparrows spent more time vigilant following the sparrow chatter playbacks than did doves and cardinals (compare light gray bars in Fig. 1c).

Playbacks at the Austin County farm site revealed that doves responded with increased vigilance ($F_{6,28}$=5.15, P= 0.001), startling ($F_{6,28}$=27.07, P<0.001), and latency to resume feeding ($F_{6,28}$=7.56, P<0.001) following the playback of startle wing-whistles and cardinal alarm calls than following nonstartle wing-whistles and sparrow social calls. Post hoc pairwise mean comparisons showed that vigilance, startle behavior, and latency to resume feeding all increased following dove startle wing-whistle and cardinal alarm call playbacks compared to the dove nonstartle wing-whistle and sparrow chatter playbacks (Fig. 2a–c).

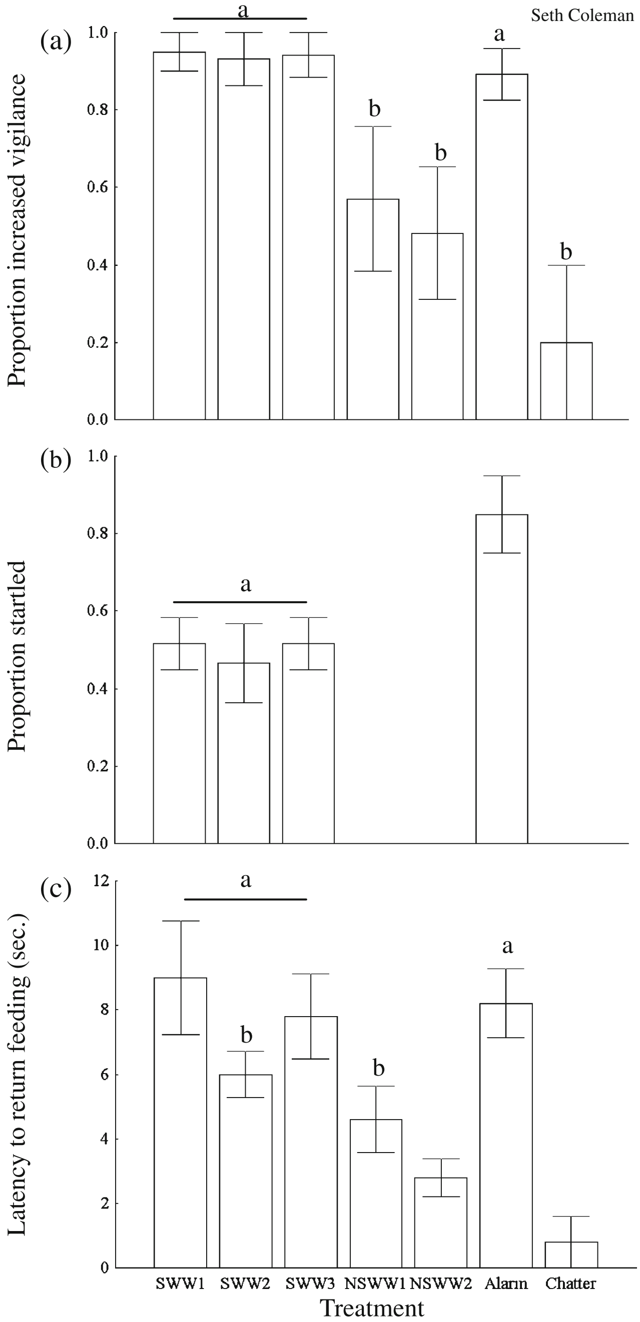

Fig. 2 Effect of playbacks of three startle wing-whistle (*SWW1*, *SWW2*, *SWW3*), two nonstartle wing-whistle (*NSWW1*, *NSWW2*), the cardinal alarm call, and the sparrow chatter on mourning dove vigilance (panel **a**), startling (panel **b**), and latency to return to feeding (panel **c**) at the Austin County farm site. *Columns* and *bars* represent means±SE. Bars that share letters above them are not significantly (P>0.05) different

Discussion

Nonvocal sounds are widespread among birds and may frequently be used in communication (see, Bostwick 2006). Here I investigate the possible functional significance of a particularly widespread nonvocal sound: the distinctive whistles that are associated with dove wing-beats. These whistles are most conspicuous when individuals are startled from the ground. I thus tested the hypothesis that foraging individuals attend to the sound of these whistles, and use information contained in them in predator avoidance. Supporting this hypothesis, I found that mourning doves, northern cardinals, and house sparrows responded to experimental playbacks of mourning dove startle wing-whistles with increased vigilance and startling behavior. Moreover, individuals of all three species responded more strongly to startle wing-whistles than they did to nonstartle wing-whistles, recorded from doves ascending with no immediate threat from a potential predator. Finally, the responses of individuals to the playback of dove startle wing-whistles were most similar to the responses following playbacks of cardinal alarm calls—a signal used to convey important threat-related information from sender to receiver (Nealen and Breitwisch 1997)—suggesting that startle wing-whistles may serve a similar communicative function.

The techniques for conducting robust playback experiments have been well documented (Hurlbert 1984; Catchpole 1989; Kroodsma 1989). This study suffers from small sample sizes and possible pseudoreplication at several levels. First, individuals were not marked, allowing for the possibility that the same individuals were tested multiple times in different groups. I attempted to minimize the potential for this type of pseudoreplication by temporally and spatially separating playback trials (see “Materials and methods”). Second, I used far fewer than the optimal number (~10) of different recordings needed to ensure that individuals are responding to the target stimulus and not to some acoustic cue associated with, but not germane to, the stimulus: at the Bryan sites, only a single recording of each type was played to each flock; at the Austin sites, only three startle wing-whistles and two nonstartle wing-whistles were used; at both sites, only a single version of the cardinal alarm call and sparrow chatter was used. Having a unique series of recordings for each stimulus type used only once at each site—the ideal experimental design (Hurlbert 1984; Catchpole 1989; Kroodsma 1989)—was beyond the scope of the present study. Third, it is possible in mixed-species flocks that increased antipredator behavior by cardinals and sparrows following startle wing-whistle playbacks reflect changes in dove behavior, rather than responses to the playbacks directly. It is widely accepted that individuals glean critical information on the threat of predation by eavesdropping on heterospecific communication (Phelps et al. 2007; Templeton and Greene 2007; Vitousek et al. 2007). Thus, it would seem to benefit a cardinal or sparrow to attend directly to information in the sound of a mourning dove wing-whistle, rather than rely on a delayed visual cue of danger. This hypothesis could be better tested in wing-whistle playback experiments to single-species flocks of cardinals and house sparrows. The shortcomings identified here, combined with results strongly supporting the central hypothesis, warrant further studies to fully elucidate the functional and evolutionary significance of dove wing-whistles in communication.

Nonvocal sounds produced by animals through the interactions among body parts with each other, or with some external medium, such as air, water, or substrate are widespread (Bostwick 2006). In some cases, these sounds have evolved into signals that convey information from a sender to a receiver; such signals have evolved independently multiple times in birds (reviewed in Bostwick 2006), spiders (Scheffer et al. 1996; Hebets and Uetz 1999; Hebets and Papaj 2005), and crickets (Huber and Moore 1989). At present, it is unclear whether the important acoustic features of startle wing-whistles are elements of an intentionally produced signal—evolved to convey information from a signaler to a receiver—or whether these elements are by-products of wing morphology, used by flock-mates as cues correlated with the presence of a threat. Regardless of whether there is intention underlying the production of sounds associated with dove wing-whistles, I suggest that individuals in many species may attend to particular acoustic features of wing-whistles, as these sounds are widespread, and may contain important information.

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