



Reliability of public information: predators provide more information about risk than conspecifics

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Animals may acquire information about predatory threats via direct cues, clues from the predator, or indirect cues from predator-elicited alarm signals from conspecifics. Although direct detection of a predator is assumed to be a better indicator of risk, only three previous studies have directly contrasted the relative information content of conspecific alarm calls to predator sounds. Studied species typically reacted equally or stronger to conspecific alarm calls than to predator sounds, suggesting that an indirect cue may be a more reliable indicator of risk. We studied zenaidura doves, *Zenaidura macroura*, responsiveness to predator sounds and conspecific alarm signals. When flushed, zenaidura doves produced voluntary mechanical wing whistles, which we predicted to be alarm signals. Observing responses to wing flap playbacks with and without whistles, we found that doves increased vigilance significantly more to wing whistles than to wing flaps without whistles or control playbacks. These results indicate that conspecifics interpret wing whistles as alarm signals. We then conducted another playback experiment, which demonstrated that red-tailed hawk, *Buteo jamaicensis*, playbacks elicited higher levels of dove vigilance than conspecific wing whistles. Contrary to other species, zenaidura doves seemingly consider predator vocalizations more informative than conspecific alarm signals. Therefore, the reliability of acoustic signals associated with predation risk may strongly influence prey responsiveness to direct and indirect cues.

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Given that all animals are potential prey, they must be able to identify, assess and manage predation risk to survive (Lima & Dill 1990; Caro 2005). Animals identify potential risk by assessing various cues such as alarm calls and predator vocalizations (Schmidt et al. 2008; Goodale et al. 2010). Alarm calls may deter predators (Zuberbühler et al. 1999b), warn conspecifics (Randall et al. 2000), or elicit mobbing (Wheeler 2008). However, these different cues provide different information. With the exception of some predatory birds (Thomsett 1987; Ellis et al. 1993; Hendrie et al. 1998; Gil-da-Costa et al. 2003), most predators do not vocalize while hunting (Brown & Amadon 1968; Boesch & Boesch 1989; Blumstein et al. 2008). Despite this, many species respond to predator vocalizations (Table 1). Species may respond because the vocalization directly indicates the predator's presence (Hauser & Wrangham 1990; Caro 2005).

Our analysis of studies that examined species responses to both predator vocalizations and conspecific alarm signals revealed

mixed results (Table 2): two species responded equally to both stimuli, two species responded more to conspecific alarm calls than to predator sounds, and four showed mixed responses, either reacting more to conspecific alarm calls or equally. None responded more to predator vocalizations than to conspecific alarm calls. Animals may thus value indirect conspecific information as much as or more than direct auditory cues produced by predators. We formally tested this concept by asking the question: do prey species respond more to conspecific alarm signals or predator vocalizations?

Given that the signaller's reliability may drive differences in response, a reliable signal requires two conditions: (1) some characteristic of the signal should be associated with an attribute of the signaller or environment, and (2) the receiver should benefit from having information from this attribute (Searcy & Nowicki 2005). Predatory threats generally elicit alarm signals (Cheney & Seyfarth 1981; Zuberbühler 2001). However, alarm signals are also uttered in nonthreatening situations that could be viewed as false alarms (Munn 1986; Haftorn 2000; Beauchamp & Ruxton 2007; Wheeler 2009). For instance, a caller may produce a false alarm by mistaking an unthreatening stimulus for a threatening one (Haftorn 2000; Beauchamp & Ruxton 2007). Callers can also produce false alarms without a stimulus to deceive and startle their audience

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Table 1
Playback studies examining focal species' responses towards predator vocalizations and conspecific alarm signals

Focal species/conspecific alarm signal	Response	Predator vocalization playback	Source
Birds			
Eurasian coot, <i>Fulica atra</i>	>	Domestic dog, <i>Canis familiaris</i>	Randler 2006b
Mammals			
Tamar wallaby, <i>Macropus eugenii</i>	>	Dingo, <i>Canis lupus dingo</i>	Blumstein et al. 2000
	>	Wedge-tailed eagle, <i>Aquila audax</i>	Blumstein et al. 2000
Red-fronted lemur, <i>Eulemur rufus</i>	=	Fossa, <i>Cytoprocta ferox</i>	Fichtel & Kappeler 2002
	=	Domestic dog	Fichtel & Kappeler 2002
	>	Harrier hawk, <i>Polyboroides radiatus</i>	Fichtel & Kappeler 2002
Verreaux's sifaka, <i>Propithecus verreauxi</i>	=	Fossa, <i>Cytoprocta ferox</i>	Fichtel & Kappeler 2002
	=	Domestic dog	Fichtel & Kappeler 2002
	=	Harrier hawk	Fichtel & Kappeler 2002
Campbell's mona monkey, <i>Cercopithecus campbelli</i>	>	Crowned hawk eagle, <i>Stephanoaetus coronatus</i>	Zuberbühler 2001
	=	Leopard, <i>Panthera pardus</i>	Zuberbühler 2001
Diana monkey, <i>Cercopithecus diana</i>	=	Crowned hawk eagle	Stephan & Zuberbühler 2008; Zuberbühler et al. 1999a*, 1997
	=	Leopard, <i>Panthera pardus</i>	Stephan & Zuberbühler 2008; Zuberbühler et al. 1999a*, 1997
Blue monkey, <i>Cercopithecus mitis stuhlmanni</i>	>	Crowned hawk eagle	Papworth et al. 2008
	=	Leopard	Papworth et al. 2008
Yellow-bellied marmot, <i>Marmota flaviventris</i>	>	Coyote, <i>Canis latrans</i> [†]	Blumstein et al. 2008
	>	Coyote [†]	Blumstein et al. 2008
	>	Golden eagle, <i>Aquila chrysaetos</i> [†]	Blumstein et al. 2008
	=	Golden eagle [†]	Blumstein et al. 2008
	>	Wolf, <i>Canis lupus</i> [†]	Blumstein et al. 2008
	>	Wolf [‡]	Blumstein et al. 2008

Prey species are listed in phylogenetic order (Wilson & Reeder 2005; Clements 2007). Focal species' responses did not differ significantly towards conspecific alarm calls and predator vocalizations (=), were greater towards conspecific alarm signals (>), or were greater towards predator vocalizations (<).

* Statistical analysis not conducted.

† Dependent variable was time allocated to foraging.

‡ Dependent variable was time allocated to increased vigilance/in burrow.

(Munn 1986; Wheeler 2009), or perhaps to signal aggression (Satischandra et al. 2010). Furthermore, individuals may have different calling thresholds (Blumstein et al. 2004; Blumstein 2007). Given the possibility of false alarms and different calling thresholds, alarm calls may not always be a reliable source of information about predators (Searcy & Nowicki 2005). Therefore, alarm signal reliability may vary and receivers may respond less to unreliable alarm signals. Caller reliability should influence receiver behaviour because antipredator behaviour is energetically expensive (Searcy & Nowicki 2005).

What then is the reliability associated with a predator's sound? When prey hear a predator, they are certain it is present, but knowledge about true predation risk is less certain. Given that some predators, particularly a variety of raptors, vocalize immediately before (Hendrie et al. 1998; Gil-da-Costa et al. 2003) or during hunting (Thomsett 1987; Smallwood 1993; Smith 2008), such predator vocalizations may reliably indicate risk. As a result, their prey may be more likely to respond to their vocalizations. However, most predators are silent hunters; thus, do prey 'know' that these predator vocalizations are not an immediate threat? If animals associate predator vocalizations with a reduced threat, they should be less likely to respond to most predator sounds.

We examined antipredator behavioural responses of zenaida doves, *Zenaida aurita*, a species that falls prey to a variety of raptors (Burger et al. 1989, 1991), towards conspecific alarm signals and predator sounds. Although zenaida doves do not utter vocal alarm signals (Griffin et al. 2005), two recent studies suggest that their relatives, crested pigeons, *Ocyphaps lophotes*, and mourning doves, *Zenaida macroura*, generate voluntary mechanical wing whistles,

which function as alarm signals (Coleman 2008; Hingee & Magrath 2009).

We first demonstrated that predator-elicited wing whistles in zenaida doves are alarm signals by comparing zenaida doves' behavioural responses towards playbacks of conspecific wing flaps with and without whistles. Then, we studied the relative information content of these signals compared to vocalizations from a common predator, the red-tailed hawk, *Buteo jamaicensis*. Supported by previous predator vocalization studies, we predicted that zenaida doves would not only recognize predator vocalizations, but that they would also react more to conspecific predator-elicited warning signals than to predator calls.

METHODS

Study Site and Subjects

We studied zenaida doves in the Virgin Islands National Park in the area surrounding the Virgin Islands Environmental Resource Station (VIERS) (18° 19' 15" N, 64° 43' 37" W) on St John, U.S. Virgin Islands, from 10 to 30 October 2009. Research was conducted under UCLA ARC Protocol number 2000-147-31, and a permit from the Virgin Islands National Park (no. VIIS-2009-SCI-0028). We walked on and off trails in a 100 km² area of the park and studied the doves we encountered. Individual zenaida doves are semiterritorial and roughly remain in the same area (Lefebvre et al. 1996). Therefore, in an effort to avoid remeasuring individuals, we walked in a different direction from VIERS each day and avoided sampling the same location twice for the same experiment.

Table 2
Playback studies examining focal species' responses only towards predator vocalizations

Focal prey species	Predator vocalization	Source
Birds		
Great blue turaco, <i>Corythaeta cristata</i>	Chimpanzee, <i>Pan troglodytes</i> Crowned hawk eagle, <i>Stephanoaetus coronatus</i>	Hauser & Wrangham 1990 Hauser & Wrangham 1990
Black-casqued hornbill, <i>Ceratogymna atrata</i>	Crowned hawk eagle Leopard, <i>Panthera pardus</i>	Rainey et al. 2004b Rainey et al. 2004b
Yellow-casqued hornbill, <i>Ceratogymna elata</i>	Crowned hawk eagle Leopard	Rainey et al. 2004a Rainey et al. 2004a
Crow, <i>Corvus brachyrhynchos hesperis</i>	Great horned owl, <i>Buteo virginianus</i> Red-shoulder hawk, <i>Buteo lineatus</i>	Hauser & Caffrey 1994 Hauser & Caffrey 1994
Black-capped chickadee, <i>Poecile atricapillus</i>	Red-shouldered hawk	Zanette & Ratcliffe 1994
Mammals		
Eastern quoll, <i>Dasyurus viverrinus</i>	Red fox, <i>Vulpes vulpes</i> Feral cat, <i>Felis catus</i> Masked owl, <i>Tyto novaehollandiae castanops</i> Tasmanian devil, <i>Sarcophilus laniarius</i>	Jones et al. 2004 Jones et al. 2004 Jones et al. 2004 Jones et al. 2004
Red-necked pademelon, <i>Thylogale thetis</i>	Dingo, <i>Canis lupus dingo</i> Wedge-tailed eagle, <i>Aquila audax</i>	Blumstein et al. 2002 Blumstein et al. 2002
Ring-tailed lemur, <i>Lemur catta</i>	Madagascar serpent eagle, <i>Eutriorchis astur</i> Henst's goshawk, <i>Accipiter henstii</i> Madagascar harrier hawk, <i>Polyboroides radiatus</i> Red-tailed hawk, <i>Buteo jamaicensis</i>	Karpanty & Grella 2001 Karpanty & Grella 2001 Macedonia & Yount 1991; Karpanty & Grella 2001 Macedonia & Yount 1991
Verreaux's sifaka, <i>Propithecus verreauxi</i>	Red-tailed hawk Fox, <i>Vulpes vulpes</i>	Fichtel & van Schaik 2006 Fichtel & van Schaik 2006
Spectral tarsier, <i>Tarsius tarsius</i>	Sulawesi serpent eagle, <i>Spilornis rufipectus</i> Spot-tailed goshawk, <i>Accipiter trinotatus</i> Sulawesi owl, <i>Tyto rosenbergii</i> Speckled boobook, <i>Ninox punctulata</i>	Gursky 2002, 2003 Gursky 2003 Gursky 2003 Gursky 2003
White-headed marmoset, <i>Callithrix geoffroyi</i>	Red-tailed hawk	Searcy & Caine 2003
Mantled howler monkey, <i>Alouatta palliata</i>	Harpy eagle, <i>Harpia harpyja</i>	Gil-da-Costa et al. 2003
Sooty mangabey, <i>Cercocebus atys</i>	Leopard Chimpanzee, <i>Pan troglodytes</i>	Zuberbühler et al. 1999b Zuberbühler et al. 1999b
Red-tailed monkey, <i>Cercopithecus ascanius</i>	Chimpanzee Crowned hawk eagle	Hauser & Wrangham 1990; Treves 1999 Hauser & Wrangham 1990; Treves 1999
Campbell's mona monkey, <i>Cercopithecus campbelli</i>	Crowned hawk eagle Leopard Human Chimpanzee	Zuberbühler 2003; Ouattara et al. 2009 Zuberbühler et al. 1999b; Zuberbühler 2003; Ouattara et al. 2009 Zuberbühler 2003 Zuberbühler et al. 1999b; Zuberbühler 2003
Diana monkey, <i>Cercopithecus diana</i>	Human Crowned hawk eagle Chimpanzee Leopard	Zuberbühler 2003 Zuberbühler 2000, 2003 Zuberbühler et al. 1999b; Zuberbühler 2003 Zuberbühler 2000, 2003; Zuberbühler et al. 1999b
Blue monkey, <i>Cercopithecus mitis</i>	Chimpanzee Crowned hawk eagle	Hauser & Wrangham 1990 Hauser & Wrangham 1990
Greater spot-nosed monkey, <i>Cercopithecus nictitans martini</i>	Crowned hawk eagle Leopard	Eckardt & Zuberbühler 2004; Arnold & Zuberbühler 2006 Eckardt & Zuberbühler 2004; Arnold & Zuberbühler 2006
Lesser spot-nosed monkey, <i>Cercopithecus petaurista</i>	Leopard Chimpanzee	Zuberbühler et al. 1999b Zuberbühler et al. 1999b
King colobus, <i>Colobus polykomos</i>	Leopard Chimpanzee	Zuberbühler et al. 1999b Zuberbühler et al. 1999b
Western red colobus, <i>Ptilocolobus badius</i>	Leopard Chimpanzee Crowned hawk eagle	Bshary & Noë 1997; Zuberbühler et al. 1999b Hauser & Wrangham 1990; Bshary & Noë 1997; Treves 1999; Zuberbühler et al. 1999b Hauser & Wrangham 1990; Gebo et al. 1994; Treves 1999
Eurasian red squirrel, <i>Sciurus vulgaris</i>	Tawny owl, <i>Strix aluco</i>	Randler 2006a
California ground squirrel, <i>Spermophilus beecheyi beecheyi</i>	Northern Pacific rattlesnakes, <i>Crotalus viridis oreganus</i>	Swaisgood et al. 1999
Eastern chipmunk, <i>Tamias striatus</i>	Broad-winged hawk, <i>Buteo platypterus</i>	Schmidt et al. 2008

(continued on next page)

Table 2 (continued)

Focal prey species	Predator vocalization	Source
Large-eared garden dormouse, <i>Eliomys melanurus</i>	Tawny owl	Hendrie et al. 1998
Lesser Egyptian jerboa, <i>Jaculus jaculus</i>	Tawny owl	Hendrie et al. 1998
Social vole, <i>Microtus socialis</i>	Tawny owl	Hendrie et al. 1998; Eilam et al. 1999
White-footed deermouse, <i>Peromyscus leucopus</i>	Barred owl, <i>Strix varia</i>	Schmidt 2006
Northeast African spiny mouse, <i>Acomys cahirinus</i>	Tawny owl	Hendrie et al. 1998; Eilam et al. 1999
Anderson's gerbil, <i>Gerbillus andersoni</i>	Barn owl, <i>Tyto alba</i>	Abramsky et al. 1996
Pale gerbil, <i>Gerbillus perpallidus</i>	Tawny owl Barn owl Peregrine falcon, <i>Falco peregrinus</i>	Kindermann et al. 2009 Kindermann et al. 2009 Kindermann et al. 2009
Greater Egyptian gerbil, <i>Gerbillus pyramidum</i>	Barn owl	Abramsky et al. 1996
Natal mastomys, <i>Mastomys natalensis</i>	Grass owl, <i>Tyto capensis</i>	Crafford et al. 1999
Domestic mouse, <i>Mus musculus</i>	Red fox, <i>Vulpes vulpes crucigera</i> Little owl, <i>Athene noctua</i> Kestrel, <i>Falco tinnunculus</i> Tawny owl Barn owl Peregrine falcon	Hendrie & Neill 1991 Hendrie & Neill 1991 Hendrie & Neill 1991 Hendrie & Neill 1991; Kindermann et al. 2009 Hendrie & Neill 1991; Kindermann et al. 2009 Kindermann et al. 2009
Norway rat, <i>Rattus norvegicus</i>	Tawny owl Barn owl Peregrine falcon	Kindermann et al. 2009 Kindermann et al. 2009 Kindermann et al. 2009
Angoni Vlei rat, <i>Otomys angoniensis</i>	Grass owl	Crafford et al. 1999
Cheetah, <i>Acinonyx jubatus</i>	Lion, <i>Panthera leo</i> Spotted hyaena, <i>Crocuta crocuta</i>	Durant 2000 Durant 2000
Harbour seal, <i>Phoca vitulina</i>	Killer whale, <i>Orcinus orca</i>	Deecke et al. 1993
Eurasian elk, <i>Alces alces</i>	Tiger, <i>Panthera tigris</i> Wolf, <i>Canis lupus</i> Coyote, <i>Canis latrans</i>	Berger et al. 2001; Berger 2007 Berger et al. 2001; Berger 2007 Berger et al. 2001
Reindeer, <i>Rangifer tarandus</i>	Tiger Wolf	Berger 2007 Berger 2007
Red deer, <i>Cervus elaphus</i>	Tiger Wolf	Berger 2007 Berger 2007
American bison, <i>Bison bison</i>	Tiger Wolf	Berger 2007 Berger 2007

Prey species are listed in phylogenetic order (Wilson & Reeder 2005; Clements 2007).

Are Wing Whistles Alarm Signals?

Production of wing whistles: are whistles produced under alarming situations?

Zenaida doves may or may not produce whistles when they take off, but their flights invariably contain obvious wing flap sounds. Since Hingee & Magrath (2009) found that take-off angles in crested pigeons may be related to alarming situations eliciting wing whistles, we analysed the relationship between take-off angle and wing whistles in zenaida doves. While one observer ran towards a dove, another observer recorded flight sounds with a unidirectional microphone (AT835b, Audio-Technica U.C., Inc., Stow, OH, U.S.A.) onto a direct-to-disk digital recorder (Marantz PMD670, Marantz America, Inc., Mahwah, NJ, U.S.A.) and noted the dove's take-off angle. After we determined that we could neither accurately nor precisely measure the take-off angle, but could reliably score take-offs as $<45^\circ$ or $\geq 45^\circ$, we categorized take-off angles into these two categories. Some of the take-off angle observations were conducted near water holes, where doves commonly aggregated at dawn and dusk; thus, a small subset of subjects may have been resampled. We defined steep take-off angles as $\geq 45^\circ$ and used a Fisher's exact test to determine whether take-off angle was associated with wing whistle production.

We then characterized the acoustic structure of escape flights with and without wing whistles. Using Canary 1.2 (Charif et al. 1995), we measured the total flapping duration (from first to last flap) and counted the number and rate of flaps and whistles (when applicable) within the first and second halves of the escape flight. The wing whistles are harmonically structured; we measured the peak frequency of the fundamental. To compare flights with and without whistles, we used *t* tests and calculated *d* scores (Cohen 1988) using the pooled variance (*d* scores >0.8 are considered large effects, those around 0.5 are considered medium effects, and those around 0.3 are considered small effects).

Perception of wing whistles: do wing whistles elicit alarm?

We conducted a playback experiment where we broadcast either escape flights with only wing flaps, escape flights with wing flaps and wing whistles, or a control sound, the song of the ubiquitous and nonthreatening bananaquit, *Coereba flaveola* (Mata & Bosque 2004). We selected the highest-quality exemplars, which contained the largest signal-to-noise ratio and the least background noise, and normalized them to 95% maximal peak amplitude using SoundEdit v.16 (Adobe System Inc., San Jose, CA, U.S.A.) to produce the final playbacks (Fig. 1). We obtained bananaquit songs from a commercial CD (Oberle 2008) and the dove flights

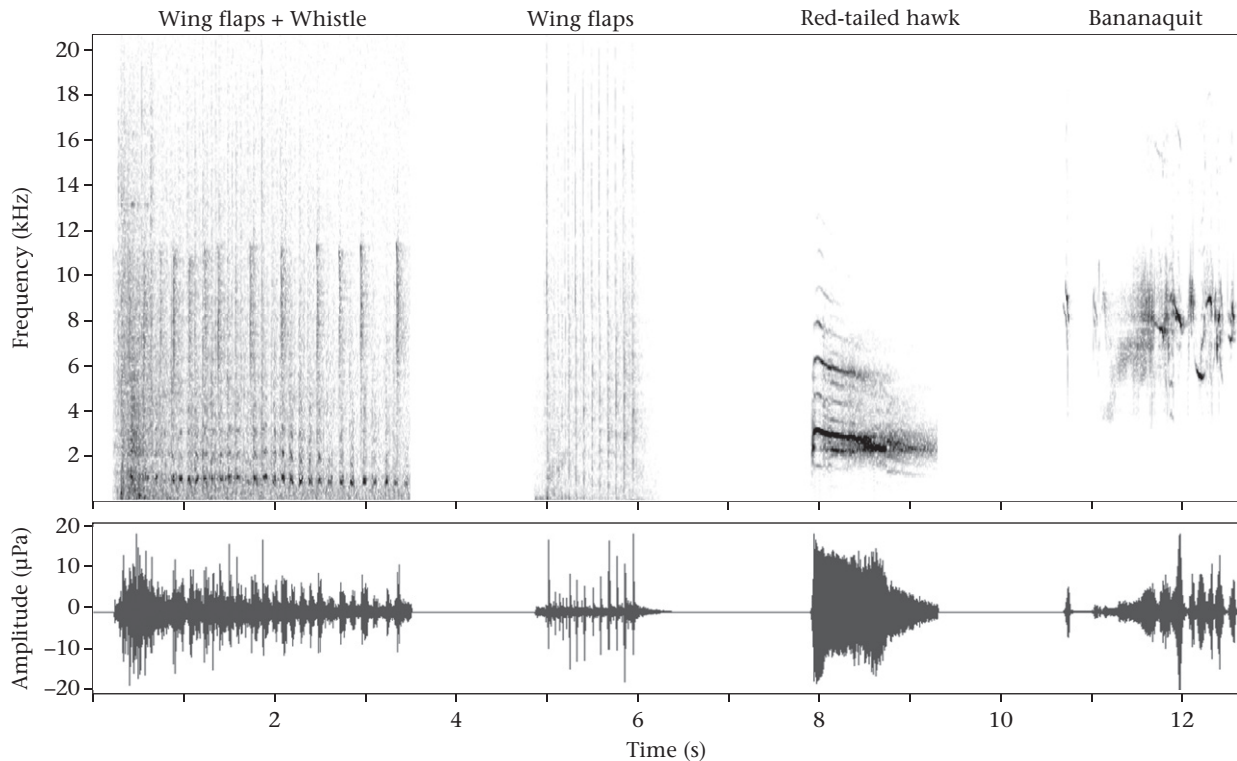


Figure 1. Spectrogram (top) and waveform (bottom) of playback stimuli. Sampling rate 44 kHz, 512 point FFT (frequency resolution 86.13 Hz), greyscale represents -80 dB from peak amplitude.

from our field recordings. Each playback exemplar (five exemplars for each stimulus) included 15 s of silence, the playback, followed by 60 s of silence.

We broadcast all stimuli through a PAL speaker (Tivoli Audio, LLC, Cambridge, MA, U.S.A.) connected to an iPod (Apple Inc., Cupertino, CA, U.S.A.). To mimic natural amplitudes of nearby bananaquits singing and flockmates flying off in alarm, we played back the controls at 76–80 dB SPL and the wing whistles and nonwhistle wing flaps at 73–78 dB SPL. All stimuli were measured with a digital sound meter (Sper Scientific Ltd., 840029, 1 m away from the speaker, weighting level A, fast response).

Upon seeing a zenaida dove approximately 20 m away, we waited until the focal individual displayed relaxed behaviour (foraging or walking), then randomly (using shuffle feature on iPod) presented a playback and conducted a 75 s focal observation (Martin & Bateson 1993). We divided the focal into a 15 s preplayback period and a 60 s period consisting of the playback and the postplayback. Our ethogram contained the following behaviours: forage (head down, in search of food), walk (slow bipedal movement), look-up (change in head position from down to up), stand-look (entire body stationary, head erect), scan (side-to-side head movement), preen (rotates head, uses bill to clean feathers), ruffle feathers (feather dishevelment), headbob (contraction and elongation of head; tail stationary), head–tailbob (contraction and elongation of head, plus tail flicks), fly away (both feet off ground and in flight, without whistle), flush (both feet off ground and in flight, whistle), and out of sight. Behavioural transitions were dictated onto a microcassette recorder using this ethogram. Following the playback and focal observation, the observer took note of the physical conditions surrounding the focal animal, including wind levels (using the Beaufort scale), distance from subject to nearest cover (± 2 m), distance from subject to observer (± 2 m) and number of conspecifics within 10 m. A single observer

later scored focal observations into JWatcher 1.0 (Blumstein & Daniel 2007). We combined the behaviours ‘stand-look’ and ‘look-up’ to form the general category of ‘looking’. We focused only on the most common activities; therefore, we designated looking as vigilant behaviour and foraging as relaxed behaviour. We focused on zenaida doves that were relaxed prior to playback. While in the field we attempted to perform focals only on animals that appeared relaxed. When we analysed relaxed behaviour with JWatcher, we rigorously define relaxed behaviour as spending less than 65% of preplayback time looking. The mean \pm SE proportion of preplayback time spent looking was 0.034 ± 0.011 .

There were no significant differences in baseline behaviours (behaviours of doves seen during the preplayback period) between treatments for either proportion of time looking (ANOVA: $F_{2,37} = 0.479$, $P = 0.623$) or foraging ($F_{2,37} = 0.162$, $P = 0.851$). Therefore, we did not adjust poststimulus time allocation data for baseline. Since the reaction to playback is transient, we focused on and reported only the first 15 s following playback. We analysed results using a linear mixed effect model (in PASW 18.0, SPSS Inc., Chicago, IL, U.S.A.) and compared treatment to proportion of time spent looking or foraging after we accounted for variation explained by the random effect of exemplar. We tested possible obscuring factors and covariates (wind speed, measured on the Beaufort scale and restricted to 0–2, distance to cover (m), distance to observer (m) and number of conspecifics within 10 m) by adding them one at a time to the basic analysis to examine whether they significantly explained variance in response.

Are Wing Whistles More Evocative Than Predator Sounds?

We obtained five exemplars of red-tailed hawk shrieks from Oberle (2008) and Peterson (1990) and used the same five

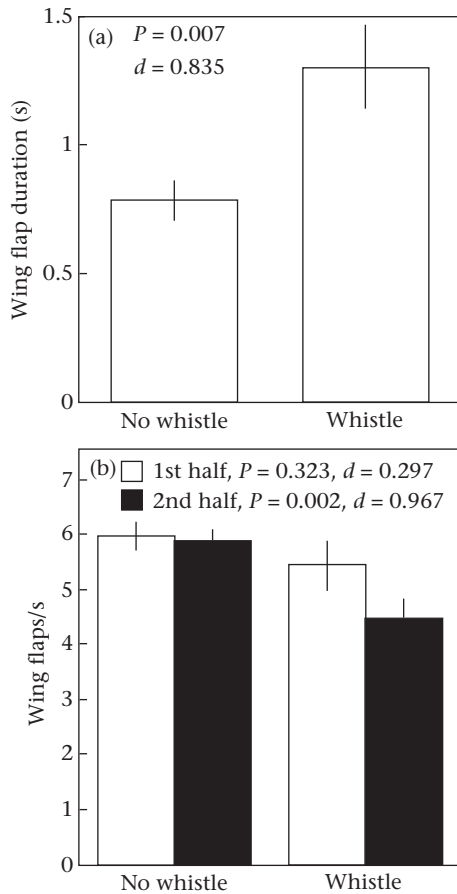


Figure 2. Mean \pm SE (a) wing-flapping duration and (b) wing-flapping rate of zenaïda doves during whistling ($N = 26$) and nonwhistling ($N = 22$) flights. In (b), rates of flapping are shown in the first and second halves of flight.

bananaquit and five flight whistle exemplars from our previous experiment. We chose to use the red-tailed hawk because it is a common predator of zenaïda doves (Burger et al. 1989). We played back hawk shrieks at 85–90 dB SPL. While in the field we heard natural red-tailed hawk shrieks; thus we chose this amplitude range to mimic a red-tailed hawk flying overhead. Alarm whistle and bananaquit amplitudes were the same as in the previous experiment (Fig. 1) and mimicked natural amplitudes of adjacent birds.

Our experiment directly contrasted the zenaïda doves' response to alarm signals and predators sounds. Experimental procedures were identical to the previous experiment. The mean \pm SE proportion of preplayback time spent looking was 0.052 ± 0.016 . There were no significant differences in baseline behaviours between treatments for either proportion of time looking ($P = 0.456$) or foraging ($P = 0.271$); therefore, we did not adjust poststimulus time allocation data for baseline. We analysed the first 15 s postplayback segment using a linear mixed effect model (in PASW 18.0) and compared treatment to proportion of time spent looking or foraging after we accounted for variation explained by the random effect of exemplar. We tested possible obscuring factors and covariates (wind speed, measured on the Beaufort scale and restricted to 0–2, distance to cover (m), distance to observer (m) and number of conspecifics within 10 m) by adding them one at a time to the analysis to examine whether they significantly explained variance in response.

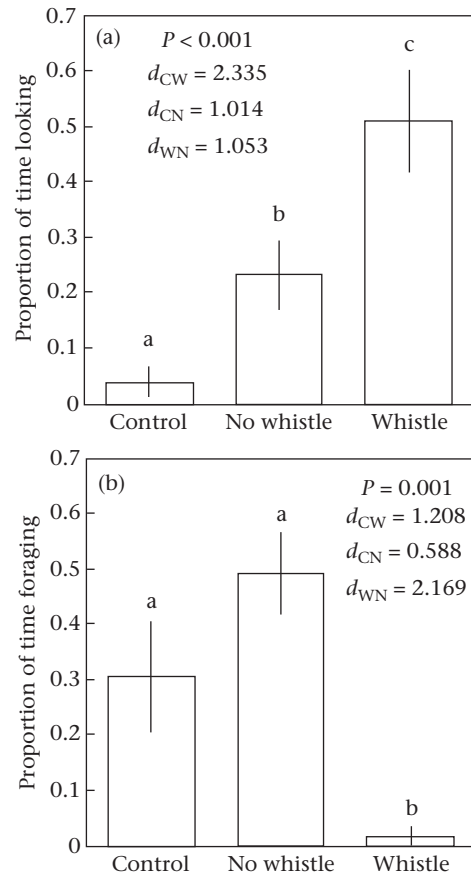


Figure 3. Mean \pm SE proportion of time spent (a) looking and (b) foraging by zenaïda doves during the first 15 s after playback of bananaquit control vocalizations ($N = 11$), and whistling ($N = 17$) and nonwhistling ($N = 9$) flights of zenaïda doves. Bars with different letters were significantly ($P < 0.05$) different from each other. Cohen's d is calculated for the comparisons: CW = Control/Whistle; CN = Control/No whistle; WN = Whistle/No whistle.

RESULTS

Are Wing Whistles Alarm Signals?

Production of wing whistles: are whistles produced under alarming situations?

We found two discernable differences between wing flaps with whistles and wing flaps without whistles. Discernable flapping lasted significantly longer for flights with whistles than without whistles (Fig. 2a), and the rate of wing flaps differed (Fig. 2b). In the first half of flapping, no significant difference was present between wing flap rates; however, the wing flap rate during the second half substantially reduced for flights with whistles. The mean \pm SE of the fundamental frequency of the whistle was $1.159 \text{ kHz} \pm 0.082 \text{ kHz}$.

Take-off angle influenced the probability of emitting a whistle. Doves that took off at steep angles ($\geq 45^\circ$) were significantly more likely to whistle ($N = 24$) than not to whistle ($N = 3$) (Fisher's exact test: $P = 0.002$), whereas doves that took off at lower angles ($< 45^\circ$) were equally likely to whistle ($N = 17$) or not whistle ($N = 18$).

Perception of wing whistles: do wing whistles elicit alarm?

Our three playback treatments elicited significantly different responses (Fig. 3). Wing whistles elicited significantly more looking than either the control ($P < 0.001$) or the nonwhistle wing flap

($P = 0.003$; Fig. 3a). Furthermore, focal individuals significantly reduced the proportion of time foraging in response to wing whistle playbacks (Fig. 3b). In comparison to the control stimulus, playbacks of nonwhistle wing flaps also elicited significantly more time spent looking ($P = 0.025$), but induced no significant difference in proportion of time spent foraging ($P = 0.077$). Measured covariates had no significant effects on proportion of time spent looking (wind: $F_{2,37} = 1.873$, $P = 0.168$; distance to cover: $F_{1,37} = 0.083$, $P = 0.775$; distance to observer: $F_{1,37} = 3.226$, $P = 0.081$; number of conspecifics within 10 m: $F_{1,37} = 0.090$, $P = 0.766$) and proportion of time spent foraging (wind: $F_{2,37} = 1.306$, $P = 0.283$; distance to cover: $F_{1,37} = 2.234$, $P = 0.143$; distance to observer: $F_{1,37} = 0.241$, $P = 0.627$; number of conspecifics within 10 m: $F_{1,37} = 1.981$, $P = 0.168$).

Are Wing Whistles More Evocative Than Predator Sounds?

Doves looked most in response to predator vocalizations, least to bananaquit controls, and at an intermediate level to alarm whistles (Fig. 4a). Both whistles and predator calls suppressed foraging compared to bananaquit songs (Fig. 4b). Measured covariates did not significantly affect time spent looking (wind: $F_{1,33.3} = 1.750$, $P = 0.190$; distance to cover: $F_{1,46.6} = 0.002$, $P = 0.962$; distance to observer: $F_{1,48.5} = 0.185$, $P = 0.669$; number

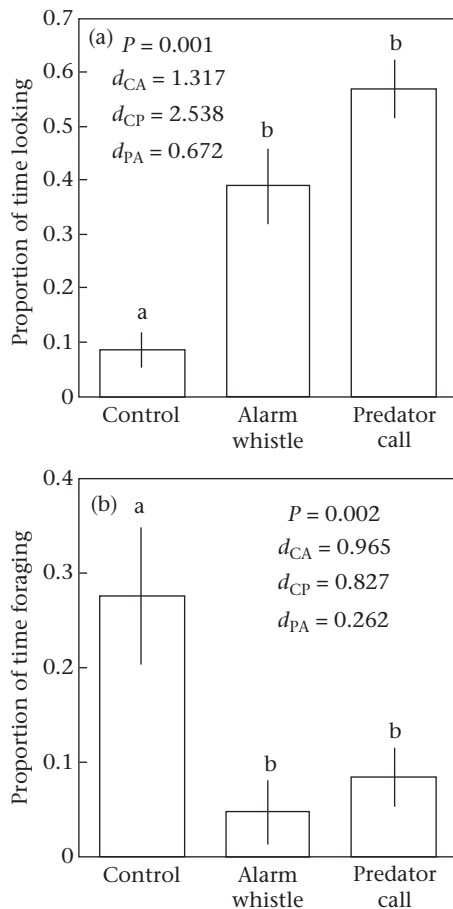


Figure 4. Mean \pm SE proportion of time spent (a) looking and (b) foraging by zenaida doves during the first 15 s after playback of bananaquit control vocalizations ($N = 18$), zenaida dove alarm whistles ($N = 19$) and red-tailed hawk shrieks ($N = 19$). Bars with different letters were significantly ($P < 0.05$) different from each other. Cohen's d is calculated for the comparisons: CA = Control/Alarm whistle; CP = Control/Predator call; PA = Predator call/Alarm whistle.

of conspecifics within 10 m: $F_{1,48.2} = 2.71$, $P = 0.106$) or foraging (wind: $F_{1,39} = 2.805$, $P = 0.102$; distance to cover: $F_{1,56} = 0.389$, $P = 0.535$; distance to observer: $F_{1,56} = 0.458$, $P = 0.501$; number of conspecifics within 10 m: $F_{1,56} = 1.663$, $P = 0.203$).

DISCUSSION

Assuming that steeper take-off angles are associated with alarm (van der Veen & Lindström 2000), wing whistles are seemingly produced when doves are under higher threat, and thus take off at steeper angles. Doves responded more to wing whistle playbacks than to those without whistles or to bananaquit songs, confirming that wing whistles are a mechanical signal (Bostwick 2000) used to communicate a predatory threat among conspecifics. However, wing flaps alone still have the potential to act as alarm signals because rapid wing sounds can provide a reliable cue for predatory risk (Hingee & Magrath 2009).

Unlike previous studies, which have demonstrated that prey appear to respond more to conspecific alarm signals (Blumstein et al. 2000; Randler 2006b), or equally to both conspecific alarm signals and predator sounds (Zuberbühler et al. 1997; Fichtel & Kappeler 2002), our results surprisingly show that, for these doves, predator vocalizations were more evocative than conspecific wing whistles. Thus, our results indicate that zenaida doves may actually value predator vocalizations more than conspecific alarm signals. One possible explanation for this result may be that, unlike many predators that are known to vocalize only in social contexts (Mulligan & Nellis 1975; Holekamp et al. 1999), many birds of prey vocalize before or during hunting (Thomsett 1987; Smallwood 1993; Hendrie et al. 1998; Gil-da-Costa et al. 2003). Red-tailed hawks (*Macedonia & Yount 1991*) and other raptors (short-tailed hawks, *Buteo brachiurus*, and harpy eagles, *Harpya harpyj*; Albuquerque 1995) call while soaring, but some also call immediately prior to a strike (e.g. harpy eagles; Gil-da-Costa et al. 2003). Vocalizations can also be used as an ambush strategy to flush prey from cover (slaty-backed forest-falcons, *Micastur mirandollei*, and collared forest-falcons, *Micastur semitorquatus*; Smith 2008). Given the variety of ways raptors call while hunting, calls are likely to be perceived as danger signals. Thus, the doves' high degree of responsiveness to hawk vocalizations could minimize their predation risk. Furthermore, we observed that zenaida doves not only produced wing whistles in response to predators, but also when they were flushed by territorial, pearly-eyed thrashers, *Margarops fuscatus*, and conspecifics. Thus, like other alarm signals, wing whistles are not uniquely elicited by predators and may therefore be less valued by conspecific listeners.

An alternative explanation may be that territorial, but group foraging, zenaida doves may be particularly vulnerable because they are not always found in groups (Jeffrey-Smith 1972; Lefebvre et al. 1996). Such vulnerability may serve as a strong driving force for prey to respond to and potentially value predator sounds more than conspecific alarm signals.

While no previous studies reported a greater response towards predator vocalizations than towards conspecific alarm calls, we are aware of one study that found that black-casqued hornbills, *Ceratogymna atrata*, reacted more to predator vocalizations than to the alarm calls of heterospecific primates (Rainey et al. 2004b). Their results support their 'information precision hypothesis', which suggests that the relative information content of predator sounds provides accurate spatial information about the predator's location, while heterospecific alarm signals do not. Rather, indirect cues, such as a conspecific or heterospecific alarm signal, may only represent the signaller's, not the listener's, encounter with the predator; thus, the direct cue of predator presence is valued more than indirect cues. The concept that alarm signals do not

provide accurate spatial information about a predator may also explain why zenaida doves responded to conspecific wing whistles with more vigilance, rather than automatic flight. Provided that signallers generate wing whistles when fleeing from a potential threat, one might expect a listening zenaida dove to also fly away. However, we observed that such wing whistles were only elicited when the signaller experienced a threat (being chased by an observer, territorial pearly-eyed thrasher, or another zenaida dove) within close range. Therefore, we might not expect wing whistle playbacks to elicit (presumably) energetically expensive flight in receivers, unless they encounter a similar degree of threat as the signaller.

At some level, a distinction between vocal and nonvocal alarm signals should not exist. Both are likely under voluntary control, and we can envision receivers being primed to learn about them (Hollén & Radford 2009). Thus, we might expect nonvocal alarm signals to be equivalent to vocal ones. However, if responsiveness to vocal and nonvocal alarm signals is not equivalent, differences in responsiveness should be explained by differences in signal reliability. Given that our results showed a greater reaction to predator sounds, we infer that the nonvocal wing whistle was less reliable, suggesting that reliability influences the receiver's evaluation of the relative information content.

The ability to respond to predator sounds may be partially driven by reliability and prey vulnerability. While previous studies have demonstrated that vulnerable, nonsocial prey have the ability to recognize interspecific alarm signals by eavesdropping on heterospecific callers (Tonkin 1983; Shriner 1999; Randler 2006c; Lea et al. 2008), they have not emphasized the role of caller reliability. To determine how strongly signal reliability, vulnerability, or both influence the responsiveness of prey towards auditory cues that communicate predation risk (predator sounds and conspecific and heterospecific alarm signals) future playback studies should focus on both social and nonsocial prey species and on predators that possess both hunting and social vocalizations.

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