



Mixed-species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*

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Aggregating with heterospecifics may be particularly beneficial for a species that is able to exploit the antipredator behaviour of another. Territorial zenaida doves vigorously exclude conspecific intruders from their territory, but forage with, and acquire novel foraging techniques from, carib grackles. Given that doves associate with no other conspecific than their mate and they have no vocal alarm signals of their own, they might benefit from attending to the conspicuous alarm calls of carib grackles. In the present study, we found that zenaida doves suppressed foraging both in response to a model predator and in response to the sound of grackle alarm vocalizations. Although doves' responses to the predator model also involved moving away from the immediate vicinity, their responses to grackle alarm vocalizations consisted of remaining alert and tail flicking. Together, these results strongly suggest that doves attend to the antipredator behaviour of carib grackles. These findings extend earlier work demonstrating that doves obtain foraging benefits from their association with grackles, to show that they may also obtain predator avoidance benefits.

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Mixed-species foraging aggregations confer advantages that can be greater than those of monospecific groupings. For example, species with different diets may obtain predator avoidance benefits while avoiding the costs of food competition (Morse 1977; Terborgh 1990). In case of dietary overlap, however, individuals may nevertheless join heterospecifics because it increases their probability of finding food and/or because it allows them to acquire information about novel foods and novel foraging techniques (Webster & Lefebvre 2001). Predator avoidance benefits may also outweigh the costs of food competition (Morse 1977; Terborgh 1990) if a species with poor antipredator detection skills is able to exploit an efficient antipredator behaviour of another species (Gaddis 1980; Munn 1986; Rasa 1990). For example, a species that does not produce any alarm call may benefit substantially from associating with one that does. Information transfer about food and predators are not mutually exclusive and there are most likely to be cases in which both operate (Wolters & Zuberbühler 2003).

The carib grackle and the zenaida dove are two urbanized avian species that are common and sympatric on several islands of the Lesser Antilles. In most areas of Barbados, zenaida dove pairs aggressively defend year-round

territories against conspecifics (Lefebvre et al. 1996). In contrast, they show little or no aggression towards carib grackles, despite considerable dietary overlap in areas where food scraps left by humans are an important source of food (Dolman et al. 1996). As a consequence, grackles, which forage in small, mobile flocks, often feed in close proximity to doves. The preferential association of doves and grackles, rather than of doves and conspecifics, has been found to drive the direction of social learning about food. Zenaida doves from territorial populations acquire a novel foraging technique from a carib grackle demonstrator more readily than from a conspecific dove (Dolman et al. 1996). In addition, grackles often land at an experimental food source before doves, raising the possibility that doves, which are relatively neophobic, may use grackles to detect and investigate novel food patches (Webster & Lefebvre 2001; D. J. White, unpublished data).

Another potential benefit that doves may obtain from their close association with grackles is heightened predator avoidance. Carib grackles travel in small flocks and give high-amplitude, broadband pulsatile chuck vocalizations, which are strongly associated with the presence of predators (Jaramillo & Burke 1999). In free-living grackles, high rates of chuck calls are typically evoked by mongooses, *Herpestes auro-punctatus*, cats, *Felis catus*, vervet monkeys, *Chlorocebus aethiops*, and dogs, *Canis familiaris*, and are sometimes accompanied by mobbing, particularly

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around nesting roosts (L. Lefebvre, personal observation; A. S. Griffin, personal observation). In addition, experimental playback of chuck calls cause receivers to take flight and to begin calling (A. S. Griffin, unpublished data). These observations, together with published reports of predator–chuck call associations in carib grackles (Jaramillo & Burke 1999), strongly suggest that chuck vocalizations function as antipredator calls. In contrast, zenaida doves do not produce vocal alarm signals and territory owners typically forage alone or with their mate. Doves may benefit from relying on grackles to look out for predators and responding to their antipredator calls for two reasons. First, an approaching predator may be more likely to be detected by a grackle than a dove because grackles are more abundant, more mobile, and spend more time perched in trees. Second, relying on grackles might allow doves to increase their food intake by reducing the time they allocate to antipredator vigilance. Given the ability of zenaida doves to acquire information about food from carib grackles and the behavioural and ecological differences between the two species, zenaida doves and carib grackles form a particularly interesting avian system in which to explore cross-species antipredator call recognition (McLean & Rhodes 1991).

There have been no previous studies of the antipredator behaviour of zenaida doves. The aims of the present study were hence two-fold. In experiment 1, we determined how zenaida doves respond to predators by quantifying their responses to a model of a prototypical mammalian predator. In experiment 2, we tested whether zenaida doves give antipredator responses to the sound of grackle antipredator calls.

EXPERIMENT 1

As in many islands, the mammalian predator community in Barbados is entirely established by humans. Dogs are thought to have been brought by the Amerindians, the original colonizers of Barbados, prior to the 1500s. Cats, Indian mongooses and vervet monkeys were introduced more recently by European settlers. Except for dogs, there is circumstantial evidence that each of these species represents some degree of threat to either doves or their offspring. Vervet monkeys are common nest predators (A. S. Griffin, personal observation), cats have been observed stalking doves (A. S. Griffin, personal observation), and mongooses are able to kill and consume vulnerable adults (J. Morand-Ferron, personal communication). There have been no systematic attempts, however, to quantify the responses of doves to predators. We considered it necessary therefore to address this question before we tested the responses of doves to grackle alarm calls.

Quantifying antipredator behaviour during natural instances of predation is often impossible. Consequently, we elected to stage predator encounters by presenting a model to free-living zenaida doves. This approach has the further advantage that attributes of the encounter that might influence response levels substantially, such as the predator's speed, gait and direction of approach, can be controlled across subjects. Furthermore, territorial doves

can be reliably resighted, so their responses to a predator stimulus can be compared with those evoked by non-predator control stimuli using a repeated measures design, which removes the effects of interindividual variation on responses (Griffin et al. 2001, 2002; Griffin & Evans 2003).

Methods

Subjects

The dove population at Bellairs Research Institute and Folkstone Park, St-James, Barbados, has been the subject of several earlier studies (Lefebvre 1996; Webster & Lefebvre 2001). All the individuals that took part in the present study were colour-banded and readily identifiable through binoculars. This dove population lives in proximity to humans, and the birds are accustomed to being fed. Each morning and evening for 10 days prior to the start of the experiment, we walked a transect around Bellairs and Folkstone Park and placed food piles at various locations. We identified the territory owner(s) by noting which birds defended the food against intruders. Doves were considered mates if they defended the food patch against conspecifics, but foraged in close proximity of each other with little or no aggression. At the end of the 10-day period, we selected 11 territory owners with the highest resighting rates as subjects for experiment 1. These individuals were distributed across 11 different territories. Zenaida doves are difficult to sex in the field, so we did not take this factor into consideration when selecting subjects. During each test, the focal bird was provided with approximately three handfuls of cooked rice.

Visual stimuli

To measure responses to a prototypical predator stimulus, we used a taxidermic mount of an ermine, *Mustela erminea*. Although ermines are unfamiliar predators to zenaida doves, their morphology is convergent with that of many mammalian predators, such as mongooses, which are abundant on the island of Barbados. To compare responses evoked by a mammalian predator with those evoked by a nonpredator-like control object of similar volume, we presented the birds with a cardboard box painted black (Maloney & McLean 1995; McLean et al. 1996; Göth 2001; Wisenden & Harter 2001). Visual stimuli were attached to a cart (0.45 × 0.65 × 0.1 m) that could be wheeled in and out of a hide. Finally, to detect spontaneous changes in behaviour over time, we conducted a blank control, in which the hide and the test device were set up on the subject's territory, but no stimulus was presented. Each of the three visual treatments was conducted once on each territory in an order that was balanced across subjects.

Test procedure

We conducted all trials in the early morning between 0545 and 0900 hours. These are the times at which zenaida doves are most likely to be found foraging on their territories and when tests were the least likely to be disturbed by visitors to Folkstone Park and Bellairs. We ran

three to five stimulus presentations per day on widely spaced territories, and tests on the same territory were separated by 2–4 days.

We began by placing a small pile of rice on the focal subject's territory. A hide ($0.5 \times 0.70 \times 0.45$ m) containing the cart and the visual stimulus was then placed 3 m away from the food source. The cart could be pulled in and out of the hide via a quiet pulley system operated by the experimenter who sat approximately 7 m away. Doves in the Bellairs population often forage within considerably closer distances of humans. Correspondingly, we observed no behaviour that indicated that the focal subject was disturbed by the experimenter. We waited for a maximum of 20 min for the territory owner to appear and begin foraging on the experimental food source. If the territory owner had not appeared after 20 min, the experiment was postponed until the next scheduled test time.

The stimulus was only presented if the subject had been foraging at the experimental food source for 30 s without being interrupted by a conspecific intruder. This controlled for baseline behaviour and distance to the hide at stimulus onset across all tests. To present the stimulus, the experimenter slowly moved the cart out of the hide (approximately 0.5 m/s) to approximately 2 m away from the food source where it remained immobile for 60 s. At the end of the 60-s presentation period, the experimenter moved the stimulus slowly back into the hide.

Data analysis

We videorecorded the doves for 30 s immediately prior to stimulus presentation (baseline), 60 s during stimulus presentation, 120 s after the stimulus had disappeared. To quantify responses to the stimulus, we measured (1) changes in pecking rates from prestimulus baseline, (2) the tendency of the birds to move away from the stimulus and (3) changes in rate of tail flicking, a flight intention movement typically shown by alarmed zenaida doves. Tail flicking consists of a rapid upwards, then downwards, movement of the whole body, accompanied by scanning, neck elongation and a characteristic jerking motion of the tail; the posture is often followed by flight if the source of alarm keeps approaching. Although tail flicking has not been studied in zenaida doves, there is evidence from other avian species that this behaviour is strongly associated with antipredator behaviours, such as alarm calling, mobbing and wing flicking (Curio et al. 1978; Vieth et al. 1980).

Because zenaida doves actively defend their territories against conspecifics, focal doves sometimes stopped foraging and left the experimental food source to chase away an intruder. To separate locomotion away from the food that was caused by conspecific intrusion from locomotion away from the food that was not, we defined a 2-m diameter circle centred on the food source. In the field, we placed natural objects, such as stones, on the borders of the circle so that we could later identify this area on video recordings. In cases where the focal bird exited the circle to chase away an intruder, the entire time spent outside the circle was scored as 'chasing'. Chases were unambiguous to score; the focal bird moved rapidly with its head

lowered towards an approaching conspecific and often began a territorial display or fight. If the bird exited the circle, but no intruder could be identified, we scored the entire time spent outside the circle as 'away'.

We defined pecking as a clear downward movement of the beak towards the ground regardless of whether the beak actually contacted food or not. We only scored pecking if it occurred within the 2-m circle area centred on the food source because we wanted to test whether the birds were willing to forage in proximity to the area where the visual stimulus was presented. In practice, foraging behaviour was very rare outside the defined zone, presumably because the experimental food was far more abundant than any naturally occurring food.

For each bird, we counted the number of pecks and tail flicks produced during the 30-s prestimulus baseline and each 60-s interval after the appearance of the stimulus. For each behaviour, we then calculated the difference between the rate of occurrence during baseline and the rate of occurrence during each 60-s interval after stimulus onset. For each behaviour, we examined effects of stimulus on the mean change in rate from baseline using a two-way repeated measures ANOVA with factors for stimulus (predator, box, blank control) and time (three 60-s intervals). Significant main effects of stimulus in ANOVA models of pecking and tail flicking were investigated further using paired *t* tests.

We calculated the mean percentage of time spent away and chasing per minute between the appearance of the stimulus and 120 s after the stimulus had disappeared. We did not calculate changes in these behaviours from prestimulus baseline because we had ensured experimentally that 'away' and 'chase' did not occur before the stimulus appeared (see test procedure). We used nonparametric statistics to analyse these data because they were not normally distributed. We tested for an effect of stimulus on the mean percentage of time spent away per minute using a nonparametric Friedman test. To ensure that any effect of stimulus on pecking and tail-flicking rates was not a consequence of differential levels of territorial defence, we also tested for an effect of stimulus on the mean percentage of time spent chasing per minute using a nonparametric Friedman test. Significant effects of stimulus were investigated further using Wilcoxon matched-pairs tests.

Significance levels were set at 0.05, except for post hoc multiple comparisons, in which we used Bonferroni-corrected *P* values adjusted for three successive comparisons. Significance levels for post hoc tests were hence set at 0.017. All analyses were carried out on untransformed data using Statview 5.2 (SAS Institute 1998).

Results and Discussion

Zenaida doves suppressed pecking more in response to a predator stimulus than in response to a similar-sized control object (box), or during blank control trials (Fig. 1a). This was reflected by both a significant ANOVA main effect of stimulus on peck rate ($F_{2,20} = 9.667$, $P = 0.001$), and the results of post hoc pairwise comparisons (paired

t tests: predator versus box, $t_{10} = -2.886$, $P = 0.016$; predator versus blank, $t_{10} = -4.080$, $P = 0.002$; box versus blank, $t_{10} = -0.268$, $P = 0.760$). There was also a main effect of time on peck rate (ANOVA: $F_{2,20} = 6.772$, $P = 0.006$), but no stimulus by time interaction ($F_{4,40} = 0.109$, $P = 0.979$). In contrast, we found no effect of stimulus presentation on tail-flick rates (ANOVA: main effect stimulus, $F_{2,20} = 2.005$, $P = 0.161$; main effect time, $F_{2,20} = 1.050$, $P = 0.369$; stimulus \times time interaction, $F_{4,40} = 0.934$, $P = 0.454$; Fig. 1b).

Doves spent significantly more time away from the experimental food patch during trials in which we presented a predator than during trials in which we presented the control stimulus or no stimulus (Fig. 2a, left panel). This was reflected by both a significant effect of stimulus (Friedman test: $\chi^2_2 = 19.579$, $N = 11$, $P < 0.001$), and the results of post hoc pairwise comparisons (Wilcoxon matched-pairs tests: predator versus box, $T = 66$, $N = 11$; $P = 0.003$; predator versus blank, $T = 66$, $N = 11$, $P = 0.003$; box versus blank, $T = 10$, $N = 11$, $P = 0.500$). In contrast, there was no effect of stimulus on time spent chasing conspecific intruders, demonstrating

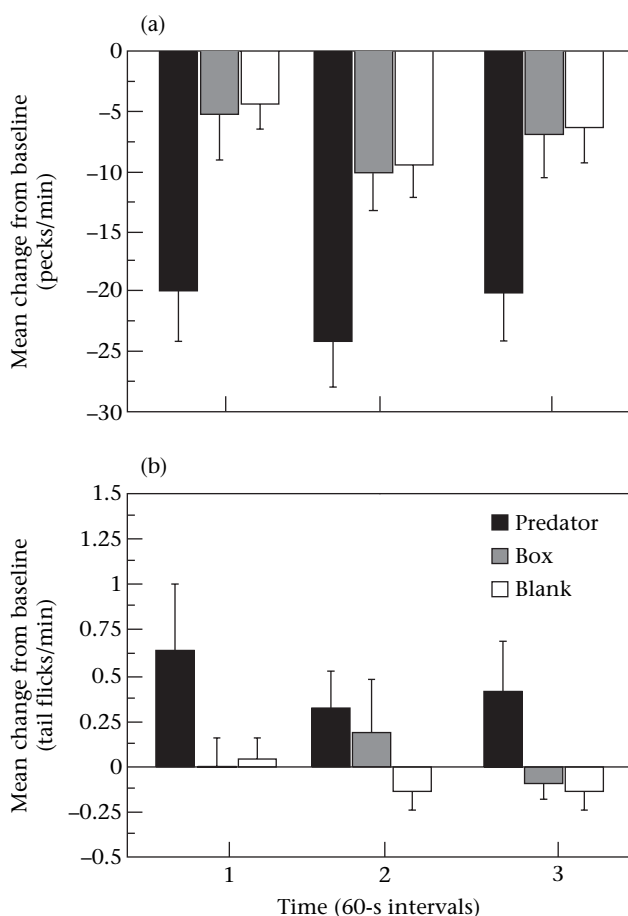


Figure 1. Behavioural responses of zenaida doves to a model predator, a box of similar volume, and during a blank control trial. Mean \pm SE ($N = 11$) changes in peck rates (a) and tail-flick rates (b) from prestimulus baseline are shown for three successive 60-s intervals from the appearance of the stimulus to 2 min after the stimulus had disappeared.

that the effects of the predator on peck rate were not attributable to differences in levels of territorial defence between stimulus treatments (Friedman test: $\chi^2_2 = 2.800$, $N = 11$, $P = 0.247$; Fig. 2b, left panel).

To the extent that our prototypical model predator was a representative exemplar of the greater category of mammalian predators, decreases in peck rates and in time spent at the food patch are consistent with the idea that doves respond more cautiously to predator stimuli than to nonpredator stimuli.

EXPERIMENT 2

Grackles may be a more common source of information about predators for zenaida doves than conspecifics. First, unlike doves, which forage alone or with their mate, grackles forage in small flocks. Consequently, there are many grackle eyes looking out for predators. Second, doves are seed eaters and forage primarily on the ground within their own territory, whereas grackles are very mobile omnivores, spending much of their time in the air or perched in trees. Therefore, grackles may be more likely to detect approaching danger, such as a troop of vervet monkeys. Third, territorial zenaida doves are found more often in close association with grackles than with conspecifics, so doves may be more likely to observe the alarm responses of grackles than those of a conspecific. Finally, unlike doves, which do not vocalize in the presence of predators, grackles give conspicuous alarm vocalizations, which can be heard tens of metres away. Responding to the calls of grackles would be a straightforward means for zenaida doves to avoid predators. The aim of experiment 2 was hence to determine whether zenaida doves respond to the sound of grackle alarm calls.

Methods

Subjects

We selected 14 territory owner zenaida doves distributed across 14 different territories in the same way as we had done for experiment 1. Six of these individuals had taken part in the previous experiment.

Acoustic stimuli

We measured the effects of grackle chuck calls on the behaviour of zenaida doves by comparing them to responses evoked by a playback of grackle song. To create the playback sequences of grackle chuck vocalizations, we evoked these calls in captive grackles by holding them in a cage and standing beside them while staring at them. To obtain playbacks of song, we recorded free-living grackles. Both kinds of acoustic stimuli were recorded using a Sony dynamic F-V620 microphone connected to a G3 iBook computer (Amadeus sound software, stereo recording, sample rate 44.1 kHz, 16-bit amplitude encoding).

Folkstone Park and Bellairs Research Institute are located close to roads, so they are relatively noisy environments in which to record sound. Using Cool Edit Pro 1.2a (Synttrillium Software 2000), we edited each stimulus

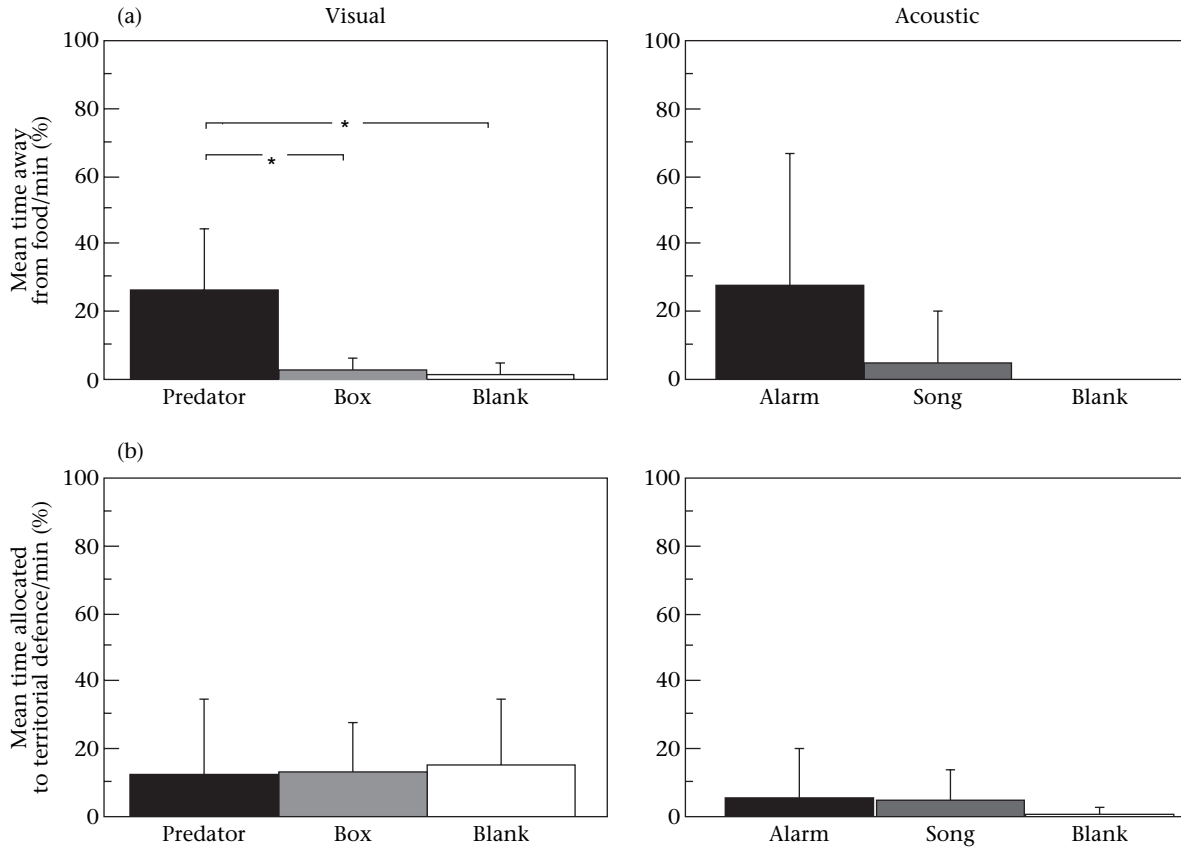


Figure 2. Mean percentage of time spent (a) away from the food source and (b) in territorial defence in response to three visual (left panel) and three acoustic (right panel) stimuli. For visual stimuli, mean + SD ($N = 11$) percentage of time per minute was averaged across the 1-min presentation period and two 1-min postpresentation intervals. For acoustic stimuli, mean + SD ($N = 14$) percentage of time was averaged across the 30-s stimulus presentation period and two 30-s poststimulus presentation intervals. * $P < 0.017$.

recording to reduce background noise. First, we used a sample of the stimulus where the birds were not vocalizing to calculate a noise reduction algorithm. We set the level of noise reduction such that the bird calls were not altered to our ear. Second, we removed a narrow frequency range of the remaining background noise, which consisted mainly of traffic sound, using parametric equalization (Cool Edit Pro 1.2a, Syntrillium Software 2000). Finally, we edited the recordings to make four distinct 30-s exemplars of alarm call sequences (Fig. 3) and four distinct exemplars of song sequences (Fig. 3) in order to sample natural variation in the acoustic structure of these vocalizations. Each exemplar began with a 2-s fade-in and ended with a 2-s fade-out to avoid startling the birds.

To examine the differential effect of alarm call versus song per se, we chose to match the volume of both stimuli to the natural volume of alarm calls. We adjusted the amplitude of all stimuli at the output using a digital sound level meter (Radioshack, model no. 33-2085) and played back the stimuli at a mean amplitude of 82 dB (A weighting; peak; ± 1 dB measured 3 m in front of the speakers). This is roughly equivalent to the birds' own alarm call output volume measured at a distance of 2 m. We played back the stimuli using an iBook G3 Apple computer laptop through two Altec Lansing 220 speakers

(frequency response 0.07–18 kHz) located 3 m away from the food source, and separated by approximately 1 m. We conducted one blank control trial and presented one randomly selected exemplar of each of the two acoustic treatments (alarm, song) on each territory, such that each exemplar was only used three or four times. Treatment order was balanced across territories.

Test procedure

As in experiment 1, we conducted all trials in the early morning between 0545 and 0900 hours. As in experiment 1, we conducted three to five stimulus presentations per day on widely separated territories, and tests on the same territory were separated by 2–4 days.

We began by placing a pile of rice on the focal subject's territory. We then placed the loudspeakers 3 m away from the food and connected them to an iBook laptop computer held by the experimenter, who sat approximately 8 m away from the food source. As in experiment 1, we waited for a maximum of 20 min for the territory owner to appear and begin foraging at the food source. If the territory owner had not appeared after 20 min, we postponed the experiment until the next scheduled test time. As in experiment 1, the stimulus was only presented if the subject had been foraging at the experimental food source without interruption for 30 s.

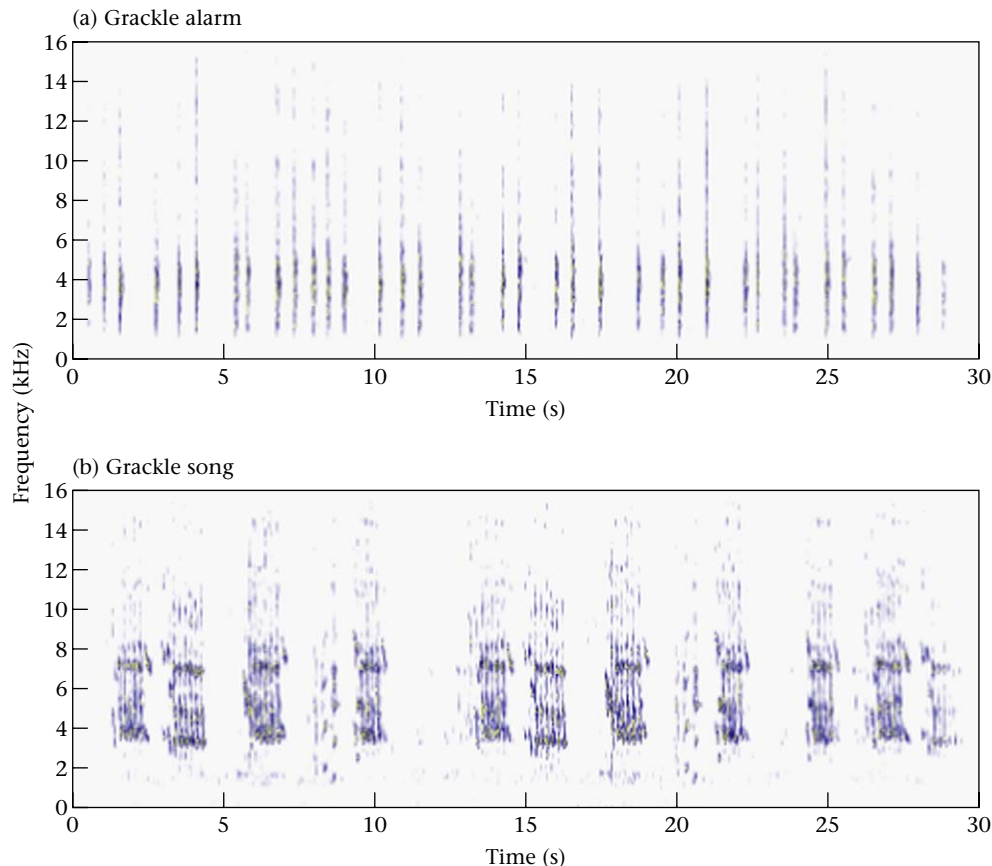


Figure 3. Sonograms and spectrograms of one of the four exemplars of acoustic stimuli used to study recognition of grackle alarm calls by zenaida doves. Sampling rate = 44.1 kHz, delta frequency = 172.3 Hz, delta time = 5.8 ms, fast Fourier transform = 256, Hanning window, cutoff values: low: -40 dB, high: -6 dB.

Data analysis

We videorecorded the doves for 30 s immediately prior to stimulus presentation (baseline), 30 s during stimulus presentation, and 1 min after the end of the stimulus. As in experiment 1, we scored and analysed changes in pecking rate and tail-flicking rate from prestimulus baseline, the percentage of time spent away from the food patch, and the percentage of time allocated to chasing away intruders.

Changes in pecking and tail-flicking rates from baseline were quantified by calculating difference scores between the 30-s prestimulus baseline and each of the three 30-s intervals after the onset of the acoustic stimulus. We calculated the mean percentage of time allocated to chasing and away from the food per minute between the onset of the acoustic stimulus and 60 s after the end of the playback.

As in experiment 1, we tested for a differential effect of stimulus on changes in pecking rate and tail-flicking rate from prestimulus baseline using two-way repeated measures ANOVAs with factors for stimulus (alarm, song, blank control) and time (three 30-s intervals). We tested for a differential effect of stimulus on the mean percentage of time away per minute and the mean percentage of time allocated to chasing per minute using nonparametric Friedman tests. Significant effects were examined further

using multiple paired t tests and Wilcoxon matched-pairs tests. Significance levels were set as in experiment 2.

Results and Discussion

The sound of grackle alarm calls evoked a sustained decrease in peck rates in zenaida doves from stimulus onset to 1 min afterward (ANOVA: stimulus main effect, $F_{2,26} = 23.523$, $P < 0.001$; time main effect, $F_{2,26} = 0.587$, $P = 0.563$; stimulus \times time interaction, $F_{4,52} = 1.578$, $P = 0.194$; Fig. 4a). The decrease was significantly greater than that evoked by either grackle song or blank control trials (paired t tests: alarm versus song, $t_{13} = -4.254$, $P < 0.001$; alarm versus blank, $t_{13} = -7.436$, $P < 0.001$; song versus blank, $t_{13} = -1.405$, $P = 0.184$). Zenaida doves also tail-flicked significantly more both during presentations of grackle alarm vocalizations and for 1 min afterward than in response to grackle song (Fig. 4b), as indicated by a main effect of stimulus on tail-flick rate (ANOVA: $F_{2,26} = 4.040$, $P = 0.030$), a nonsignificant main effect of time ($F_{2,26} = 0.811$, $P = 0.455$) and a nonsignificant stimulus by time interaction ($F_{4,52} = 0.390$, $P = 0.815$). This effect was, however, small and was not apparent in Bonferroni-corrected t tests (alarm versus song, $t_{13} = 2.110$, $P = 0.055$; alarm versus blank, $t_{13} = 2.580$, $P = 0.230$; song versus blank, $t_{13} = -0.906$, $P = 0.382$).

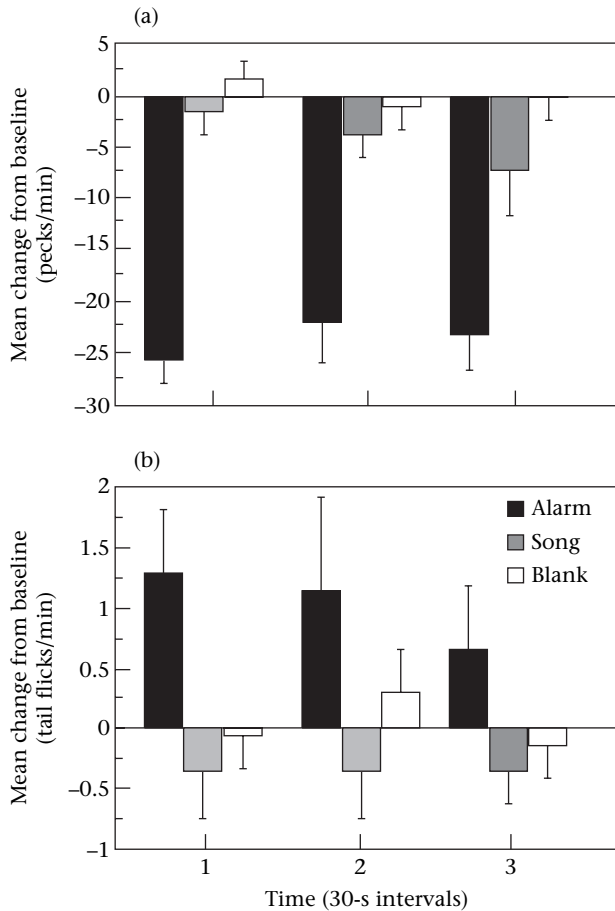


Figure 4. Behavioural responses of zenaida doves to a playback of grackle alarm calls, grackle song, and during a blank control trial. Mean + SE ($N = 14$) changes in peck rates (a) and tail-flick rates (b) from prestimulus baseline are shown for three successive 30-s intervals from the appearance of the stimulus to 1 min after the end of the stimulus.

Contrary to the results obtained during presentations of a model predator, there was no main effect of stimulus on time away from the food source (Friedman test: $\chi^2_2 = 2.649$, $N = 14$, $P = 0.266$; Fig. 2a, right panel). There was also no effect of stimulus on time allocated to chasing, confirming that, as in experiment 1, effects of stimulus on peck rate and tail-flick rate were not attributable to differential levels of territorial defence (Friedman test: $\chi^2_2 = 2.632$, $N = 14$, $P = 0.268$, Fig. 2b; right panel).

In four of 14 alarm call presentation trials, the playback stimulus attracted nearby grackles and triggered alarm calling in these individuals. The observation that our playback stimulus facilitated alarm calling in free-ranging grackles provides excellent support that the acoustic stimulus reliably reproduced the sound of grackle alarm calls. However, we cannot exclude the possibility that during these trials the doves responded to the alarm behaviour of the live grackles, rather than to the playback stimulus. We ensured therefore that removing these trials from the data set did not change the outcome of our analyses. Main effects of stimulus on pecking rate remained significant. The effect of stimulus on tail flicking

was absent from this reduced data set, but there was a significant stimulus by time interaction, revealing that alarm stimuli continued to evoke significantly more tail flicking, but only during stimulus presentation (Fig. 4b).

Insofar as our exemplars of grackle alarm calls and song were representative of the greater category of these vocalizations, our results are consistent with the idea that zenaida doves adjust their levels of foraging in response to the vocal alarm behaviour of grackles. First, changes in foraging were evoked by grackle alarm calls, but not by a control stimulus of similar amplitude (grackle song), indicating that changes in dove behaviour do not simply reflect a response to loud sounds played back from nearby loudspeakers. Second, changes in behaviour are unlikely to reflect a startle response to broadband noises. We gradually increased the volume of all playbacks over a 2-s period until the stimulus reached maximum volume, thereby reducing the likelihood of a startle reaction. In addition, the doves' responses were long-lasting, unlike startle responses; subjects did not resume foraging after the end of the playback, but rather remained vigilant for at least 60 s afterward.

However, we cannot exclude the possibility that zenaida doves are, in general, more fearful of broadband noises that are more similar in frequency composition to grackle alarm calls than to grackle song. Such responsiveness would be sufficient to allow doves to use grackle alarm calls as a signal for danger. Heterospecific alarm calls are usually considered to be recognized as alarm calls per se, rather than inherently aversive sounds, if they trigger responses that are qualitatively similar to those evoked by conspecific alarm calls, such as alarm calling and mobbing (Evans 1972; Krams & Krama 2002). Zenaida doves do not display these responses, so we have to rely on more general changes in behaviour to quantify recognition. In the present experiment, subjects did not move away from the origin of the sound, the loudspeakers. Rather, they adopted an alert erect posture and tail-flicked, as if scanning their surroundings, and maintained this behavioural state for 60 s after the end of the alarm stimulus. In contrast, in experiment 1, the presence of the predator model caused the birds to move away from the food, suggesting that the model was inherently aversive. We suggest therefore that grackle alarm calls may not be inherently frightening to doves, but rather that they are recognized as a sound associated with danger.

GENERAL DISCUSSION

This study represents the first attempt to characterize the responses of zenaida doves to predators, and to determine whether doves respond with antipredator behaviour to the alarm calls of a closely associated species, the carib grackle. We found that zenaida doves suppressed foraging both in response to a model predator and in response to the sound of grackle alarm vocalizations. Responses to the predator model also involved moving away from the immediate vicinity, whereas responses to grackle alarm calls consisted of remaining alert and tail flicking. Together, these results strongly suggest that doves respond adaptively to the antipredator behaviour of carib grackles.

Empirical demonstrations of heterospecific alarm call recognition that employ experimental playback to tease

apart the effects of the vocalization from other environmental events, such as the behaviour of social companions, remain relatively rare in birds compared with the huge literature on intraspecific communication (Frings et al. 1955; Nuechterlein 1981; Sullivan 1984, 1985; Göth 2001; Krams & Krama 2002). This is rather surprising since heterospecific communication has been suggested to play a role in the evolution of alarm call structure (Marler 1957). The paucity of data in birds stands in stark contrast to the large literature on heterospecific chemical alarm substance recognition in fish, the mechanisms of which are now well understood. Heterospecific alarm substances that are structurally similar to those released by conspecifics evoke responses that are not dependent upon prior experience, suggesting that these chemicals are recognized by simple generalization from conspecific alarm signal recognition (Chivers & Smith 1998; Magurran 1999). In contrast, heterospecific signals that bear little structural similarity to those released by conspecifics elicit responses that arise as a consequence of associative learning (Chivers et al. 1995; Mirza & Chivers 2001, 2003).

Zenaida doves do not produce any vocal alarm signals of their own, so generalization from conspecific alarm call recognition can be ruled out. They may, however, respond to broadband pulsatile grackle alarm calls through a general sensitivity to loud broadband sounds. We consider this unlikely, however, because our subjects did not move away from the source of the sound during the entire 30-s playback, suggesting that they did not find the acoustic stimulus inherently aversive. We suggest, therefore, that responses to grackle alarm calls may be acquired through associative learning in which grackle alarm behaviours become associated with the presence of predators. Our thinking is analogous to that proposed to explain the results of cross-species learning about food in the grackle-zenaida dove system. Dolman et al. (1996) found that territorial doves acquire a novel foraging technique more readily from a demonstrator grackle than from a conspecific dove, whereas doves from a group-feeding harbour population learn more readily from a conspecific. Territorial doves caught at a site adjacent to the harbour, which experience both group-feeding at the harbour and aggressive defence at their site of residence, learn equally well from doves and grackles (Carlier & Lefebvre 1997). Given the lack of isolation between dove populations with different tutor preferences, the rapid changes in defence brought about by manipulations of food distribution in the field (Goldberg et al. 2001) and the lack of differences between group-feeding and territorial doves kept for long periods under identical conditions in aviaries (B. Livoreil, unpublished data), learning is the most plausible mechanism for the differences in response to feeding information. During ontogeny, territorial doves learn to associate food with the presence of grackles and to associate conspecifics with territorial aggression. The idea that doves may learn to behave adaptively to the alarm calls of carib grackles is supported by evidence that associative learning can mediate the acquisition of antipredator responses to novel acoustic stimuli (Shriner 1999).

Information parasitism of one species' alarm system by another is likely to be an important benefit of polyspecific

groupings (Rasa 1990), particularly if the ecology of the eavesdropping species puts it at a disadvantage that is compensated for by the antipredator behaviour of the producer species. For example, Sullivan (1985) found that downy woodpeckers, *Picoides pubescens*, which often forage alone, respond to the alarm vocalizations of black-capped chickadees, *Parus atricapillus*, which associate with conspecifics and have a high propensity to call. Western grebes, *Aechmophorus occidentalis*, have reduced flying capabilities during the breeding season and use the aerial alarm calls of Forster's terns, *Sterna forsteri*, to detect overhead danger, thereby perhaps reducing their vulnerability to predators (Nuechterlein 1981). The alarm calls of antbirds and tanagers in Amazonian polyspecific flocks are exploited by a variety of gleaner and prober species, which find food by scanning the ground with their bills close to the substrate (Munn 1986). Similarly, in the grackle-dove system, an approaching predator is more likely to be detected by a grackle than a dove because of the differences in these species' social systems, their use of habitat and their alarm behaviour. Grackles are hence an ideal source of predatory information for doves. Earlier work has shown that doves can parasitize information from grackles about food and novel foraging techniques. The benefits grackles may provide for doves, both in terms of antipredator vigilance and information about food availability (Webster & Lefebvre 2001) and novel foraging techniques, may explain why doves forage with grackles so readily, despite considerable dietary overlap in areas where anthropogenic food is an important resource (Dolman et al. 1996). More specifically, relying on grackles to signal danger may outweigh the costs of enhanced foraging competition, particularly if searching for food or intruders is dependent upon the use of search images or diverts the dove's attention from other environmental stimuli, such as predators (Dukas & Kamil 2000, 2001). Finally, our results raise the possibility that grackle alarm responses may facilitate avoidance learning of novel predators in doves. This question awaits future research.

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