

Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*

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Predation pressure is an important selective force in many animal populations. In response to such pressure, prey species have evolved diverse sensory mechanisms and behavioural responses designed to increase the probability of survival (Endler 1991). Studies of anti-predator adaptations typically focus on behavioural tactics such as vigilance, alarm calling and mobbing. Less information is available regarding the sorts of environmental cues available to prey for detecting predators, together with the design features of the sensory mechanisms facilitating detection and recognition. Several recent studies, however, have indicated that prey are capable of using auditory cues associated with the predator (e.g. alarm calls) to increase the probability of early detection (Rowe et al. 1986; Cheney & Seyfarth 1990; Hauser & Wrangham 1990). We designed a series of playback experiments to determine whether western American crows (1) recognize the calls of their predators and (2) discriminate between these ecologically significant sounds and acoustically similar, but ecologically unimportant sounds.

Experiments were conducted on a population of crows in Encino, California. Marked individuals from this population have been under intensive observation since 1985 and detailed information is available on their social organization and behaviour, demography, and breeding biology (Caffrey 1991, 1992). Predation on nestlings and fledglings by great horned owls, *Bubo virginianus* and red-shouldered hawks, *Buteo lineatus*, is the major source of mortality in this population; great horned owls also prey on adult crows. Only 43% of 147 nesting attempts monitored over 6 years fledged young; 29% of fledglings failed to survive 2 months (Caffrey 1991). Evidence of the identity of predator species came from observed attacks, predator feathers found in association with

depredated nests and carcasses, and the remains of crows found in pellets and below predator nests.

To determine whether crows recognize calls of their two primary predators, we conducted playback experiments using recordings (Cornell Laboratory of Ornithology) of each predator species (*B. virginianus*, *B. lineatus*) and as controls (recordings from J. Macedonia), the call of the Madagascar harrier hawk, *Gymnogenys radiatus*, and the song of the wood thrush, *Hylocichla mustelina*; for each species, recordings from three individuals were obtained, but playback trials consisted of only one exemplar (Fig. 1). Crows in Encino will have had no experience with either species, as they do not occur there. The call of *G. radiatus* is of particular interest as a control because although it is spectrally similar to the call of *B. lineatus* only *B. lineatus* is a threat to this crow population.

We conducted playbacks over a period of 6 days between 1200 and 1600 hours at five acoustically separated locations on the site; young had already fledged by the time our playbacks were conducted. Calls were broadcast from an AR-572 Powered Partner speaker placed 3–5 m up into a tree, approximately 15 m from the cassette-recorder (Sony TCD-5M), and 15–25 m from the crows. To recruit crows to the playback area, peanuts were thrown on the ground. As soon as two or more individuals arrived and began feeding, we waited 30 s and then initiated a 30-s playback presentation. We recorded the number of individuals present just prior to the playback, the number and direction of individuals flying away within 30 s of the playback, and the number exhibiting flight intention movements (an unambiguous posture involving crouching with wings prepared for flight and momentarily freezing). We conducted a total of 22 playback trials,

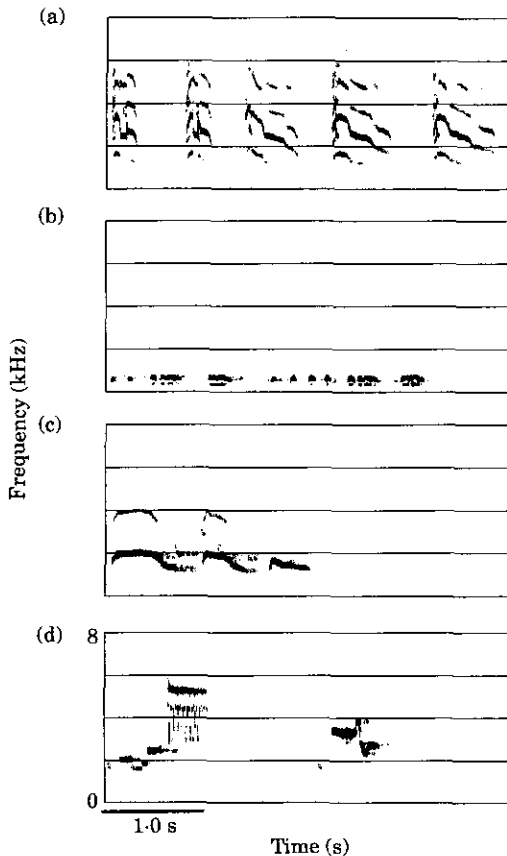


Figure 1. Spectrograms of exemplar calls from two crow predators: (a) red-shouldered hawk and (b) great horned owl; and two non-predators: (c) Madagascar harrier hawk and (d) wood thrush used in playback experiments.

including seven with *B. lineatus*, seven with *B. virginianus*, three with *G. radiatus* and five with *H. mustelina*. The number of individuals present during a given trial ranged from four to 17 ($\bar{X} \pm \text{SD} = 10.8 \pm 0.8$). No playback site was used more than once on a given day with a particular stimulus exemplar; in addition, when two playbacks were conducted at a site on one day, one trial involved a predator call and the other trial involved a non-predator call. Although most individuals tested were banded, and thus recognized individually, we cannot rule out the possibility that some unbanded individuals were tested in more than one trial. However, the probability of repeated tests on the same individual was low because trials were conducted in different locations.

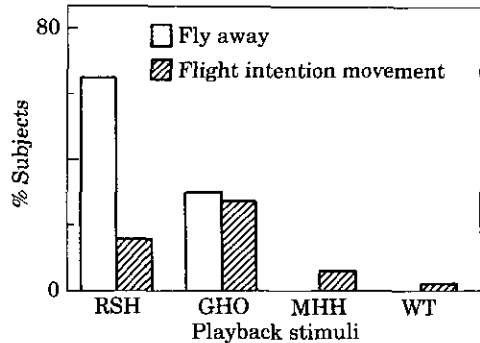


Figure 2. The mean proportion of subjects taking flight and exhibiting flight intention movements in response to the four playback stimuli: RSH: red-shouldered hawk; GHO: great horned owl; MHH: Madagascar harrier hawk; WT: wood thrush.

In response to calls of *B. virginianus*, and particularly *B. lineatus*, subjects often took flight (Fig. 2). Subjects never left the ground in response to *G. radiatus* and *H. mustelina*. The proportion of individuals taking flight in response to *B. lineatus* and *B. virginianus* differed ($t = 1.67$, $df = 13$, $P = 0.0001$). Moreover, whereas all subjects flew away from the speaker in response to calls of *B. lineatus*, 86.5% of all individuals that took flight in response to *B. virginianus* flew towards the speaker, with four individuals actually alighting in the tree next to the speaker, giving alarm calls.

Subjects that remained on the ground often responded to playbacks with flight intention movements. A greater proportion of individuals exhibited such movements in response to the predator calls than to the non-predator calls ($t = 2.41$, $df = 20$, $P < 0.03$).

Our results indicate that members of the Encino population of western American crows recognize at least one call from two of their major avian predators. This recognition system is based on fine-grained perceptual distinctions, as evidenced by the lack of an overt response to the Madagascar harrier hawk call which is spectrally similar to the call of the red-shouldered hawk. Moreover, the difference in their reactions to the calls of these predators reflects adaptive responses. Crows flew away from the call of the red-shouldered hawk, a diurnal predator posing an actual threat to foraging crows, especially young individuals. Although we were unable to make sufficiently rapid identifications of immature and

adult crows during our tests, it would be interesting for future experiments to examine how the observed anti-predator responses develop over time. Crows flew towards the source of the great horned owl call, a nocturnal predator that under natural conditions is mobbed if found roosting in a tree during the day; landing near the speaker and vocalizing may therefore have represented a mobbing response to the owl playbacks. Results from our playback experiments, together with other studies of anti-predator behaviour (Cheney & Seyfarth 1990; Hauser & Wrangham 1990), suggest that differentiated prey responses co-evolve with predator-specific hunting strategies.

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REFERENCES

- Caffrey, C. 1991. Breeding group structure and the effects of helpers in cooperatively breeding western American crows. Ph.D. thesis, University of California, Los Angeles.
- Caffrey, C. 1992. Female-biased delayed dispersal and helping in American crows. *Auk*, **109**, 609-619.
- Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: Chicago University Press.
- Endler, J. A. 1991. Interactions between predators and prey. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 169-202. Oxford: Blackwell Scientific Publications.
- Hauser, M. D. & Wrangham, R. W. 1990. Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. *Ethology*, **86**, 116-130.
- Rowe, M. P., Coss, R. G. & Owings, D. H. 1986. Rattlesnake rattles and burrowing owl hisses: a case of acoustic Batesian mimicry. *Ethology*, **72**, 53-71.