



Wild American crows gather around their dead to learn about danger



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While a growing number of animals demonstrate avoidance of areas associated with conspecific death, the extent to which wild populations may use these experiences to learn about novel predators remains unclear. Here we demonstrate with experiments that wild American crows, *Corvus brachyrhynchos*, respond to dead conspecifics by mobbing, increasing the time to approach food in areas associated with these events, and learning new predators based on their proximity to dead crows and hawks. Avoidance of either dead conspecifics or areas associated with them is not shared by another urban bird, the rock pigeon, *Columba livia*. Crows mobbed and increased the time to approach food over the next 72 h after observing novel humans paired with a dead crow, a red-tailed hawk, *Buteo jamaicensis*, or a hawk with a dead crow. The sight of a dead pigeon did not elicit these responses. These findings suggest that, for crows, dead conspecifics, but not dead heterospecifics, represent a salient danger akin to the observation of a predator. On the day the stimulus was presented, the number of trials that resulted in mobbing and avoidance of the food was strongest when crows were presented a hawk with a dead crow. In addition, we demonstrate that crows use the proximity of a human to predators, to dead conspecifics and to predators with dead conspecifics as cues to learn to recognize and subsequently scold the associated human after only one training event, and that this association can last 6 weeks. Together, our results support previous findings that crows learn places associated with conspecific death, and further demonstrate that crows can learn and remember people who appear complicit in these events.

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Animals can reduce their risk of predation by attending to cues in the environment such as predator odours (Eichholz, Dassow, Stafford, & Weatherhead, 2012), observations of predators (Cooper, 2005) and observations of predators with prey (Conover & Perito, 1981; Kruuk, 1976). Risk may also be communicated through conspecific and heterospecific alarms such as vocalizations (Shriner, 1998; Templeton, Greene, & Davis, 2005) and olfactory cues (Ferrari, Wisenden, & Chivers, 2010). In fish, these cues trigger area avoidance and increased shelter activity (Lawrence & Smith, 1989). Less is known, however, about the extent to which animals use visual remains of conspecifics as evidence of predation risk.

Humans place substantial significance on conspecific death (Tattersall, 1998), whereas few animals have been reported to show more than a passing interest. Black-billed magpies, *Pica hudsonia* (Miller & Bringham, 1998), western scrub-jays, *Aphelocoma californica* (Iglesias, McElreath, & Patricelli, 2012), chimpanzees, *Pan troglodytes* (Stewart, Piel, & O'Malley, 2012), African elephants, *Loxodonta africana* (Douglas-Hamilton, Bhalla, Wittemyer, &

Vollrath, 2006), and bottlenose dolphins, *Tursiops aduncus* (Dudzinski et al., 2003), are among those that congregate around or touch and groom dead conspecifics. The evolutionary basis for these behaviours in mammals remains unclear (McComb, Baker, & Moss, 2006). Emerging evidence suggests that, for some birds, these interactions are used to assess danger and trigger antipredator behaviours.

Wild common ravens, *Corvus corax*, and American crows, *Corvus brachyrhynchos*, mob in response to distress call playbacks paired with a dead conspecific and avoid areas where they are present (Avery, Tillman, & Humphrey, 2008; Peterson & Colwell, 2014). Western scrub-jays also mob in response to dead conspecifics, and they do so in the absence of artificial distress calls (Iglesias et al., 2012). Furthermore, following carcass removal, scrub-jays show reduced feeding activity in the area for 24 h. A similar effect was seen when scrub-jays were presented an upright-mounted great-horned owl, *Bubo virginianus*, suggesting that dead conspecifics are used as indirect evidence of predators. These behaviours were not observed in response to jay-like, novel objects or upright-mounted scrub-jays. A subsequent study showed that mobbing and area avoidance are also extended to sympatric and allopatric jay-sized heterospecifics (Iglesias, Stetkevitch, & Patricelli, 2014). Together,

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these studies suggest that dead conspecifics, and certain heterospecifics, can elicit learning and avoidance of places associated with death. What remains unclear, however, is whether the presence of dead conspecifics is an effective trigger to induce conditional learning of a novel predator in wild populations.

Through classical conditioning, naïve animals can learn about novel predators through exposure to an unfamiliar predator in association with conspecific alarm cues, such as odours or vocalizations, or by watching responses of knowledgeable individuals (Griffin, Blumstein, & Evans, 2000). These stimuli subsequently prompt antipredator behaviours such as mobbing (Curio, Ernst, & Vieth, 1978) and site avoidance, even at the cost of avoiding high-quality or abundant food (Lima & Dill, 1990). Fear can be extinguished, however, through repeated exposure to the conditioned stimulus without reinforcing its predictive value of the unconditioned stimulus (Myers & Davis, 2007). While brain-imaging studies suggest that captive American crows learn to recognize people associated with dead crows (Cross et al., 2013), it remains untested whether wild animals can use dead conspecifics to infer novel predators in the absence of alarm call playbacks. Understanding this potential, and its vulnerability to extinction, could inform management for both the reintroduction of naïve individuals, and as a means to create more effective 'scarecrows'.

Here, we add to previous studies by testing whether, as in scrub-jays, wild crows reduce feeding activity after only a brief exposure to a predator, to a dead conspecific or to a dead, similarly sized heterospecific. Furthermore, we expand by asking whether crows' interest in dead conspecifics facilitates learning of novel, threatening people and whether this knowledge is resistant to extinction. Lastly, we also determine whether another urban bird, the rock pigeon, *Columba livia*, uses dead conspecifics to assess risk. To test danger learning, we conducted three experiments on wild crows. In experiment 1, we examined (1) whether the sight of a dead conspecific is sufficient to elicit alarm calling and recruitment, or whether the presence of an unconditioned predator is also necessary, (2) whether crows learn areas associated with these dangers and subsequently avoid them, (3) whether crows use dead conspecifics to identify novel predators and, if so, how this process compares to conditioned learning when novel predators are paired with unconditioned stimuli (hawks), and (4) whether fear extinction can be achieved with a minimum of three additional exposures. For experiment 2, we determined whether a dead conspecific is a more salient source of dangerous information than a similarly sized, dead heterospecific. In experiment 3, we compared responses of rock pigeons and crows to dead conspecifics.

METHODS

General Information

We conducted the three experiments, consisting of three phases each (conditioning, stimulus presentation, post-exposure; Fig. 1), at sites in Washington, U.S.A. (in and around the cities of Seattle, Redmond, Kirkland and Bellevue, and Mercer Island; 47°34'9"–47°49'14"N, 121°33'13"–122°13'56"W). In our study area, crows live on small (25–150 ha) territories as pairs or small families (Marzluff, McGowan, Donnelly, & Knight, 2001). We assumed that no more than two adult birds occupied each territory, as helping behaviour occurs infrequently in crow populations in the northwestern United States (Verbeek & Butler, 1981).

A single observer and data collector (K.N.S.) provided food at a consistent location at roughly the same time daily throughout all phases of each experiment. Crows received a 2:1 mix of raw, unshelled peanuts and cheese puffs. Pigeons received a 2:1 mix of birdseed and crumbled white bread. After providing food, the

observer monitored the food pile from 15–25 m away, for up to 2.5 h, and measured the birds' latency to approach within 2 m of the food pile ('food discovery time').

Conditioning phase

Once the birds at each site approached the food within the 2.5 h observation period for 3 consecutive days (in most tests, birds met the criterion in 3 days; in seven tests, birds took up to 10 days to meet the criterion), we began the stimulus presentation phase on the following day (day 4).

Stimulus presentation phase

During the stimulus presentation phase, we provided food as normal, after which a volunteer exposed an experimental or a control stimulus 2 m from the food pile (see below). Volunteers wore one of six realistic facemasks with neutral expressions (to preclude contaminating effects of facial expression; see Figure 1b in Marzluff, Walls, Cornell, Withey, & Craig, 2010) and a white sign around their neck that read 'UW CROW STUDY' to limit interruptions by pedestrians or police. During stimulus presentation, the data collector recorded instances and durations of scolds and typical crow contact calls, and the number of birds present within 25 m of the stimulus. We define mob formation as the presence of more than two scolding individuals within 25 m of the stimulus. We calculated mob size as the maximum number of individuals present during the stimulus event. Because mobs are highly mobile and most birds were not individually marked, we did not determine whether all individuals within a mob actively scolded beyond the three-bird minimum. The volunteer removed the stimulus 30 min after the first bird perched within 25 m of the stimulus and was observed gazing towards the experimental set-up ('stimulus discovery time'). Following stimulus removal, for up to 2.5 h, the observer recorded the birds' latency to approach within 2 m of the food pile ('food discovery time'). We removed all but a small amount (five pieces) of food after 2.5 h. If birds approached the pile in the presence of the stimulus, we recorded the food discovery time as 0 s. The observer used plumage, profile, voice and mouth lining to discriminate between hatch-year and older birds (dos Anjos, Debus, Madge, & Marzluff, 2009; Emlen, 1936). Only birds older than 1 year of age were counted for stimulus discovery time, food discovery time and mob or group size.

Post-exposure phase

During the post-exposure phase, on days 5–7, we split the experiment into two trial types: A and B. In trial type A, we continued to provide food (as described above) to test for site aversion. In trial type B, following standard feeding by the observer (as during conditioning), a volunteer wearing the same mask as seen during the stimulus exposure phase arrived and stood 2 m from the food pile. The experimental procedure during test trial B otherwise matched that of the stimulus exposure phase, allowing us to test for novel predator learning and to evaluate the influence of varying levels of exposure to danger on fear extinction. Only experiment 1 used both trial types. Experiments 2 and 3 used trial type A during the post-exposure phase.

Ethical Note

No animals were trapped or handled during the course of this study and any marked individuals were banded 5 years before the onset of the present experiment. Experimental locations were established 35–45 m from nest sites to limit nest disturbance. All procedures were approved by the Institutional Animal Care and Use Committee of the University of Washington (IACUC; protocol number 3077-01).

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