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Lasting recognition of threatening people by wild American crows

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While many domestic and laboratory animals recognize familiar humans, such ability in wild animals is only anecdotally known. Here we demonstrate experimentally that a cognitively advanced, social bird, the American crow, *Corvus brachyrhynchos*, quickly and accurately learns to recognize the face of a dangerous person and continues to do so for at least 2.7 years. We exposed wild crows to a novel 'dangerous face' by wearing a unique face mask as we trapped, banded and released 7–15 birds at five sites near Seattle, WA, U.S.A. After trapping, crows consistently used harsh vocalizations to scold and mob people of different sizes, ages, genders and walking gaits who wore the dangerous mask, even when they were in crowds. In contrast, prior to trapping, few crows scolded people who wore the dangerous mask. Furthermore, after trapping, few crows scolded trappers who wore no mask or who wore a mask that had not been worn during trapping. In a fully crossed, balanced experiment in which each site had a unique trapping (dangerous) mask and five neutral masks, crows scolded and mobbed a mask more when it was the dangerous mask at that site than when it was a neutral mask at another site. When simultaneously presented with a person in the dangerous mask and a person in the neutral mask, crows typically ignored the neutral mask and followed and scolded the person wearing the dangerous mask. Risky, aggressive scolding by crows was sensitive to variable costs across study sites; aggression was less where people persecuted crows most. We suggest that conditioned and observational learning of specific threats may allow local bird behaviours to include aversions to individual people.

Many animals recognize individual members of their own species using well-developed acoustic, olfactory and visual cues (Wilson 1975). These abilities have fitness benefits such as guiding preferential care of mates and kin (Marzluff & Balda 1992), reducing costly displays and fights with familiar competitors (Brooks & Falls 1975), and maintaining stable social bonds (Barnard & Burk 1979). While the benefits of recognizing members of one's own species are obvious, the benefits of recognizing individuals of a different species are less clear. For example, recognizing another species' general, rather than individually distinct, alarm calls may be sufficient to lower the risk of predation (Templeton & Greene 2007). However, for animals that have close associations with individuals of another species, heterospecific individual recognition may be advantageous. This may explain why domestic animals, from honeybees to pigeons, recognize familiar human faces (Herrnstein & Loveland 1964; Peirce et al. 2001; Dyer et al. 2005; Adachi et al. 2007) and why in research settings, primates and other nondomestic animals appear to associate specific people with past experiences (Ristau 1983; Davis 2002; Levey et al. 2009).

As science turns its lens towards processes in cities, towns, farms and other human-dominated environments, we are learning that humans and nature have strongly coupled mutual interactions (Liu et al. 2007) that may favour the evolution of human recognition by animals (Levey et al. 2009). Familiar birds like crows, for example, routinely encounter hundreds of people but appear to recognize individuals who feed or harass them. Pioneering ethologist, Konrad Lorenz (1952) reported that hooded crow, *Corvus cornix*, recognized and mobbed a man who often walked with a tame crow perched on his shoulder. Apparently wild crows saw the tame crow as 'being carried by an enemy' and later recognized and harassed the man wherever they saw him, whether the tame crow was with him or not. Lorenz was so convinced of crows' abilities to recognize people and hold a grudge, that he wore a devil costume when banding a close relative, the jackdaw, *Corvus monedula*, a practice only slightly modified by raven, *Corvus corax*, researchers on the North Slope of Alaska, U.S.A., who disguise their appearance to increase their chances of recapturing study animals (Rozell 2007). Such precautions appear warranted, as common ravens and American crows that we captured and banded appeared exceptionally alert

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and occasionally directed alarm calls at us when we approached them after banding, but ignored our colleagues who had not harassed them previously (Marzluff & Angell 2005). Recognizing benevolent people also occurs. In Bellevue, Washington, U.S.A., a woman who routinely fed crows nearly lost her job as a bus driver because the birds would pick her out of a crowd and follow her far from her home for food (Singer 2003). Because corvids are cognitively advanced (Emery & Clayton 2004), capable of individual (Bednekoff et al. 1997) and social learning (Fritz & Kotrschal 1999), and often live closely with people who hold strong positive and negative attitudes towards them (Marzluff & Angell 2005), it seems likely that they may develop the ability to recognize specific humans.

We have taken a functional perspective towards studying ecologically relevant, conditioned responses (Domjan 2005). To assess experimentally wild crows' abilities to recognize a person's face, we paired a threatening experience (being trapped for routine banding; the unconditioned stimulus) with a particular face (a conditioned stimulus with natural connection to the unconditioned stimulus) and then observed the response of crows to subsequent encounters with that face. We used commercially available and custom-made, rubber masks that covered our entire head (Fig. 1) so that a 'dangerous' (mask used for trapping) and a 'neutral' (mask not used for trapping) face could be presented to crows on demand and by people of various morphologies and knowledge about the experiment. Our use of masks, while standardizing some unique facial aspects such as expression, allowed us to gauge the response of crows to a single consistent aspect of a human (face) regardless of random variation in other physical (body size and shape), cultural (dress) and mechanical (walking gait, demeanor and posture) human qualities. We devised three experiments that involved five distinct populations of crows in the Seattle, WA, U.S.A., area.

METHODS

Ethical Note

All crows were trapped, handled and marked using devices and protocols consistent with Gaunt et al. (1997), and supported by the United States Bird Banding Laboratory (permit 22489) and the University of Washington Animal Care and Use Committee (protocol 3077-01). We purposefully trapped a small number of birds at each site, conducted all experiments in the wild rather than in captivity, limited our trials to either once per day for a few months (experiments 2, 3), or infrequently for a longer time period (experiment 1), and only marked birds using leg bands (including colour bands that did not reinforce coloration known to be associated with status) to minimize long-term stress on the crows. We did not measure stress during the actual capture and handling, but acted to minimize it by trapping on soft natural surfaces, immediately removing all birds from the net upon capture and placing them in confining and calming socks when they were not being handled, and marking, measuring and releasing birds as quickly as possible. We took no blood, feather or tissue samples from any birds.

Study Species, Long-term Research and Study Sites

American crows in our study area live as pairs or small family groups on territories of 25–150 ha (Marzluff et al. 2001). Territorial birds flock at local food bonanzas (feeders, infested lawns, road kill and rubbish) throughout the year, and small groups of 5–15 nonbreeders are common, especially in autumn and winter. Large flocks are exceptional, except early and late in the day as birds commute to large communal roosts. The population has increased dramatically over the last four decades and has not been reduced by West Nile virus (Pecoraro et al. 2007).

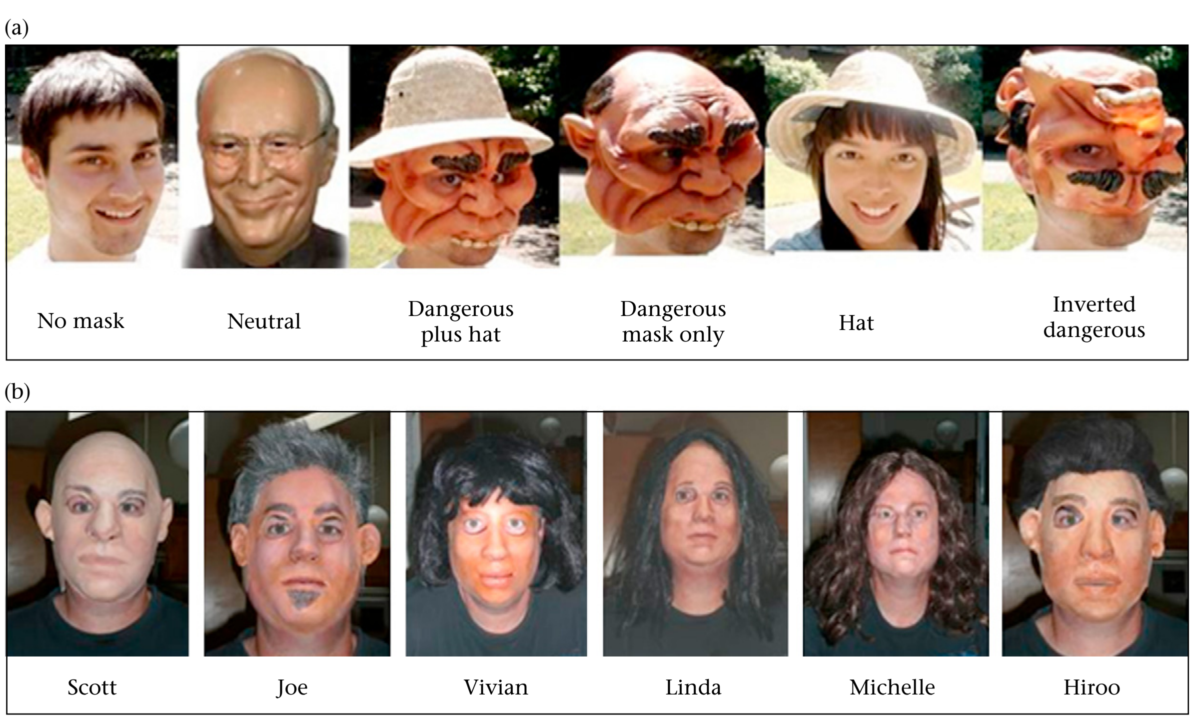

Figure 1. (a) Treatments for experiment 1, from left to right: no mask, neutral mask, dangerous mask plus hat, dangerous mask alone, dangerous hat alone, and inverted dangerous mask. (b) Treatments for experiment 2 and 3. Each of the first four masks (from left) was used in a single site as the dangerous mask; the last two masks (from right) were always neutral masks. These masks were custom-made by taking moulds from three males and three females, half of Asian descent and half of European descent.

We have studied crows in the Seattle area since 1997. Our focus has not been to trap and tag every animal, or to follow each breeding attempt precisely as is needed for a long-term demographic study. Instead, the intensity of our research has ebbed and flowed as we studied general population and behavioural responses to urbanization (Hepinstall et al. 2008; Withey & Marzluff 2009), dispersal (Withey & Marzluff 2005), and the role of crows as nest predators (Marzluff & Neatherlin 2006; Marzluff et al. 2007). During the course of these studies, we routinely trapped, handled, measured and marked crows in downtown Seattle, the nearby University of Washington campus, and more distant, less populated neighbourhoods. For the experiments reported here we worked within some of these study areas (at three sites), and because previous trapping may have influenced our current results, we also initiated new research in two areas (at two sites), as follows. (1) The University of Washington (UW) main campus, where we studied crows from 1997 to 2004, regularly capturing and banding nestlings and free-flying older birds (number of nestlings/number of independent breeders and nonbreeders tagged per year starting in 1997: 0/74, 9/65, 13/11, 9/19, 16/32, 11/4, 6/19, 4/23). At the start of experiments (2006), approximately 15% of the campus population was uniquely colour-banded from these previous efforts. No birds had been captured for 1 year before experiments began. (2) Freeway Park in downtown Seattle, WA, 5.5 km southwest of UW, where we studied crows for 2 years, capturing and banding seven individuals (3 nestlings in 2002; 4 breeding adults in 2004). In 2008, approximately 20% of the population was banded. (3) Maltby, WA, a suburban area 22 km northeast of UW characterized by extensive second-growth coniferous forest and patchy development. We captured and banded crows here from 1997 to 2003 (number of nestlings/number of independent breeders and nonbreeders tagged per year starting in 1997: 0/9, 15/4, 16/22, 10/9, 2/17, 7/5, 0/4). In 2008, 60% of the population was banded and no trapping had been done for 5 years. (4) Magnuson Park, a dense subdivision 3.5 km east of UW with no prior crow research. (5) Bellevue, a dense urban settlement 9 km east of UW with no prior research.

Experiment 1: Recognition of an Extraordinary Face

Two trappers wore identical 'caveman' masks and straw hats ('dangerous mask plus hat'; Fig. 1a) and fired a net launcher at small foraging groups of wild crows during 8–12 February 2006 in four locations on the University of Washington campus. During these capture attempts, seven birds were caught (three others were present but avoided the net), uniquely colour-banded, and released within 20 min. Trappers wore masks and hats during the entire banding process and were visible to the birds being banded and to birds in the immediate area; groups of 10–30 crows from the campus population ($\sim$5–15% of the entire resident population) circled the trappers and gave harsh alarm vocalizations ('scolding') from a height of 10–30 m for 5–10 min immediately after the trappers deployed the net. Based on plumage (outer rectrices narrow and pointed, plumage often brown and worn in young birds relative to adults; Emlen 1936) and colour of the mouth lining (black in mated pairs and proximally to completely pink in young birds), we captured four adult (after second year of life) and three younger independent (a mix of juvenile, yearling, and less dominant birds in the second year of life) crows. After releasing the banded birds, trappers removed masks when inside a nearby building. Prior to these experiments no birds had been trapped by people wearing a mask.

To survey the responses of the crow populations at each site to people with and without masks, before and after capture, observers surveyed crows and their responses to themselves as they slowly walked a 2.5 km long route for 1–2 h that included the trapping sites and intersected 20–30 crow territories. Observers randomly wore no mask, a previously unseen neutral mask, or one of four variants of the dangerous mask during each survey (Fig. 1a) opportunistically over the 2.7-year experiment. Pretrapping trials of the dangerous and neutral mask were conducted by three people immediately before trapping (25 January 2006–7 February 2006). Pretrapping trials of no mask were done during the same time period, but only by two people who had not captured crows at the site for the past 3 years.

Surveys were done from 1 h after sunrise until midday when people were normally active at the site. Wearing a mask, observers walked in crowds of people while crows were breeding, not breeding, tending recently fledged young, foraging alone on their territories or foraging in mixed groups outside of territories. During surveys, which were limited to no more than one per day, observers paused briefly to look at each crow encountered and categorized its behaviour either as 'scolding' (harsh, alarm 'kaw' directed repeatedly at the observer, and accompanied by agitated wing and tail flicking; Yorzinski & Vehrencamp 2009), or as 'otherwise'. To reduce object-specific recognition, observers carried a small notebook, which concealed a micro-audio/video recorder for all trials, but they did not use binoculars. During each survey, observers selectively approached three to five crows while the crows were foraging on the ground and they recorded vocal (as above) and locomotory (flee, approach, or neutral) responses, including the minimum flight distance between each focal crow and the observer.

All trials were conducted by the authors, except for 10 replications of four treatments (no mask, neutral mask, dangerous mask, inverted dangerous mask) that were done by naïve, 'blind' observers during July–December 2006. 'Blind' observers either had no prior experience, or had moderate prior experience observing crows, did not know the experimental objectives, and were unaware that masks were used previously in the study area. They listened to recorded calls of scolding crows, learned about basic crow behaviour, and were instructed how to survey crows using our methods to determine crow identity (band combination), scolding frequency and behavioural response. They were given a map and then simply told to walk a route while wearing each mask in a specified, random order, and to record the crows' responses. To minimize the effect of interindividual variation, possibly due to varying experience with crows, we analysed the treatment-specific responses of crows as a randomized, balanced, repeated measures experiment ($N = 10$ observers; 40 trials). To standardize variation in the absolute number of crows encountered over the several years of observation at UW (mean of 77 surveys = 26.5 crows, range 7–84), we present the percentage of crows that scolded during each survey in addition to the absolute number of scolders. In all cases percentages were transformed (arcsine square root) prior to analysis to increase normality (transformation was successful: maximum kurtosis/SE <0.57).

Experiment 2: Recognition of Ordinary Faces

As in experiment 1, we paired a negative experience (trapping) with a particular human face, and surveyed the response of crows to dangerous and neutral faces during standard surveys before and after trapping. Experiment 2 began in 2007 and differed from experiment 1 in the type of mask (custom-made for these experiments from real people; Fig. 1b) and research sites (Freeway Park, Maltby, Magnuson and Bellevue, described above).

At each site, two trappers wore identical masks and a red cloth armband as they captured 6–15 crows during 1 day ($N = 3$ sites) or 2 days ($N = 1$ site) of trapping at two to four locations per site. A

different mask was used during trapping at each site, but each mask was tested at every site, including two masks that were never used for trapping. Pretrapping trials of the dangerous mask, of each neutral mask and of no mask were conducted by two people in the month immediately before trapping.

Captured birds were colour-banded and released within 20 min, during which time groups of five (Maltby) or 20–40 (other sites) crows circled and gave scolding vocalizations from a height of 10–30 m. The ratio of adult to younger crows captured at each site was 5:1 (Freeway Park), 8:7 (Maltby), 9:5 (Magnuson) and 4:2 (Bellevue). Prior to this experiment, no birds had been trapped using masks at any of these sites. We also had not previously conducted any research at Bellevue or Magnuson. We had captured and banded 70 breeding and nonbreeding independent birds and 50 nestlings at Maltby and four breeding adults and three nestlings at Freeway Park prior to experiments (see above for years and effort/year).

After trapping at each site, 10 observers who were blind to our trapping activity donned one of six masks (Fig. 1b) in random order and scored crow responses along 3.8 km (Freeway Park), 2.3 km (Maltby), 3.6 km (Magnuson) and 3.6 km (Bellevue) long survey routes. Half of the masks (the dangerous mask and the most and least similar neutral masks based on gender, race and hair of the wearer) were worn twice within the random sequence; once with the red armband used during trapping and once without the armband. This resulted in 90 trials per site (one per day). Masked participants self-reported their gender, race, weight and height, and wore clothing of their own choice. The authors verified responses at these sites by: (1) conducting separate trials; (2) following each blind observer on two trials and independently scoring responses; and (3) reviewing videotapes and spectrographically analysing audiotapes. Blind observers varied in their accuracy, and tended to underestimate the scolding response of crows to the dangerous mask (correctly identifying calls as scolds to masks used for trapping in 53% of a random sample of 807 calls versus 75% correct identification of 1537 calls to masks not used for trapping; Fisher's exact test statistic = 122, $df = 1$, $P < 0.001$). This bias is conservative, relative to our hypothesis.

We used a completely randomized, fully crossed design in which each site had a unique trapping (dangerous) mask and five neutral masks. Because two neutral masks and the dangerous mask were worn twice to test the effects of the red armband, there were nine repeated measures for each of 10 independent observers at each site. We analysed these responses with a two-factor (site, mask, site × mask), repeated measures ANOVA. Because surveys were done within a few months during the nonbreeding season, when consistent numbers of birds were encountered along each route, we analysed the absolute number of crows scolding and the number of scolding groups (>2 crows scolding = 'mob'). Only a few independent (1–6) scolding mobs could be assembled during any single experiment; mobs would follow masked observers, thereby reducing the number of unique mobs that could form during the limited course of the survey route. However, despite the low average, the distribution of mobs per mask per site was normal (range of kurtosis/SE = −0.92, 1.5).

Experiment 3: Discrimination among Faces

In experiments 1 and 2 crows could choose to scold or ignore a single, masked person walking a set route. In experiment 3, we provided crows a choice between responding to either or both of two masked people encountered simultaneously. Two masked observers, one wearing the dangerous mask and the other a neutral mask, centred themselves in front of a perched crow within a territory where they had been reliably scolded during experiment 2. When the bird noticed them (typically by scolding), they walked apart approximately 50 m in opposite directions, paused for 1 min, returned to the starting point, paused, crossed and walked in the opposite direction, paused, returned, paused, and crossed a second time before returning to the starting position to end the trial. A third person, blind to the identity of the dangerous versus neutral mask, filmed and scored the intensity of the response by the bird (1 = no response; 2 = looking at person; 3 = looking and scolding person; 4 = scolding and following person as they walked). We conducted 44 trials, each of which presented a unique pair of masks to crows in a specific territory (site 1: 11 trials in 2 territories; site 2: 10 trials in 2 territories; site 3: 6 trials in 1 territory; site 3: 17 trials in 3 territories).

RESULTS

Experiment 1: Recognition and Long-term Memory of an Extraordinary Face

Crows responded strongly and consistently to the dangerous mask of the trappers. The percentage of crows giving scolding vocalizations to people wearing all variants of the dangerous mask increased after trapping (Fig. 2). Prior to trapping, less than 5% of the crows scolded people with masks ($N = 15$ trials). After trapping, a similar proportion of crows scolded observers when they wore no mask or the neutral mask, but an average ± SE of 8.3 ± 1.0 birds ($N = 33$), or 20–40% of those observed, scolded when observers wore any variant of the dangerous mask (overall ANOVA: $F_{8,24} = 12.7$, $P < 0.0001$). Scolding of the dangerous mask alone, the dangerous mask with the hat, and the dangerous mask worn upside down ('inverted') was similar after trapping ($P > 0.19$ in all post hoc LSD comparisons). Response to the dangerous hat alone after

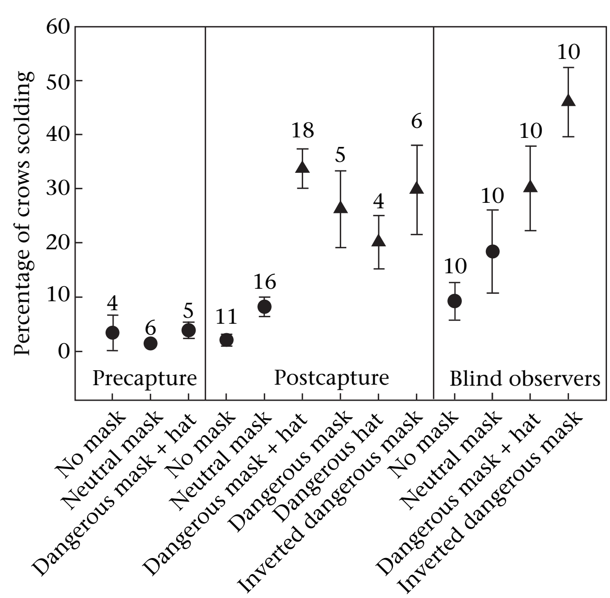

Figure 2. Mean ± SE proportion of wild crows that directed harsh 'kaw' vocalizations (scolding) at people wearing a variety of masks. The far left panel shows responses before the negative stimulus of trapping by people wearing the dangerous mask plus a hat. The centre panel shows responses for the first 1.5 years post-trapping. All observations in the left and centre panel were made by the authors and were considered to be independent (N = number of trials, indicated above error bar), as they were conducted in random order on different days under a variety of biological (e.g. breeding and nonbreeding season) and ambient conditions. Observations in the right panel were done post-trapping by naïve people using a randomized, repeated measures design (N = number of observers, indicated above error bar). Responses to variants of the dangerous mask after trapping (triangles) are distinguished from those in control (circles) situations.

trapping was significantly less than that to the dangerous mask and hat (post hoc LSD: $P = 0.03$) and only slightly greater than the post-trapping response to the neutral mask (post hoc LSD: $P = 0.07$). Responses to no mask or the neutral mask were similar before and after trapping (post hoc LSD: $P = 0.84$ and 0.22, respectively). Minimally trained observers, who were blind to the study design and objectives, confirmed significantly greater scolding responses to the dangerous mask worn with the hat or inverted relative to the neutral mask or no mask (repeated measures ANOVA $F_{3,7} = 11.2$, $P = 0.005$; Fig. 2). Crows consistently scolded the dangerous mask when it was worn by different people who varied in gender (eight male, five female), race (10 white, two Asian, one Hispanic), age (20–48 years), height (155–190 cm), weight (45–100 kg), style of walking and approaching crows, and attire.

The percentage of crows scolding the dangerous mask increased rapidly immediately after trapping and continued to increase slightly for 2.7 years (Fig. 3a). On average, 26% of crows ($\bar{x} = 7.3$ individuals; Table 1) scolded the dangerous mask immediately after trapping. The prevalence of scolding increased steadily to 66% ($\bar{x} = 19.0$ individuals) at the end of observation (Fig. 3a; regression line: percentage scolding = 26.2 + 0.04 (day); $F_{1,33} = 10.7$, $P = 0.003$, $r^2_{adj} = 0.23$), and this response was not limited to the breeding season (Table 1). In contrast, few crows scolded the neutral mask through the first 1.5 years (Fig. 3b, Table 1). Overall, scolding of the neutral mask was consistently rare (Fig. 3b; regression line: percentage scolding = 12.2 + 0.005 (day); $F_{1,30} = 0.13$, $P = 0.72$, $r^2_{adj} = -0.03$); however, the largest average responses were recorded 600–993 days after trapping (Table 1).

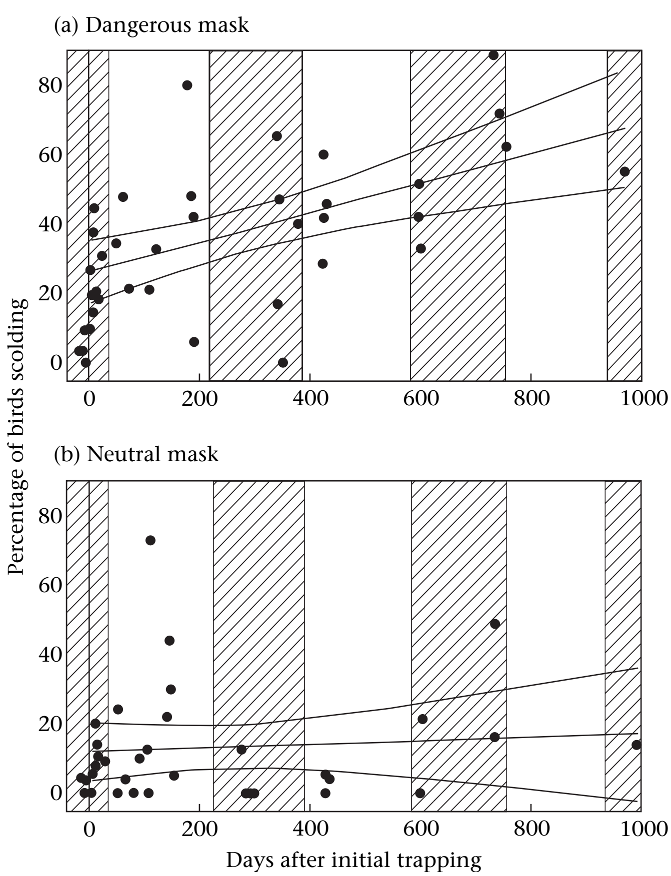

Figure 3. Scolding in response to (a) dangerous and (b) neutral masks through time by wild crows. Observations before and after trapping with the dangerous mask are separated by the vertical line at day 0. Nonbreeding (▨) and breeding (□) portions of the annual cycle are indicated. Least squares linear regression lines and 95% confidence intervals are provided.

Table 1
Mean ± SE number of crows scolding the dangerous and neutral masks on the University of Washington campus through time

	Mask worn by person	
	Dangerous	Neutral
Pretrapping (day −16 to −1)	0.83±0.31	0.33±0.21
Nonbreeding (day 4–27)	7.3±1.5	2.6±1.6
Breeding (day 49–194)	12.3±4.1	4.5±1.6
Nonbreeding (day 324–380)	10.0±3.6	0.5±0.5
Breeding (day 470–480)	8.3±1.0	0.7±0.3
Nonbreeding (day 600–993)	19.0±5.7	7.0±3.6

Experiment 2: Recognition of Ordinary Faces

Crows responded immediately to the brief, essentially single, negative trapping experience at each site. Scolding was extremely rare before trapping at all sites ($\bar{x} \pm SE = 0.1 \pm 0.10$ crows/survey; not different from a mean of zero: $t_{23} = 1.7$, $P = 0.10$). Scolding was greater immediately after trapping (8, 16, 19 and 5 crows scolded at the initial presentation of the dangerous mask on day 4, 4, 3 and 5 after trapping, respectively; all greater than the upper 95% confidence interval (0.37) around pretrapping responses).

Despite variation in observer dress, morphology and experience, the dangerous mask was scolded most frequently at all sites (Fig. 4a). Neutral masks were scolded, often substantially, at each site, but the dangerous mask was scolded significantly more than the neutral masks ($N = 1$–3 neutral masks/site) at each site (Fig. 4a). The formation of mobs (groups of 2–14 crows cooperatively scolding and following masked people) was especially indicative of dangerous masks (Fig. 4b). Mobs were formed significantly more around dangerous masks than nearly every neutral mask (Fig. 4b). Each of the four dangerous masks was scolded and mobbed more at the site where it was used for trapping than at the sites where it was used as a neutral mask (interaction of mask × site: scolding: $F_{9,108} = 2.2$, $P = 0.03$; mob formation: $F_{9,108} = 5.4$, $P < 0.001$). In contrast, scolding and forming mobs at the sight of the two masks that were neutral at all sites did not vary by site (site × mask interaction: scolding: $F_{3,36} = 0.63$, $P = 0.60$; mob formation: $F_{3,36} = 0.20$, $P = 0.90$).

The difference between the total number of birds scolding (Fig. 4a) and the formation of mobs (Fig. 4b) reflects the less discriminatory scolding of individual birds that did not attract others to form a mob. During the 10 trials per site, observers recorded at least one lone bird scolding each mask. Observations of single scolding birds were not especially common during trials involving the dangerous mask. At only one site (site 2, Bellevue) was the dangerous mask scolded most frequently by single birds (10 such cases versus at most 5 to any other mask). Across all trials there was no significant interaction between mask and site on the average occurrence of single birds scolding ($F_{9,108} = 1.7$, $P = 0.09$).

The amount of scolding directed at neutral masks was not related to apparent physical similarities between dangerous and neutral masks. Neutral masks could be of the same gender, race or hair colour as dangerous masks, but the total number of these features held in common was not consistently associated with the relative degree to which the neutral mask was scolded. The neutral mask that was most similar to the dangerous mask was scolded more frequently than the less similar neutral masks only at Bellevue, where the neutral mask was of the same race and gender as the dangerous mask. Across all sites, however, physical similarity of dangerous and neutral masks did not influence scolding of neutral masks (gender: $F_{1,36} = 0.002$, $P = 0.96$; race: $F_{1,36} = 0.79$, $P = 0.38$; hair colour: $F_{1,18} = 1.04$, $P = 0.32$).

Scolding responses were not equal among sites. There was a consistent effect of site on scolding that was robust to the site-by-mask interaction (scolding: $F_{3,36} = 3.0$, $P = 0.04$; formation of

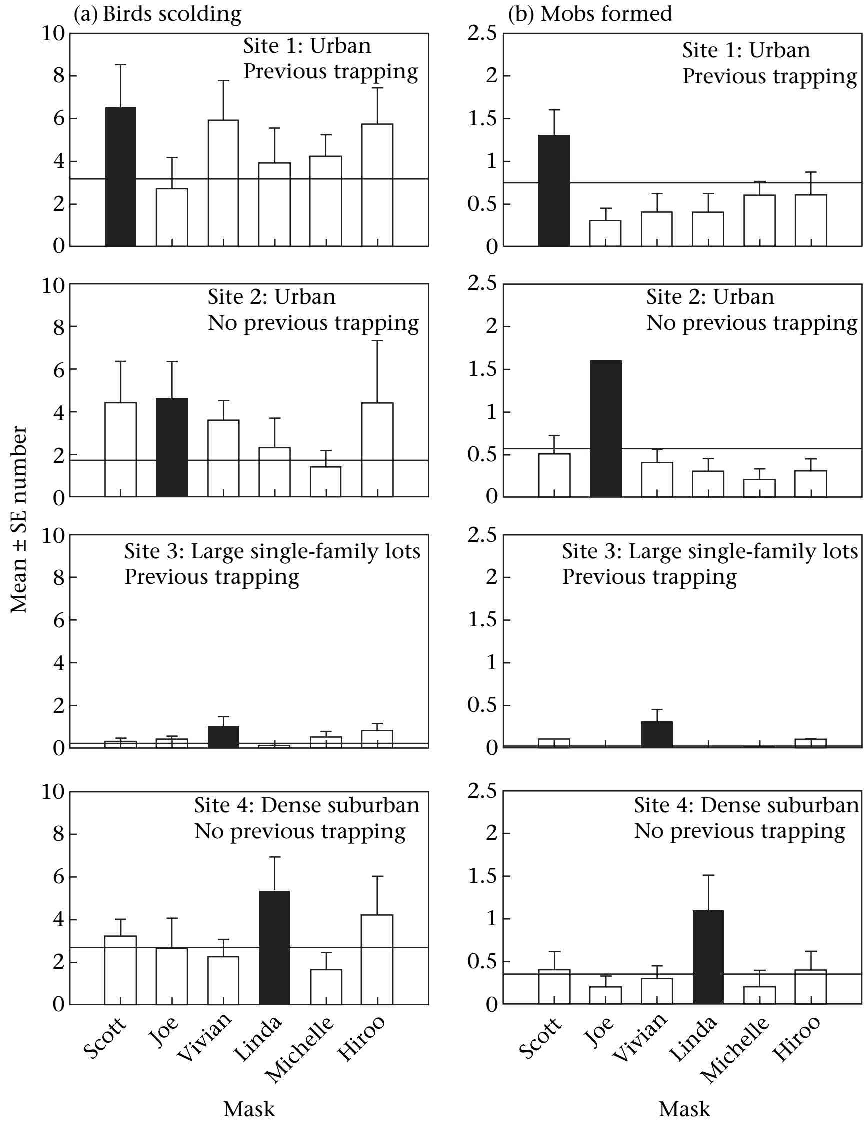

Figure 4. Mean + SE number of wild American crows that (a) scolded and (b) formed mobs in response to six masks at four study sites, as recorded by 10 observers at each site who were blind to the experimental design. ■: dangerous mask; □: neutral masks; horizontal line: 95% confidence interval of mean response to the dangerous mask.

mobs: $F_{3,36} = 2.5$, $P = 0.07$; Fig. 4). Site 3 (Maltby, see Methods) had extremely low rates of scolding and mobbing. While trapping at this site, few crows mobbed us. When we approached crows that were foraging on the ground or perched near the ground at this site, they also had the greatest average flight initiation distance ($\bar{x} \pm SE = 18.9 \pm 3.9$ m; $F_{3,39} = 13.2$, $P < 0.001$).

Presence of the red armband, used during trapping, did not affect crow responses after trapping. Of the three masks tested with and without the armband at each site (the dangerous mask, and the most similar and least similar neutral masks), the dangerous mask was scolded by the most crows ($F_{2,72} = 3.36$, $P = 0.04$), but there was no effect of the armband ($\bar{x} \pm SE$ number of crows scolding: person with armband: 8.6 ± 3.5; person without armband: 10.4 ± 3.9; $F_{1,36} = 1.57$, $P = 0.22$).

Experiment 3: Discrimination among Ordinary Faces

Crows accurately discriminated among simultaneously viewed neutral and dangerous masks. Regardless of site, crows responded strongly to the dangerous mask while typically ignoring the neutral mask. Crows scolded and followed the person with the dangerous mask 16 times, but scolded and followed the neutral mask only once (Fig. 5a). There were only four instances (9% of trials) where the crow responded most strongly to the neutral mask (permutation test statistic = 5.04, $P < 0.001$; Fig. 5b, negative values). In fact, the typical trial consisted of the crow either looking and scolding or scolding and following the dangerous mask while ignoring the neutral mask (Fig. 5b, values of 2 and 3, respectively).

DISCUSSION

Our study is unique in that we demonstrated rapid learning to a brief, single experience, long-term memory retention, and fine-feature discrimination between individuals of a different species in wild free-ranging birds. American crows in five distinct landscapes were able to recognize the facial qualities of people with whom they had prior experience. Consistent scolding by crows of a variety of extraordinary (experiment 1) and ordinary (experiments 2, 3) dangerous masks worn by human males and females, especially when worn without the hat or armbands used during trapping,

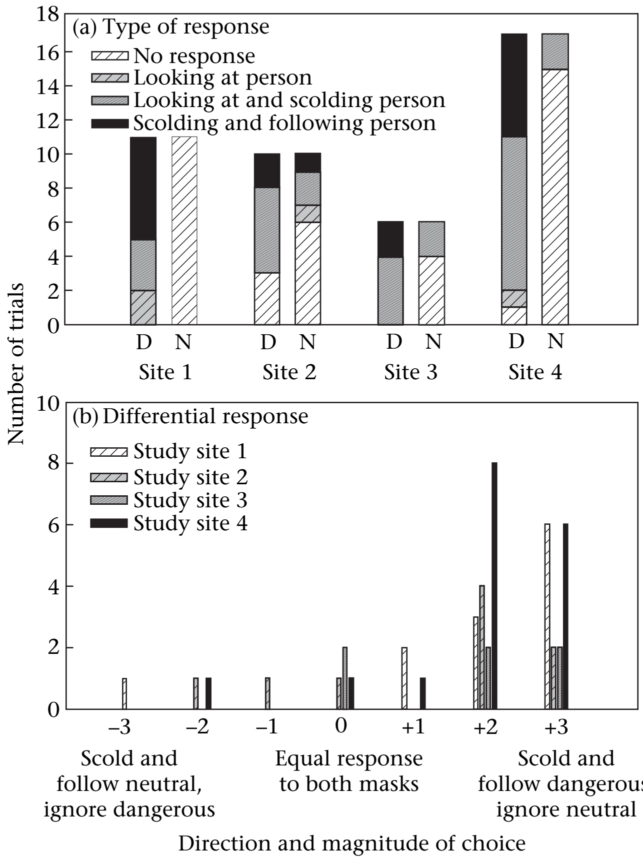

Figure 5. (a) Distribution of responses by wild American crows to 44 paired presentations of two people each wearing a different mask (one dangerous, D; one neutral, N) at four sites near Seattle, WA. (b) Differential responses of crows to two masked people during a choice trial, when each person walked away from the test crow in opposite directions, were scored as follows: 1 = no response; 2 = looking at person; 3 = looking and scolding person; 4 = scolding and following person as the person walked.

suggest that properties of the human face are recognized and remembered for long periods after only a brief negative experience. That the inanimate objects associated with the face (hat), but not the arm (band), triggered moderate responses also suggests that crows pay attention to people's faces, not other, typically variable, aspects of the human body, movement and attire. These abilities are adaptive for crows that exploit anthropogenic resources from people who may ignore, persecute or assist them.

The discriminatory abilities of crows may be exaggerated under the uncontrolled natural environment characterizing our experiments because scolding is an attractive signal that often stimulates unknowing individuals to join a mob and call. It is probable that our measure of the number of scolding birds (Fig. 4a) included birds that had actually learned to recognize the dangerous mask and those that had only been stimulated to join in the scolding mob. However, the number of mobbing incidents (Fig. 4b), a more conservative measure that is independent of size of mob, was less influenced by the confounding effect of social facilitation, and more indicative of crows' abilities to accurately discriminate among people.

Many of the scolding birds that appeared inaccurate in discriminating dangerous from neutral masks in experiment 2 were ineffective at stimulating a mob. These lone scolders may in fact be poor discriminators, or they may subtly indicate the threat posed by a particular person. Harsh crow calls assemble or disperse mobs (Frings & Frings 1957), and naïve observers could easily have incorrectly discerned among these calls, noting both as 'scolds'. However, it is also possible that crows scolded known dangerous masks with a call that assembled a mob while also scolding similar (masked) people in a less intense, or simply alarming, manner. Crow scolds vary in intensity, which may reflect predator threat (Yorzinski & Vehrencamp 2009). Ongoing analysis of calls recorded during our experiments will test these possibilities.

Our results are consistent with studies of fear conditioning and facial recognition by humans and other mammals. Whether 'expert' methods or specific neural cells, such as the fusiform gyrus (Peirce et al. 2001), are involved in facial recognition by birds is unknown, but they are suggested by these and previous studies on pigeons (Herrnstein & Loveland 1964). The one-trial learning and long-term memory we report are consistent with other findings on predator avoidance and fear conditioning (Griffin 2004). As in mammals, these learned responses may be facilitated by an amygdala with subnuclei that regulate behavioural expressions of fear (e.g. scolding and mobbing) and avoidance behaviours (e.g. increased flight distance), and is closely associated with a hippocampus that allows learning the spatial and temporal context of the cues associated with danger (Olsson & Phelps 2007; Adolphs 2008). Crows have large brains with a well-developed hippocampus (Emery & Clayton 2004; Marzluff & Angell 2005), but the occurrence of an avian homologue to the mammalian amygdala is unresolved (Butler & Cotterill 2006). That crows have complex responses to danger facilitated by facial recognition, learning and memory is consistent with structures, probably in the meso-, nido- or arcopallium, that have functions similar to those of the mammalian amygdala and fusiform gyrus, suggesting that crows would be an excellent candidate as a model study species for avian neurophysiology.

Recognition of individual people allowed crows across our study sites to adjust their behaviour relative to specific people at particular places by scolding and mobbing, or remaining distant from potentially dangerous people with a known history of trapping crows. Differential responses among study sites also suggested general crow population responses to site-specific threats. Crows were not especially discriminatory or responsive at sites where our previous research involved trapping or banding of nestlings (sites 1, 3; Fig. 4). Likewise, discrimination was equal at sites with dense human populations (sites 1, 2 and 4) and at the least populated site (site 3; Fig. 4). However, aggression (mobbing and scolding) was significantly reduced, and caution (reflected in lengthy flight initiation distances) was extreme at site 3 (Maltby). This relatively rural site bordered agricultural areas where crows had been hunted or actively persecuted by humans. Persecution in this study area resulted in two of our banded birds being shot during the course of experiment 2. Increased caution and reduced aggression in persecuted corvid populations are well known (Knight 1984; Knight et al. 1987).

The precise way that configurational cues are used in face recognition by birds and mammals appears to differ. Mammals, including older humans, are less able to recognize and remember familiar faces that are inverted (Yin 1969), but an upside down variant of the dangerous mask was accurately scolded by crows in experiment 1. Facial inversion may not confuse birds because they often see people from above and are able to correct for facial orientation by turning their head; for example, we observed crows turn their head completely upside down in response to the inverted dangerous mask in experiment 1. Crows, like pigeons (Jitsumori & Makino 2004), may also be capable of rotation generalization, the recognition of faces from a variety of novel viewpoints.

Crows also appear to generalize the apparent life-threatening danger of some people. This was evident in the apparent mistakes that crows made when scolding neutral faces in experiment 2, the slight elevation in scolding of the neutral mask 2 years after trapping in experiment 1, and the generally low level of scolding and large minimum flight distance at the Maltby study area (site 3).

Scolding of neutral faces (experiment 2) by crows that were clearly able to distinguish dangerous from neutral faces (experiment 3) has several explanations. Some mistakes may simply reflect inaccurate scoring of crow responses by naïve observers (see Methods). Audio and video recordings confirmed that observers underestimated scolding to the dangerous mask, but in all study areas, some crows scolded neutral masks. Facial recognition in people begins with the eye region, which is influenced by the brow, and rapid responses to eyes drive fear responses (Sadr et al. 2003; Adolphs 2008). In experiment 2, the eye region of our masks was variable; cutout portions allowed each observer's eyes to be visible. Corvids are attentive to human gaze (Bugnyar et al. 2004), so it is possible that because the same people wore neutral and dangerous masks at each site, the consistency in eyes between neutral and dangerous faces or the variability in eyes of the dangerous face, confused crows. However, in experiment 1, crows rarely responded to trappers without masks after trapping, despite being able to see the trappers' eyes during trapping. Perhaps the prominent brow of the mask in experiment 1 enabled more accurate discrimination, despite eye variability. Although the crows' mistakes that we documented may indicate individual variability in crows, they are also consistent with risk averse behaviour and object categorization, as expected when the costs of a behaviour are low but the benefits are high (Real & Caraco 1986; Jitsumori & Makino 2004).

Our procedures may have influenced our results in three ways. First, it is possible that the crows we trapped were especially bold (Biro & Dingemanse 2008) and therefore especially apt to scold in later trials. This is unlikely to bias our results because the majority of birds we recorded scolding were not previously trapped (H. N. Cornell, J. M. Marzluff & S. Peccorro, unpublished data). Second, our previous trapping and nest monitoring at the UW site may have increased the saliency of trapping and lowered the likelihood that scolding behaviour would be extinguished even years after trapping. However, the longevity of scolding after trapping ceased was more closely related to the uniqueness of the dangerous mask and the variety of people inhabiting each site than it was to our past research activity (H. N. Cornell, J. M. Marzluff & S. Peccorro, unpublished data). Third, our use of two trappers, each of whom wore identical masks, could have enforced 'stiff' or masked faces as generally dangerous. This may increase discrimination among faces and reduce the extinction of discrimination. While we did not formally monitor the responses of trapped crows to our faces in the early years of study when we did not use masks, both the intensity and the longevity of crows' alarm response to unmasked trappers were certainly less than those reported here to masked trappers. Controlled tests using unmasked trappers would clarify the degree of this effect.

Rapid learning and lasting memory of dangerous people is consistent with classical conditioning to stimuli indicative of biological danger, such as novel predators, parasites and pests (Kavaliers et al. 2003). A trapper holding a crow or sitting next to a crow that has been captured under a net, which may appear dead or distressed to flockmates, is an intense, salient and biologically significant stimulus. A trapper is thus a naturalistic, conditioned stimulus, which is quickly learned and immune to extinction in a variety of species (Domjan et al. 2004; Domjan 2005). The trapper, the net and the bird in distress are all related features of a dangerous object, which may further accelerate learning (Domjan 2005).

Recognition of humans may also be important in the development of close, personal bonds between particular crows and people (e.g. Lorenz and his jackdaws, the poet Poe and his raven, or the Kwakiutl shamans and their crows) that have influenced human culture for millennia (Lorenz 1952; Marzluff & Angell 2005). In this way, recognition of humans by crows is a mechanism that can support the mutual coevolution of human and animal cultures (Marzluff & Angell 2005).

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