THE EFFECT OF PREDATOR TYPE AND DANGER LEVEL ON THE MOB CALLS OF THE AMERICAN CROW

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Abstract. Flee-inducing alarm calls often communicate information about the type of predator and the danger associated with it. Less is known about how approach-inducing mob calls encode this information. We studied the mob calls of the American Crow to determine whether these calls convey information about the predator type or the level of danger by presenting a model owl (representing an avian predator) and raccoon (representing a mammalian predator). We found that crows emit the same types of vocalizations in response to both of these predator classes. Our results, however, suggest that calls with a longer duration, higher rate, and shorter interval between caws reflect a higher degree of danger. We also found significant differences in call structure from trial to trial, possibly reflecting variations in call structure among individuals or groups. The ability to encode specific information about urgency and individual or group identity while mobbing may be particularly important for efficient coordination of group activities in species—such as the American Crow—that live in stable social groups.

Key words: acoustic communication, alarm vocalizations, American Crow, call structure, Corvus brachyrhynchos, *mobbing, referential calls.*

Efectos del Tipo de Depredador y del Nivel de Peligro sobre las Llamadas de Asedio de *Corvus brachyrhynchos*

Resumen. Las llamadas de alarma que inducen la huida frecuentemente comunican información sobre el tipo de depredador y el peligro asociado con éste. Sin embargo, se conoce menos sobre como las llamadas de asedio que inducen el acercamiento codifican esta información. Estudiamos las llamadas de asedio de *Corvus brachyrhynchos* para determinar si estas llamadas proporcionan información sobre el depredador o sobre el nivel de peligro mediante la presentación de un modelo de lechuza (que representa un ave depredadora) y de un mapache (*Procyon lotor*, que representa un mamífero depredador). Encontramos que *C. brachyrhynchos* emite los mismos tipos de vocalizaciones en respuesta a ambas clases de depredadores. Sin embrago, nuestros resultados sugieren que las llamadas con una duración mayor, tasas mayores e intervalos más cortos entre llamadas, reflejan un mayor grado de peligro. También encontramos diferencias significativas en la estructura de las llamadas entre las pruebas; éstas pueden reflejar diferencias en la estructura de las llamadas entre los individuos o entre los grupos. La habilidad para codificar información específica sobre la urgencia y la identidad individual o grupal durante el asedio puede ser particularmente importante en las especies—como *Corvus brachyrhynchos*—que viven en grupos sociales estables, de manera de poder coordinar eficientemente las actividades del grupo.

INTRODUCTION

Animals threatened by an imminent attack from a predator may emit flee-inducing alarm calls (Bradbury and Vehrencamp 1998). These vocalizations often contain specific information about the type of predator (referential signaling) and the level of danger (urgency-based signaling) that helps the receivers respond appropriately. Referential signaling is often used by species that employ different escape tactics to avoid different classes of predators (reviewed in Fichtel and Kappeler 2002). In contrast, urgency-based signaling is often used by species that respond in the same qualitative manner to all predators but vary quantitatively in the probability or speed of response (Owings and Hennessy 1984, Macedonia and Evans 1993, Leavesley and Magrath 2005). It is likely that many alarm calls contain both referential and urgency-based information (Marler et al. 1992, Blumstein 1999b, Manser 2001).

Unlike flee-alarm calls that cause animals to disperse, mob calls cause animals to approach and gather around predators (Curio 1978). Compared to flee-alarm calls, less

is known about how mob calls encode information about predators. Several studies have shown that mob calls convey information about the level of danger associated with the predator (Cully and Ligon 1986, Zimmermann and Curio 1988, Naguib et al. 1999, Baker and Becker 2002, Templeton et al. 2005, Ellis 2008). To our knowledge, only one study has explored whether animals use their mob calls to communicate not only the level of risk but also the type of predator: Naguib et al. (1999) found that the mob calls of the Arabian Babbler (*Turdoides squamiceps*) encoded information about the danger of the predator but not the type of predator. More research investigating the association between structural variation in mob calls and specific contexts is needed to assess whether mob calls ever do encode information about predator type.

We studied the vocalizations of the American Crow (*Corvus brachyrhynchos*) during experimentally staged mobbing events. The American Crow is a cooperative breeder that spends much of its time in extended family groups. These groups usually include a single breeding pair, offspring from multiple broods, and immigrants (Kilham 1984, 1989, Caffrey 1999, McGowan 2001, Verbeek and Caffrey 2002). Family members defend a group territory, defend and feed dependent young, and guard each other while foraging together (Serrell 2003). The American Crow has a rich repertoire of calls with many modulations and intergradations associated with warning against and mobbing predators (reviewed in Verbeek and Caffrey 2002). Great Horned Owls (*Bubo virginianus*) and raccoons (*Procyon lotor*) are among the crow's greatest threats (Verbeek and Caffrey 2002).

The aim of this study was to determine whether crows have a referential or urgency-based communication system in the predator context. We presented crows with a model owl, representing an avian predator, and a raccoon, representing a mammalian predator. If crows rely on referential communication, we would expect them to use specific vocalizations for each predator class. If they rely on urgency-based communication, we would expect them to use the same types of vocalizations for both predator classes but vary them according to the perceived level of danger. To investigate whether the vocalizations change with the level of danger, we explored whether calls differ with the distance between the crows and the predators. If crows rely on both referential and urgency-based communication, we would expect them to emit specific vocalizations for each predator class and vary structural components of the vocalizations according to the level of danger.

METHODS

STUDY SITE AND MODELS

Our experiments, with the eastern subspecies of American Crow (*C. b. brachyrhynchos*), took place between 0700 hr and 1630 hr in the post-breeding season between September and December 2003 in Ithaca and Cayuga Heights, New York. To elicit mobbing behavior, we used taxidermic mounts of a Great Horned Owl and a raccoon. The owl was perched on a log; the raccoon was standing on top of a log. We placed the predators in fields and cemeteries and around schools, churches, and residential areas where we had observed crows previously.

We considered the experiments successful when at least one crow approached and vocalized in response to the predator. Of the 34 successful trials, 18 were with the owl, 16 with the raccoon. Trial locations were separated by at least 1500 m and therefore included the territory of only one crow family (average territory size 8.7 ha; McGowan 2001). We conducted both an owl experiment and raccoon experiment at each location (with at least 1 day separating the trials) for 24 of the 34 trials. Because of equipment failure, we were able to use only 26 trials (14 trials in which both predators were presented at the same location) for the analysis of initial vocalizations. Three owl experiments and three raccoon experiments were unsuccessful because crows never approached and vocalized in response to the models. Because most subjects were unmarked, we did not know their ages, sexes, or whether the same birds responded to both trials at the same site. Therefore, it is possible that some of the same individuals were tested repeatedly with different stimuli; even so, the effects of this type of resampling on the statistical analyses are likely minimal (Coss et al. 2005).

PRESENTATIONS

We placed the predators in open locations (not hidden behind trees or buildings) so that crows could easily detect them while randomly flying past. The owl was put on top of a 2-m black stake driven into the ground; the raccoon was placed on the ground. The predator was left exposed for 10 minutes after the first bird discovered it. If >1 hr passed and no crows detected the predator, the experiment was aborted. We recorded all experiments continuously with a video camera (Sony Hi8 CCD-TRV87) and a digital audio tape (DAT) recorder (Tascam model DA-P1, serial number 540055) with an Audio-Technica AT4071a directional microphone. The experimenter was always fully concealed behind a sheet whenever approaching the models.

During the experiments, the observer dictated into the video camera, noting the maximum number of crows present, the number of times crows swooped (flying within 2 m of the predator) and flew by (flying 2 to 10 m above the predator), and the movement of vocalizing crows (sitting, flying, or swooping). We recorded the times of the following events: predator uncovered, first discovery by a crow (indicated by movement toward the predator), first and last vocalizations, and predator removed. Because the video or audio equipment
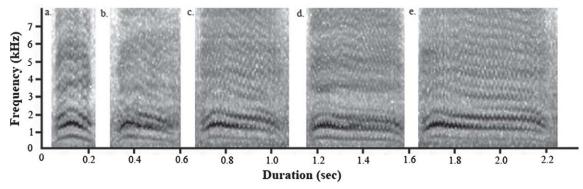
FIGURE 1.   Spectrograms of mob calls of crows, displayed in order of increasing duration: (a) typical inflected alarm call, (b–d) typical range of variation in caw structure, (e) the scream call, which acoustically and visually is an especially long caw (512-point FFT; window function: Hanning; 50% overlap; 124-Hz bandwidth; 256 points per frame).

sometimes failed (e.g., batteries or tape expired), data for some trials were incomplete.

ACOUSTIC MEASUREMENTS

Recordings of the mob vocalizations were digitized (sample rate 44 100 Hz; sample size 16 bit) with Raven 1.2 (Charif et al. 2004) and converted into spectrograms (512-point fast Fourier transform [FFT]; window function: Hanning; 50% overlap; 124-Hz bandwidth; 256 points per frame; frequency

86.1 Hz). Over 99% of the mob vocalizations belonged to a graded set of calls composed of inflected alarm caws, mixed caws, alert caws, and screams (Brown 1985, Yorzinski et al. 2006; Figure 1, Table 1). The remaining 0.6% of calls were "two-syllable caws" (Parr 1997), noncaws ("growl calls," "squalling calls," "moribund calls," "rattling notes" (Chamberlain and Cornwell 1971), and unclassified. We analyzed the caws emitted in response to the models to see if any quantitative features of the vocalizations differed.

TABLE 1.   Acoustic measurements of the mob calls of crows displayed in Figure 1. The call with the shortest duration (a) has the lowest bandwidth, lowest frequency modulation, highest center frequency, and highest frequency spectrum skew compared to the calls of longer duration (b–e). U_F = upper frequency (highest encountered, Hz); CTR_F = concentration spectrum range (Hz); LUR_F = upper minus lower frequency (Hz); IPR_F = interpercentile range (Hz); CFC-CumAbsDer = center frequency contour cumulative absolute derivative; CFC-AvgAbsDer center frequency contour average absolute derivative; PES_F = peak energy spectrum (Hz); $Peak_F$ = value of loudest frequency bin (Hz); $P1_F$ = initial percentile frequency (Hz); M_F = median frequency (Hz); PS_F = percentile skewness of frequency; LS_F = asymmetry of lower minus upper frequency range relative to median. Variables are described further by Cortopassi (2006a, b).

	Call				
	a	b	c	d	e
Bandwidth					
U_F (Hz)	1550	1637	1895	1723	1895
CTR_F (Hz)	345	517	689	689	689
LUR_F (Hz)	258	431	689	603	689
IPR_F (Hz)	431	517	775	861	775
Frequency modulation					
CFC-CumAbsDer	103 864	296 755	890 263	1 083 154	1 468 935
CFC-AvgAbsDer	8655	10 991	24 730	24 617	23 692
Center Frequency					
PES_F	1464	1378	1464	1464	1378
$Peak_F$ (Hz)	1464	1292	1378	1292	1378
$P1_F$ (Hz)	1292	1206	1206	1120	1206
M_F (Hz)	1464	1378	1464	1378	1378
Frequency spectrum skew					
PS_F	0.40	0.33	0.33	0.30	0.22
LS_F	0.67	0.40	0.38	0.43	0.25
Duration (msec)	150	211	311	383	539

We used XBAT 0.3 (Figueroa 2006), a sound-analysis platform that supports custom algorithm plugins, to measure the vocalizations (spectrogram settings: FFT size = 512 points; window size = 512 points; window function = Hanning; overlap = 256 points). We characterized frequency and bandwidth by using 12 acoustic measurements from the plug-in for energy-distribution measurement (EDM). This plug-in (Cortopassi 2006a, b) computes robust measurements on the basis of a user-specified interior percentage of energy in an acoustic signal, reducing the effects of outliers, background noise, and variable recording levels (Fristrup and Watkins 1992, Yorzinski et al. 2006). We specified 75% of the energy within the frequency range 550–6000 Hz (analysis settings: data length = 512 points, overlap = 256 points).

Because calls sometimes overlapped, we measured call duration by hand with Raven. Similarly, the total number of calls could not always be determined. Therefore, to calculate the time crows spent vocalizing, we summed the total amount of time (in sec) crows vocalized during each 1-min period.

STATISTICAL ANALYSES

For simple comparisons of means of the experiments' results, we used two-sample *t*-tests when variables were normally distributed and Wilcoxon two-sample tests when variables were not normally distributed. All other analyses were based on measurements of multiple calls given by mobbing crows, so we employed mixed models to control for repeated measures and trial effects. We used the PROC MIXED procedure in SAS version 9.1 (SAS Institute 2002). Variables not distributed normally were transformed as needed to meet the conditions for these parametric analyses. In cases of pairwise post-hoc comparisons of means, we report the Tukey-adjusted *P* values indicated as $t_{df,k}$, where df represents the usual degrees of freedom for the *t*-test and *k* is the total number of means compared.

To compare differences in the mean and slope of time spent vocalizing as a function of time in experiments comparing responses to the raccoon to those to the owl, we conducted a random-coefficient analysis with PROC MIXED. The model contained fixed effects (predator type, time period, and their interaction as well as the maximum number of mobbers) and included the intercept and time period as random variables along with an unstructured covariance structure to account for differences between trials in slope and mean. We also tested the individual slopes with separate random-intercept models for each predator.

To address the question of whether different vocal parameters were associated with the two predators, we focused on the initial vocal responses. The initial vocalizations usually consisted of a series of calls (mean 9.9 calls; range 1–41 calls) within 500 msec of each other that were emitted by a single individual. We used the 12 XBAT measurements and the duration measurement to analyze the calls emitted in the first series

for each trial. Because the measurements were correlated, we reduced them to a smaller set of orthogonal factors by means of a factor analysis with Varimax rotation (Tabachnick and Fidell 2001). We transformed the factors to meet underlying assumptions of the models and tested the scores of each of the factors separately to determine whether the responses to the two predators differed. The statistical model contained the main effect of predator type. We included the predator type × trial ID interaction as a random variable to control for differences among trials and tested the significance of this effect with a Wald *Z*-test.

We tested the same factors separately to determine whether they differed by predator type and the distance of the crow that initially discovered the predator. The first vocalizations this crow emitted were given either before it reached the predator and was relatively far from the predator (distant trials) or after it had flown around the predator and was relatively close to the predator (close trials). The experiments with the raccoon included only close trials because crows rarely (*n* = 2) emitted the first vocalization before circling around the predator. Some analyses therefore compared acoustic parameters for three contexts: owl-distant, owl-close, and raccoon.

Because the duration of the initial calls varied with the distance between the crow that discovered the predator and the predator type (see Results), we conducted two follow-up analyses. The first was to determine how the duration of the calls changed while the crows were mobbing. We measured more than 6900 calls in all trials combined and numbered them sequentially for each trial (for example, the first call given in response to a predator was numbered 1, referred to as call number in sequence). We used a random-coefficient model with fixed effects (predator type, call number in sequence, and their interaction), declared the intercept and call number as random variables, and specified an unstructured covariance. Such a model reduced the denominator's degrees of freedom for subsequent statistical comparisons to a value that reflected the number of trials in the analysis. We were particularly interested in testing the differences in slope among the predator categories (the interaction effects). We also tested the individual slopes with separate random-intercept models for each predator type.

We conducted the second follow-up analysis to determine how call duration and intercaw interval varied with respect to the movement of vocalizing crows (categorized as sit, flyby, or swoop) for the owl experiments. Intercaw interval was the amount of time that lapsed between two consecutive vocalizations. Raccoon experiments were excluded because crows rarely swooped at the raccoon (see Results). We used a random sample of 500 vocalizations emitted while crows were sitting and another 500 vocalizations emitted while crows were flying by the predators. We used all of the calls given when crows were swooping because slightly fewer than 500
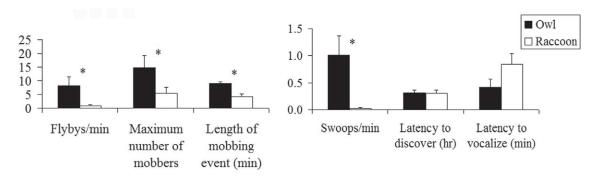
FIGURE 2.   Comparison of approach responses to the owl and to the raccoon. Asterisks indicate significant differences.

vocalizations were recorded for this behavior. As mentioned above, we made post-hoc comparisons among all pairs of means using Tukey–Kramer adjusted P values. Means ± SE are provided in graphs to illustrate effect sizes. Our criterion for significance was $P < 0.05$.

RESULTS

APPROACH BEHAVIORS AND RATES

Figure 2 compares the response of crows to the owl and to the raccoon. The period from the presentation of the two predators to their initial discovery by a crow (latency to discovery) did not differ ($t = 0.15$, df = 25, $P = 0.8791$). Crows tended to wait longer to emit the first vocalization after they discovered the raccoon than after they discovered the owl ($W = 189.5$, df = 25, $P = 0.0919$). Crows mobbed the owl longer than they mobbed the raccoon ($W = 177$, df = 32, $P = 0.0005$). In all but two of the owl experiments, crows continued mobbing the predator for the full 10 min. In contrast, crows mobbed the raccoon for the full 10 min in only two experiments. More mobbers assembled in response to the owl than to the raccoon ($t = 2.26$, df = 31, $P = 0.031$). Crows flew by ($W = 113.5$, df = 27, $P = 0.0067$) and swooped ($W = 198.5$, df = 31, $P = 0.0037$) in response to the owl more often than to the raccoon.

The total time crows spent vocalizing in response to the owl and raccoon differed even after we controlled for the maximum number of mobbers present. The length of time crows vocalized at the beginning of the trial was greater for the owl than for the raccoon (comparison of intercepts: $t = 2.14$, df = 32.4, $P = 0.040$). As the mobbing progressed, the amount of time crows spent vocalizing remained the same in the owl experiments ($t = 0.76$, df = 17, $P = 0.46$) and decreased in the raccoon experiments ($t = 4.56$, df = 16, $P = 0.0003$; comparison of slopes: $t = 2.59$, df = 33, $P = 0.0143$; Figure 3).

INITIAL VOCALIZATIONS
WITH RESPECT TO PREDATOR TYPE

The first vocalizations given in response to the owl and raccoon were similar. Four orthogonal factors, characterizing call bandwidth and frequency modulation (fine-scale frequency modulation and shape of the chevron), center frequency, frequency-spectrum skew, and duration, explained over 85% of the variation in call structure. The first vocalizations given in response to the two predators did not differ significantly in any of these factors (summarized in Table 2). Figure 1 displays exemplar spectrograms of mob calls given in response to the two predators, and Table 1 explains their acoustic properties in terms of energy distribution and duration.

INITIAL VOCALIZATIONS
WITH RESPECT TO DISTANCE

Even though no relationship existed between the durations of the initial vocalizations and the type of predator, the duration of the initial calls was related to whether the crows first called before reaching the predator (owl-distant) or after they circled around the predator (owl-close). Post-hoc tests show that call duration was significantly longer in the owl-close trials than in both the owl-distant ($t_{21,3} = 3.67$, $P = 0.004$) and raccoon ($t_{21,3} = 2.89$, $P = 0.023$) trials; the latter two trial categories did not differ significantly from each other with respect to duration ($t_{21,3} = 0.87$, $P = 0.664$). Inflected alarm caws (somewhat distinguishable from other caws by their shorter duration, lower frequency modulation, and higher pitch) at the beginning of the owl-distant trials likely explain part of this pattern. However, there were no differences related to the distance and predators in the other factors of call structure (Table 2).

OTHER DETERMINANTS OF VOCALIZATION
STRUCTURE

Despite the large amount of structural variation captured by our factor analyses of the measurements of energy distribution, none of this variation was associated with predator type or distance. We therefore explored other possible correlates of the structural factors. Cumulative frequency modulation was significantly correlated with call duration, but this effect is a consequence of the greater number of modulation cycles
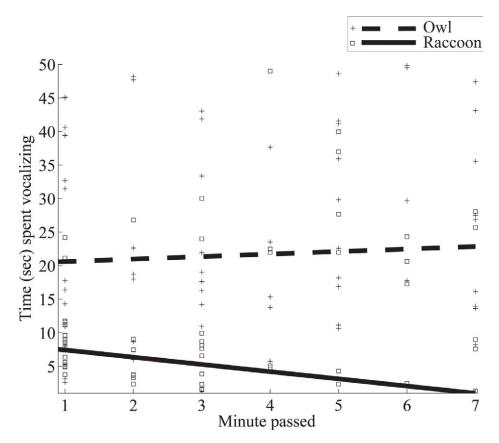
FIGURE 3.   The change in the amount of time (sec) that crows spent vocalizing during each minute of mobbing with respect to predator type. Each point is an acoustic measurement randomly selected from a mobbing trial.

in longer calls. All of the factors differed significantly as a function of the particular trial (Table 2). Because the same individual likely emitted all of the initial calls within a given trial (we do not know whether the same individual gave the initial calls in both experiments to the same group of crows), this finding suggests that variation in the acoustic structure of the calls was partially explained by individual or group differences.

TABLE 2.   Summary of analyses of acoustic measurement factors extracted from the calls in the first series of the mobbing events. Each orthogonal factor was analyzed separately with respect to predator type or distance/ predator type. Variance explained by each factor, F statistic, degrees of freedom, and P values are shown. Variables loading on each factor are given in footnotes and further described by Cortopassi (2006a, b).

| Treatment comparison | Statistic | Acoustic factors | | | |
		1	2	3	4
		Bandwidth and frequency modulation[a]	Center frequency[b]	Frequency spectrum skew[c]	Duration
Owl vs. raccoon	$F_{1,24}(P)$	3.81 (0.063)	1.21 (0.281)	0.54 (0.472)	0.46 (0.503)
Trial effects: owl vs. raccoon	$Z(P)$	3.17 (0.0008)	3.35 (0.0004)	3.15 (0.0008)	3.11 (0.0009)
Owl distant	$X \pm SE$	1.50 ± 0.018	0.070 ± 0.115	-0.086 ± 0.076	0.406 ± 0.053
Raccoon close	$X \pm SE$	1.72 ± 0.029	0.359 ± 0.103	0.519 ± 0.165	0.240 ± 0.128
Owl close	$X \pm SE$	1.60 ± 0.013	-0.277 ± 0.064	-0.021 ± 0.087	-0.795 ± 0.120
Distance and predator type	$F_{2,21}(P)$	1.89 (0.177)	1.06 (0.363)	1.27 (0.302)	7.26 (0.004)
Trial effects: distance and predator type	$Z(P)$	2.98 (0.0015)	3.14 (0.0008)	2.90 (0.0019)	2.75 (0.003)
Explained variance (%)		47.6	20	13.5	6.7

[a] U_F, CTR_F, LUR_F, IPR_F, CFC-CumAbsDer, -AvgAbsDer.
[b] PES_F, $Peak_F$, $P1_F$, M_F.
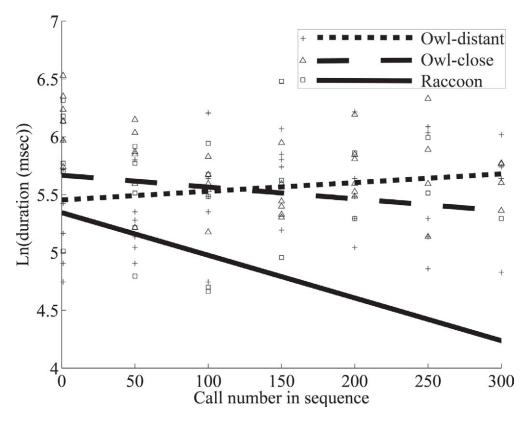[c] PS_F, LS_F.

FIGURE 4.   The change in the natural log of call duration vs. time during mobbing with respect to distance and predator type. Each point is an acoustic measurement randomly selected from a mobbing trial.

CHANGES IN CALL DURATION DURING MOBBING

Because the duration of the initial calls varied depending on the predator type and the distance between the predator and the crow that discovered it, we conducted a follow-up analysis to determine how the duration of the calls changed during the mobbing event. As the mobbing progressed, many individuals emitted a mixture of mob calls. The calls' duration remained similar in the owl-distant trials ($t = 0.93$, df $= 5.02$, $P = 0.39$) and owl-close trials (owl-close: $t = 1.01$, df $= 2.39$, $P = 0.40$) but decreased during the raccoon trials (raccoon: $t = 2.44$, df $= 8.02$, $P = 0.04$). The calls' duration tended to decrease more in the raccoon trials than in the owl-close trials and to increase more in the owl-distant trials than in the raccoon trials (post-hoc tests of slope differences: owl-close versus raccoon: $t_{15.3,2} = 1.76$, $P = 0.098$; owl-distant versus raccoon: $t_{15.2,2} = 3.01$, $P = 0.0087$; Figure 4).

VOCALIZATIONS WITH RESPECT
TO CROWS' ACTIONS

In the second follow-up analysis, we explored how duration and intercaw interval changed with the crows' movement. Crows that were swooping emitted caws of longer duration ($t_{31,3} = 3.20$, $P = 0.0076$) with shorter intervals between them ($t_{31,3} = 6.28$, $P < 0.0001$) than crows that were sitting. Crows that were flying emitted caws with longer intervals between them than crows that were swooping ($t_{31,3} = 2.41$, $P = 0.0544$). Last, crows that were sitting emitted caws with longer intervals between them than crows that were flying ($t_{31,3} = 4.91$, $P < 0.0001$; Figure 5). No other structural variables or factors varied as a function of movement behavior.

Crows also emitted various noncaw vocalizations that varied with their movements. Each type of noncaw vocalization was recorded in three or fewer different trials (this
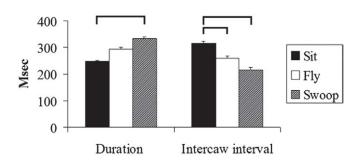

FIGURE 5.   Acoustic measurements of calls associated with different movements of crows during the owl trials. Significant differences are connected by lines.

small sample size precluded statistical analyses). They were mostly flying by the predator when emitting the moribund (56% of observations for this call type; $n = 34$), growl (48% of observations for this call type; $n = 31$), and squall (100% of observations for this call type; $n = 3$) vocalizations. The crows emitting rattling notes were sitting ($n = 2$). These rare call types were most often associated with the owl experiments (84%, $n = 64$). Most of the rare calls given in response to the raccoon were emitted during a single trial by a particular individual. This individual was the only crow observed to fly down to the ground and stand within 1 m of the raccoon while emitting moribund calls.

DISCUSSION

Our results suggest that American Crows do not use referential signals to label different classes of predators (avian vs. mammalian). They emitted the same types of vocalizations when mobbing both predators. Variation in caw duration, caw rate, and intercaw interval suggest, however, that American Crows use an urgency-based system to communicate about predators.

Different types of predators pose varied levels of danger to American Crows. Among their avian predators, the Great Horned Owl is extremely dangerous to both adult and young crows (Chamberlain-Auger et al. 1990, Caffrey 1992, McGowan 2001). In contrast, the raccoon largely preys upon eggs and chicks and represents little danger to the adults (Kilham 1989, Caffrey 1991, 2000, Verbeek and Caffrey 2002). Results from this study, conducted during the post-breeding season, also suggest that crows view owls as more dangerous than raccoons. Crows mobbed longer, performed more behaviors to deter the predator (flying by and swooping), and assembled in greater numbers in the owl trials than in the raccoon trials. Because the owl and raccoon represent different levels of danger, it could be important for crows to encode information about danger level in their calls. Encoding information about the type of predator, however, may not provide very useful information because crows respond in the same manner to stationary threats of both types of predator (they approach and mob them).

Our results suggest that rather than encoding information about predator type, the mob vocalizations of the American Crow indicate the level of danger. The close trials with the owl likely represent the highest danger level because the owl is the most dangerous threat and the crow is very close to it. The distant trials with the owl likely represent a lower danger level because the crow is not as close to the owl. Furthermore, the close trials with the raccoon also likely represent a lesser danger because the raccoon is not a very dangerous predator to adult crows yet the crows are still very close to the potential threat.

The only acoustic measurement of the calls that differed with distance and predator types was call duration. The duration was the longest for the presumably most dangerous context (owl-close). The duration was similar, however, for both of the low-danger contexts (owl-distant and raccoon) even though the predators were different. In the raccoon trials, as the mobbing progressed and the crows got closer to the predator, the duration of calls gradually decreased as the level of danger presumably decreased. In addition, duration also varied depending on the crows' movement. Crows emitted the longest calls while performing the most dangerous behaviors (swooping).

The caw rate and intercaw intervals during mobbing also appeared to indicate the level of danger. The caw rate was higher in the owl experiments than in the raccoon experiments; intercaw intervals were shortest when crows were swooping. Overall, these results suggest that longer, more frequent calls with shorter intervals between them reflect a higher degree of danger.

In addition to caws, the crows occasionally emitted other call types in response to the predators, especially the owl. Like Good (1952), we observed crows emitting growls most frequently when they were closest to the predator (i.e., flying by and swooping). We observed crows emitting moribund and squall calls while mobbing the predators even though Chamberlain and Cornwell (1971) recorded these calls only when crows were dying and struggling to escape from a predator, respectively. Interestingly, during the few times when these rare call types were emitted in response to the raccoon, the individual emitting these calls put itself in an unusually high-risk situation by standing within 1 m of the predator. These three call types likely indicate a high degree of danger and arousal level when a crow is mobbing any predator. We also heard crows making rattling notes while perched near the predator. Because rattling notes have previously been heard only within roosts and flocks and in the context of courtship (Townsend 1927, Chamberlain and Cornwell 1971), they could have functions apart from mobbing (e.g., self-advertisement; Slagsvold 1984) when emitted in mobbing contexts. Last, the results suggest that variation in the acoustic structure of mob calls is explained partly by the individual or group member producing the calls.

The results agree generally with those of previous studies of the mob vocalizations of the American Crow. Previous observations and playback experiments on the American Crow suggest that calls with long durations and high call rate are associated with high-intensity mobbing (Chamberlain and Cornwell 1971, Richards and Thompson 1978, Brown 1985, Verbeek and Caffrey 2002). They have also shown that variation in the acoustic structure of alarm and mobbing calls may be used by crows to encode the caller's identity (Yorzinski et al. 2006). Our results are also consistent with studies of the alarm and mobbing vocalizations of other species. Like the American Crow, many other species alter the duration, rate, and other acoustic properties of their alarm and mob calls to indicate a higher level of danger (e.g., Cully and Ligon 1986,

Zimmermann and Curio 1988, Blumstein 1999a, Le Roux et al. 2001, Manser 2001, Baker and Becker 2002, Ellis 2008). Species that respond with the same antipredator behavior to different predator classes rely primarily on an urgency-based signaling system (Owings and Hennessy 1984, Macedonia and Evans 1993, Naguib et al. 1999, Leavesley and Magrath 2005). Individual distinctiveness of alarm calls has also been documented in at least one other species that lives in small kin groups (Sproul et al. 2006).

Encoding specific information about urgency during mobbing may be particularly important in the Corvidae and other families that live in relatively stable social groups (Naguib et al. 1999, Griesser 2007). By knowing the specific danger associated with the predator along with the identity of the caller (Yorzinski et al. 2006), group members can make informed decisions about joining the mobbing. Their decision to join may reflect trade-offs between participating in mobbing and in other group activities, such as foraging, defending the territory, acting as sentinels, and establishing affiliative relationships. Of interest would be further studies examining how crows respond to mob vocalizations of differing levels of danger as a function of the crows' distance to the predator, age, relatedness, mated status, or other variables.

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