FUNCTIONAL AND ADAPTIVE SIGNIFICANCE

OF MOBBING AND ALARM CALLS OF

THE COMMON CROW (Corvus brachyrhynchos)

by

Eleanor Deis Brown

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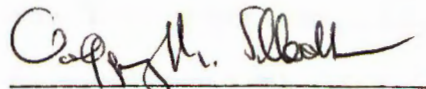the degree of
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APPROVAL SHEET

Title of Dissertation: Functional and Adaptive Significance
of Mobbing and Alarm Calls of the
Common Crow (Corvus brachyrhynchos)

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ABSTRACT

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Dissertation directed by: Wolfgang M. Schleidt, Professor
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This study is an analysis of the functional and adaptive
significance of "caw" calls used by common crows (Corvus
brachyrhynchos) in contexts involving danger. Seven tame
birds, including three siblings and several birds familiar
to the siblings (i.e., within their sight and hearing), were
the subjects of playback experiments. Four types of caws
associated with danger were played back as test calls:
screams, mixed caws, inflected alarm caws, and alert caws.
These four test caws were recorded from each of six
different individuals (senders) and played back to the
experimental subjects (receivers). The vocalizations of the
three sibling receivers were tape recorded during playback
trials, and three types of response caws were scored: mixed
caws, alert caws, and long caws. By counting caws in each
10 s interval during the 1 min before, 20 s during, and 20 s

after playback, the following functional interrelationships among cawtypes were found. Mixed caw responses were elicited immediately by, and only by, screams and mixed caws. These caws are used in harassing a predator, and seem to function in part to assemble and coordinate a mobbing group. Alert caw responses were suppressed over the 20 s during which caws were played back for all types of presentations except those of alert caws, but reached a peak just after playback. Alert caws seem to be multifunctional, probably indicating either mildly threatening objects or cessation of danger. Long caw responses were suppressed during the 20 s presentations of all cawtypes, but reached a peak after scream and mixed caw playbacks. Long caws seem to indicate either cessation of danger or continuation of normal activities. By further subdividing numbers of responses on the basis of social familiarity between senders and receivers, the effect of social relationship on responses was examined. The senders were either siblings of, familiar to (heard and seen only from a distance), or unknown to the receivers. The receivers did not respond more to the voices of senders from any particular social category (G goodness-of-fit tests) although the data were not conclusive.

The results are discussed in terms of the information encoded in mobbing and alarm calls, the functions of those calls, and the sources of natural selection which may have shaped the evolution of mobbing and alarm vocalizations.

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INTRODUCTION

Common crows (Corvus brachyrhynchos) are noisy and gregarious birds in whose lives vocal communication plays a major role. Crows have long-term relationships and close social bonds with conspecifics, remaining in the vicinity of their birth and maintaining associations with many individuals. Among and within the many social units in crow society, the main type of long-distance broadcast vocalization is cawing. Birds may communicate by cawing when they are up to .5-1 km apart, out of visual range; when they are ranging across a field or woodlot; or when they are engaged in social interactions, even within 1 m of each other.

Cawing is particularly important in situations involving potential danger, when widely scattered crows may convene to participate in harassing, or mobbing, a predator, both verbally and physically. Factors affecting mobbing behavior, particularly vocalizations, are the subject of this study, and were approached through the technique of playing back tape recorded vocalizations.

In the first part of the study, I examine the functions of a range of cawtypes, all associated with contexts involving potential danger. This part focuses on vocal responses to playbacks of these vocalizations. From the different responses to different vocalizations tested, I

infer their interrelationships and functional significance, and then discuss the selective forces which may have shaped such a system.

In the second part of the study, I examine the degree of social familiarity between sender and receiver as a variable affecting responses to the foregoing calls. I test the hypothesis that crows respond more strongly to the voices of well-known (kin) or familiar individuals than of unknown, anonymous crows. The outcome is relevant to the question of which types of selective forces may have shaped mobbing behaviors.

INTRODUCTION

In many bird species, the vocal repertoire is a complex of varied but interrelated sounds used in a wide variety of contexts. Similar vocalizations may be used in different contexts (Beer 1970); conversely, different vocalizations may appear in the same or related contexts (Mulligan and Olsen 1969). Common crows (Corvus brachyrhychos) are a suitable species for a fine-grained analysis of inter-relationships among calls, since they are noisy and gregarious birds in whose lives vocal communication plays a major role.

Among and within the various social units within crow society the main type of long-distance vocalization is cawing. Birds may communicate by cawing when they are up to .5 - 1 km apart, out of visual range; when they are in a flock or family group, scattered across a field or woodlot; or when they are engaged in various social interactions, even within 1 m of each other.

All the many types of caws have a number of physical features in common (Brown 1979). Caws are high-amplitude vocalizations (about 90 dB at 1 m). They are usually inflected to some degree; the peak fundamental frequency is around 250-350 Hz. The tonal quality is rather hoarse; harmonics 4-6 are highest in relative amplitude, but the energy is spread, usually, over a wide frequency range.

Caws are often given in sequences lasting about 1-3 s, although single caws may also occur. In regular-patterned cawing, called structured cawing by Thompson (1975), cawtype and intercaw interval are held constant within a sequence; a series of like sequences is commonly uttered. In irregular cawing, called unstructured cawing by Thompson (1975), cawtype and intercaw intervals may vary within a sequence, and series of like sequences are unusual.

Cawtypes and caw sequences may intergrade along many variables simultaneously, including such parameters as frequency, amplitude, tonal quality, caw duration, intercaw interval within a sequence, sequence duration, and intersequence interval.

The role of cawing is especially important in situations involving potential danger, when many different vocalizations may be used and when widely scattered crows may convene to participate in harassing, or mobbing, a predator. Mobbing behavior is widespread among birds (Altmann 1956), including the Corvidae (Goodwin 1976; Bent 1946). Many experimental studies have focused on factors eliciting or affecting mobbing behavior (Hinde 1954; Andrew 1961; Shalter 1978; Curio, Ernst, and Vieth 1978; Frankenberg 1981); a live or stuffed predator is commonly used to induce mobbing. The technique of playing back recorded vocalizations (Weeden and Falls 1959) has been used extensively in studies of song function or song learning in passerines (reviewed by Marker

and Mundinger 1971; Verner and Milligan 1971; Emlen 1972),
but also has been used in studies involving mobbing or alarm
behavior (Stefanski and Falls 1972; Chamberlain and Cornwell
1971; Curio 1971).

In this paper I examine the functions of a range of
cawtypes associated with related contexts, all involving
potential danger. Three of the cawtypes included in the
study, screams, mixed caws, and inflected alarm caws, occur
only in "danger" contexts; the remaining two types, alert
and long caws, occur in both "danger" and "business-as-usual"
contexts. The study focuses on vocal responses to playbacks
of these vocalizations. From the different responses to
different vocalizations tested, I infer their inter-
relationships and functional significance, and then discuss
the selective forces which may have shaped such a system.

MATERIALS AND METHODS

Data for this study were drawn from observations, and tape recordings of the vocalizations, of seven captive common crows (Corvus brachyrhynchos). Supporting data were drawn from field observations of this species in Prince George's County, Maryland, and from previous studies of crow behavior (Brown 1979).

Of the seven captive crows, three were siblings hand-reared from the age of two weeks (May 1976). Two of these birds, G and RU, were females housed together in an outdoor aviary 3.3 x 5 x 8 m. The third sibling, P (sex not known but probably female), was housed in another outdoor aviary 5.3 x 4 x 2.6 m at 24 m distance from G and RU (Fig. 1).

Two other crows, J, a hand-reared female, and N, a wild crow of unknown sex, were housed adjacent to G and RU in an aviary 3.3 x 2.6 x 6 m. These birds were acquired in July 1977, and were about the same age as the siblings.

Finally, BN and LN, male and female adults, were housed in an aviary 2.6 x 3.3 x 3.3 m. These birds were acquired in March 1978, and were about the same age as the other birds.

All the crows were well settled in their aviaries, having lived there since I acquired them. The aviaries were situated in my backyard, which contained many large trees and was in the center of a one square mile block of fields

Figure 1. Placement of avaries, microphones, speaker, and
tape recorder. Letters represent individual
crows.

J
N
G
RU
P
BN
LN

0   5   10 15 20 m

S
W
E
N
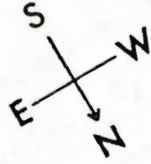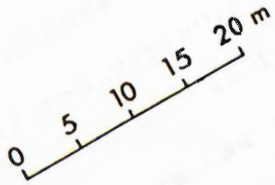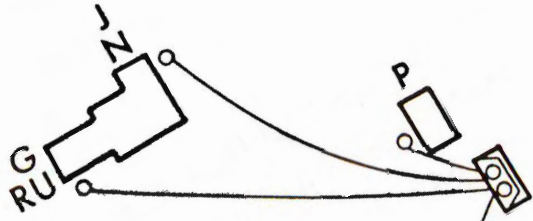
and woods. The tame birds thus had ample and long experience with local wild crows, with whom they interacted every day, and with the full panoply of local predators, including hawks, owls, snakes, raccoons, opossums, dogs, cats, foxes, and hunters.

Preparation of test tapes for playback experiments

I classified vocalizations used in contexts of danger into a graded series of categories on the basis of sound and of measurements of caw frequency, duration, and intercaw interval from sonagrams. The crow vocal repertoire cannot be easily divided into simple, discrete categories; caws and caw sequences intergrade along many variables. In order to find division points for breaking the continuum into convenient categories, I measured caw duration, intercaw interval, and various frequency-related variables such as fundamental frequency at onset and fundamental frequency at highest point, for samples of the various caw types made by different individuals. By taking the coefficients of variation (CV) of the measurements, I inferred, when low CVs were obtained, that my category system corresponded to real differences (Schleidt 1982). I chose four separate and recognizable types, screams, mixed irregular mobbing caws (= mixed caws), inflected alarm caws, and alert caws, to serve as test caws for playback. Part of the process choosing these types included plotting caw duration against

intercaw interval (Fig. 2) in order to assure further that my categories were appropriate, and that the caw types to be played back were clearly different from each other. I tape recorded each type from each of 6 different individual crows: RU, G, P, J, BN, and a wild crow (wild crow tapes made in this geographical region by D. R. Chamberlain and obtained courtesy of the Library of Natural Sounds, Cornell Laboratory of Ornithology). After measuring natural sequence and interval lengths, I chose the particular recordings which most closely approximated the 8 s caw sequence - 4 s pause - 8 s caw sequence which I had determined as a standard suitable for all 4 caw types, and whose measurements matched best the regions defined by plotting caw duration against interval (Fig. 2).

In order to standardize the test sequences further, and to control for variations in the signal's message and which might be encoded in caw duration and intercaw interval (Hinde 1954), I used a PDP-11 computer with an interactive program (WAVES) originally designed for the alteration of speech sounds (sampling rate = 10k) and thus suitable for the range of frequencies found in crow sounds. The input signal was played on a Uher 4200 Report-S tape recorder and passed through a Bruel and Kjaer Spectrum Shaper, Model 123, with a 315-5000 Hz bandpass filter. Once digitized, the caws were manipulated in such a way, e.g., by transposing caws within a sequence, changing intercaw intervals,

Figure 2.   Plot of caw duration against intercaw interval
within caw sequences, for playback caws from
sender to RU. This graph is a sample of those
used in defining categories, and in making
choices of recordings which clearly fell into
different categories. Numbers are used rather
than dots, and indicate each caw's position in
its caw sequence.
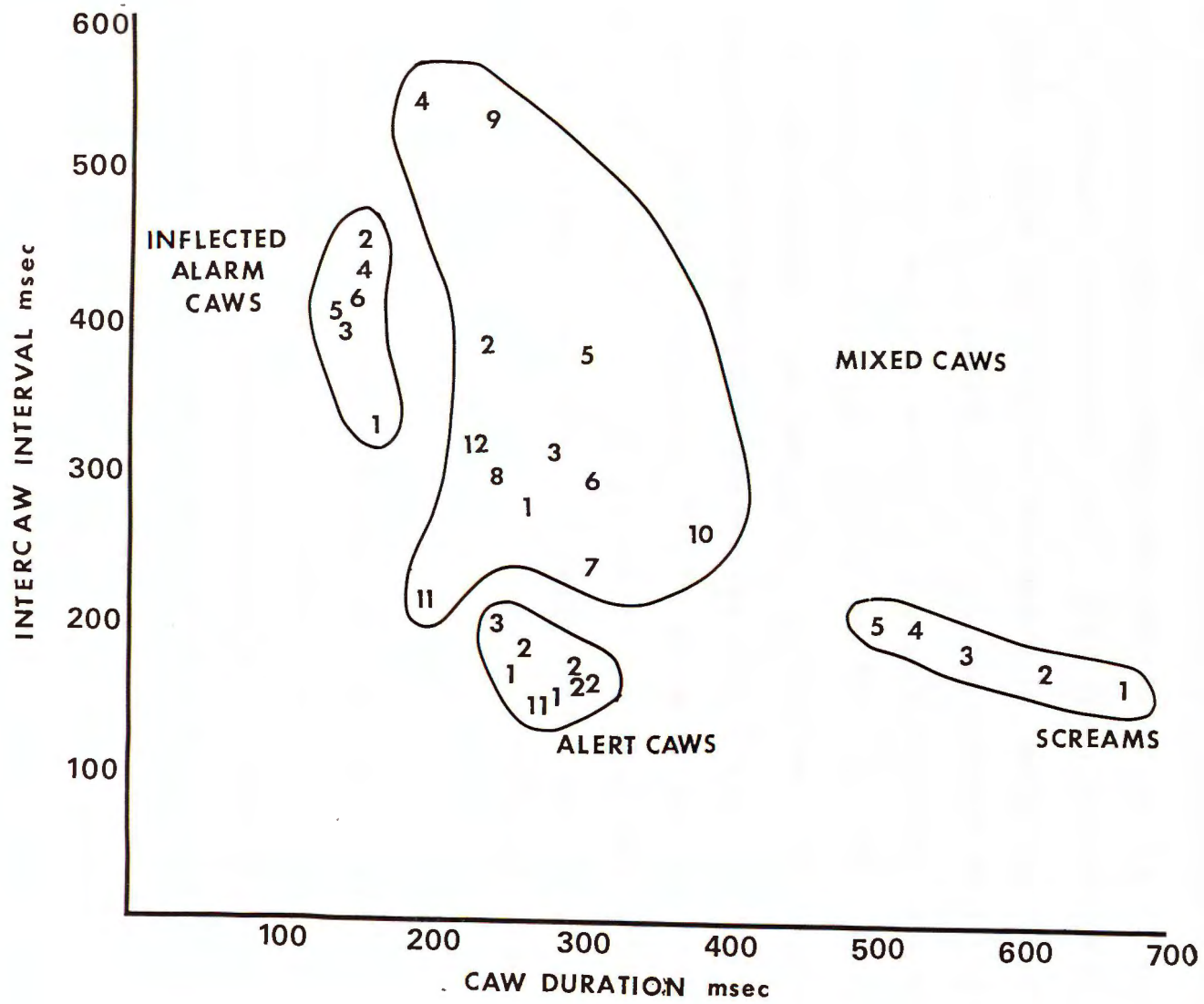
splicing caws together, etc., as to standardize the temporal patterning of sequences of caws made by different individuals. As a final step in the editing process, white noise was added at a mean level of 30 dB below the mean level of the signal in order to cover any low-amplitude switching transients at the beginning and end of edited fragments.

Experimental apparatus

The edited master playback tapes were played on a Uher 4200 Report-S tape recorder (3 3/4 ips) connected to a 100 W Altec amplifier, Model 9477A. The signal was then emitted through an array of three Amperex amplifier speakers, Model AD0260/SQ3, permanently installed about equidistant from the cages (Fig. 1). Frequency responses of the speakers and tape recorder were within 1 dB within the desired frequency range. The tapes were played back at 97 dB, a level determined by measuring caw amplitude at 1 m from the crow (General Radio Model 1551-C SPL meter, C weighting scale) and matching speaker-to-cage attenuation with observed cage-to-cage attenuation. Vocal responses of the receiving crows were picked up with Uher M517 microphones hung adjacent to each cage and connected to a 4-channel Sony tape recorder, Model TC 654-4; responses of different birds were thus recorded simultaneously on different tracks of a single tape (Fig. 1).

Experimental procedure

The 42 playback trials were spread over the period from February 21, 1981 - October 15, 1981, with an average interval of 6 days between playback trials. Each trial consisted of the 4 test caw types emitted by one of the 6 different senders (Fig. 3). There were 7 replicates of each sender, but since the first trial was a built-in pilot experiment, only data from replicates 2-7 were analyzed. Playbacks were always done in the morning, beginning between 0800 and 1000 h when the crows were most vocal. On any given day, the four vocalizations of a single sender were played at 15 min intervals. The four vocalizations were always played in the same order (Fig. 3) to (1) reduce the possibility that disturbances created by screams would affect responses to the next cawtype; and (2) to avoid making numerous copies, with inevitable loss of fidelity, of the master tape. The tape deck used to monitor the trial was switched on 8 min before the first caw was played back, and continued uninterrupted for the next 60 min. Thus the vocal activity of the subjects not only during but before and after each playback was available for analysis. The birds were observed during each trial.

Data analysis

I transcribed each of the 4 tracks, containing sounds made by receivers in their respective cages, of each tape

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Figure 3. Flowcharts of a complete replicate of playback
trials and of responses.

Top, flow chart of a single complete replicate of
playback trials. One trial was conducted on any
given day, and consisted of 4 caw types, by the
same sender, played at 15 min intervals. Several
days separated trials. Six complete replicates
were used in the analysis.

Bottom, flow chart of responses. The tape-
recorded sender's caw reached the ears of the 3
receivers singled out for analysis. The 3
response types scored for each receiver were
mixed, alert, and long caws.

TRIAL 1	TRIAL 2	TRIAL 3	TRIAL 4	TRIAL 5	TRIAL 6
SENDER RU ALERT CAWS	SENDER G ALERT CAWS	SENDER P ALERT CAWS	SENDER J ALERT CAWS	SENDER BN ALERT CAWS	SENDER WI ALERT CAWS
SENDER RU ALARM CAWS	SENDER G ALARM CAWS	SENDER P ALARM CAWS	SENDER J ALARM CAWS	SENDER BN ALARM CAWS	SENDER WI ALARM CAWS
SENDER RU MIXED CAWS	SENDER G MIXED CAWS	SENDER P MIXED CAWS	SENDER J MIXED CAWS	SENDER BN MIXED CAWS	SENDER WI MIXED CAWS
SENDER RU SCREAMS	SENDER G SCREAMS	SENDER P SCREAMS	SENDER J SCREAMS	SENDER BN SCREAMS	SENDER WI SCREAMS

SENDER'S CAW

RECEIVER G   RECEIVER RU   RECEIVER P

MIXED CAWS	ALERT CAWS	LONG CAWS	MIXED CAWS	ALERT CAWS	LONG CAWS	MIXED CAWS	ALERT CAWS	LONG CAWS

made of a playback trial (Figs. 1 & 3). I noted the type of
vocalization given, the identity of the vocalizer, and the
time with respect to playback onset for the 2 min previous
to, 20 s during, and 2 min after playback. I ordered these
data into numerous sequential records which I called bird-
sequences. A bird-sequence was defined as the record of
caws occurring in the sequential series of 10 s intervals
from -60 to 80 s during a given playback trial, for a given
individual. For example, with respect to a single alert caw
playback, receiver G may have uttered an alert caw in the
-20 to -10 s interval, a long caw in the 0 to 10 s interval
during playback, and another long caw in the 40 to 50 s
interval after playback; this record over time would be one
bird-sequence. During any single playback trial, all three
receivers scored (G, P, and RU) could potentially respond.
Since there were 36 trials of each playback type, and three
potential respondents, a total of 108 bird-sequences was
potentially possible for each playback type/response type
combination. I then tallied three types of responses
(mixed, alert, and long caws) for each 10 s interval in the
foregoing time periods. Response types were tallied
separately for the 4 separate types of test caws played
back. Data from the 3 most vocal receivers (the siblings G,
P, and RU) were combined. Few data were obtained from BN,
LN, or N. Although the remaining receiver, J, did respond,
I did not lump her response with those of the siblings

because I wished to use the same pool of data to test for effect of social relationship on responses. Clearly J, an unrelated bird, could not be classified in the same social category with the siblings G, RU, and P.

A series of G tests (Sokal and Rohlf 1969), including both single-classification goodness of fit tests and two-way tests of independence, was performed on caws distributed over the intervals before, during, and after playback, with respect to type of response caw and type of playback caw.

RESULTS

Cawtypes and the contexts in which they occur

In general, the factors affecting a crow's use of
certain cawtypes in a particular situation seem to be the
following: distance of the predator or other eliciting
object; degree of surprise involved in the appearance of the
object; severity of the danger associated with the object;
degree of familiarity of the object; and movements of the
object (e.g., behavior of a predator).

Screams (Fig. 4), called assembly calls by Chamberlain
and Cornwell (1971), are used during high-intensity mobbing
behavior directed at a dangerous predator like an owl, and
in similar contexts (Table 1). Screams are variable in
frequency and duration, but are long (about 500-700 msec),
harsh low-frequency vocalizations with a broad energy
distribution. Both the intercaw (about 125-160 msec) and
intersequence intervals vary with motivation.

Mixed caws (Fig. 4) are also used during mobbing and in
similar contexts (Table 1); screams usually grade into mixed
caws as motivation changes. It is unclear whether
Chamberlain and Cornwell (1911) include what I call mixed
caws in their assembly call category. Mixed caws are also
harsh, low-frequency sounds with variable duration (about
150-450 msec) and intercaw interval (about 150-350 msec).
Intercaw and intersequence interval, as well as sequence

TABLE 1

Representative contexts in which the tame crows
used various types of caws

Caw type	Screams	Mixed caws	Alert caws
	1. seeing a struggling crow held in the hand	1. seeing or hearing wild crows mob, approximately 10-350 m away	1. hearing a faraway (500 m?) mob
	2. seeing and hearing wild crows scream while mobbing a hawk close by (10 m)	2. seeing an unknown person walk close to their aviaries	2. seeing wild crows fly overhead
	3. seeing an unknown person waving a coat, 250 m away	3. seeing an unknown person walking 50 m away	3. after hearing wild crows at a distance of 20-500 m give alert caws
	4. seeing a particularly hated cat trot suddenly into view at 20 m	4. seeing a rifle carried within 40 m (having had prior experience with gunshots)	4. while 4-5 wild crows foraged within 20 m
	5. seeing a fox run out of the undergrowth 6 m away	5. seeing a fox walk in a field, 70 m away	5. when I appeared in the yard
		6. seeing a vulture or <u>Buteo</u> hawk soar overhead at 12 m	6. when I called their names from approx. 40 m away
		7. seeing an unknown cat walking 6 m away	7. seeing a <u>Buteo</u> hawk soar overhead at about 70 m
			8. hearing the arrival of a car in driveway 30 m away
			9. seeing an unknown person walking 250 m away
			10. during an aggressive interaction, 1-3 m separating participants
			11. during "business as usual" e.g., interspersed with other activities
Cawtype	Inflected alarm caws	Long caws	
	1. seeing a vulture or <u>Buteo</u> hawk soar overhead at 30 m	1. during and after hearing wild crows give a short bout of low-intensity mixed caws	
	2. seeing a <u>Buteo</u> hawk soar overhead at 12 m	2. after hearing wild crows at a distance of 20-500 m give long caws	
	3. seeing a vulture or <u>Buteo</u> hawk soaring at 30 m, approximately 100 m away	3. during "business as usual" e.g., interspersed with other activities such as preening and eating	
		4. when I appeared in the yard	

Figure 4. Cawtypes used in the study.

Top, screams given by RU.

Bottom, beginning of a mixed caw sequence by RU.

SCREAMS

MIXED CAWS
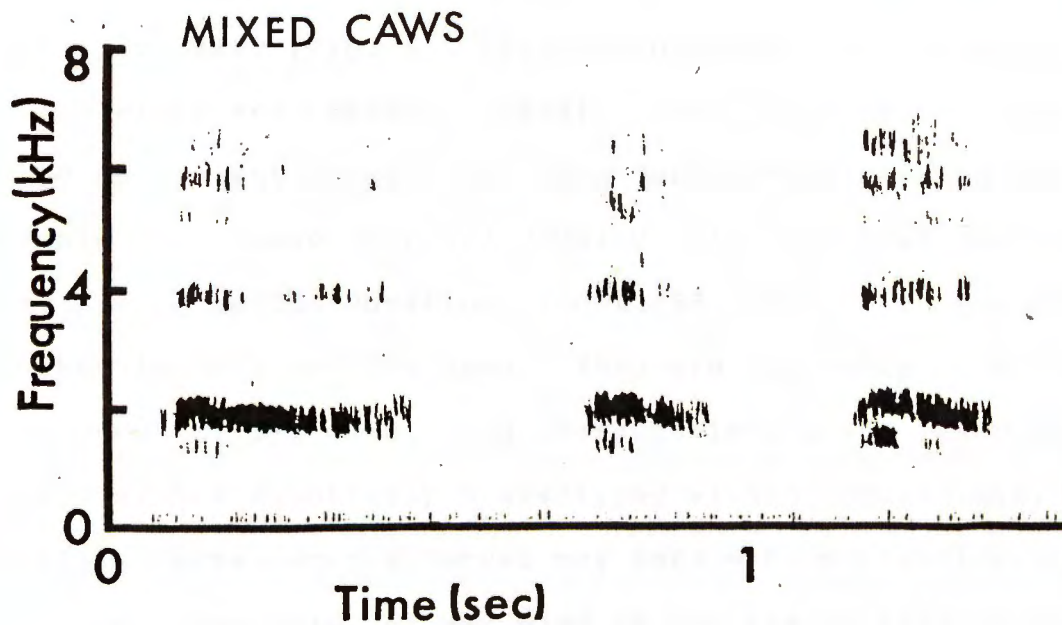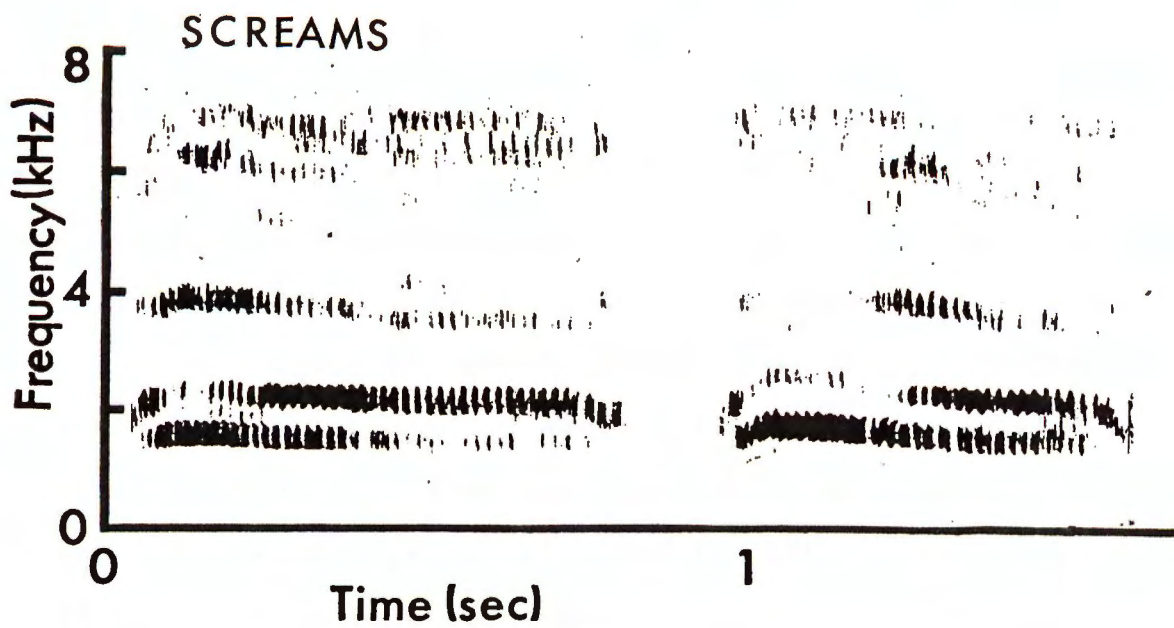
duration, vary with motivation and with changes in the
mobbed object's movements. Typically, sequences lasting
from about 3 s (4-5 caws) to 15 s (20 caws) are given.

Inflected alarm caws (Fig. 5) are given in the presence
of a soaring raptor at certain altitudes (Table 1). These
caws seem to be included as alarm calls by Chamberlain and
Cornwell (1971), but since many physically dissimilar
sounds are placed together in broad functional categories,
it is very difficult to interpret their results. They are
short (about 100-150 msec) sharp bursts of sound, less
hoarse than other caws. Intercaw intervals (about 325-500
msec) are long and variable, and vary with motivation.
Inflected alarm caws with short intercaw intervals are used
in other different contexts.

Alert caws (Fig. 5), part of the alert call category of
Chamberlain and Cornwell (1971), occur in contexts involving
mild or distant danger, but also during "business as usual"
(Table 1). These caws are usually inflected near the onset
and are of medium duration (about 250 msec), with intercaw
intervals of about 160 msec. They are typically given in
sequences of 3-5 caws. Caw characteristics and intercaw
interval are relatively stereotyped within individuals,
while intersequence interval may vary with motivation.

Long caws (Fig. 6) may also be associated with mild or
distant danger and with "business as usual" (Table 1).
These caws, like alerts, are inflected near the onset but

Figure 5. Cawtypes used in the study.

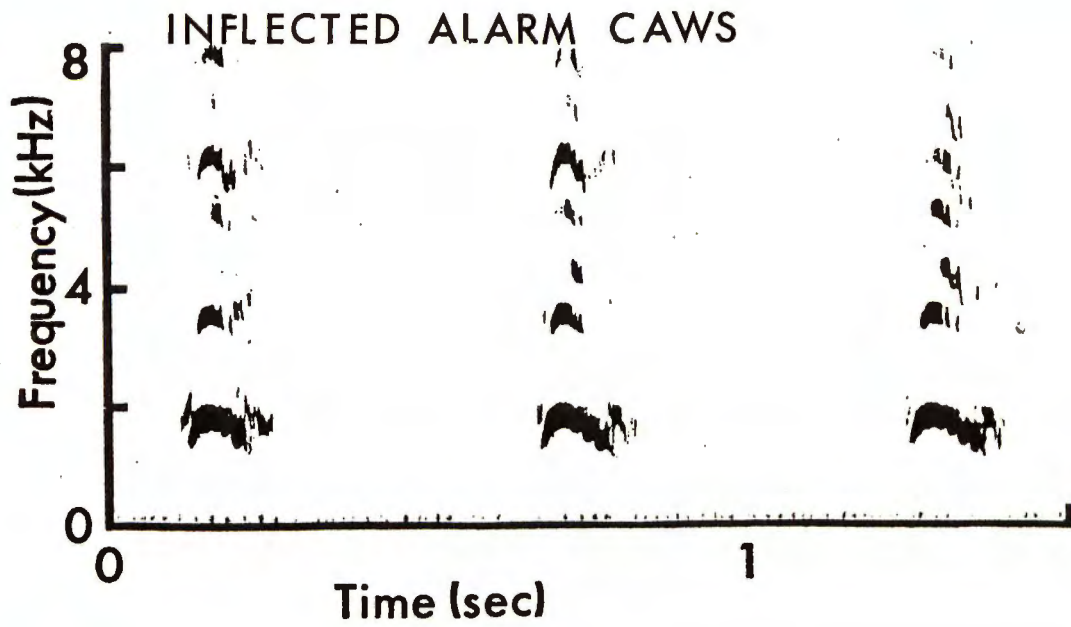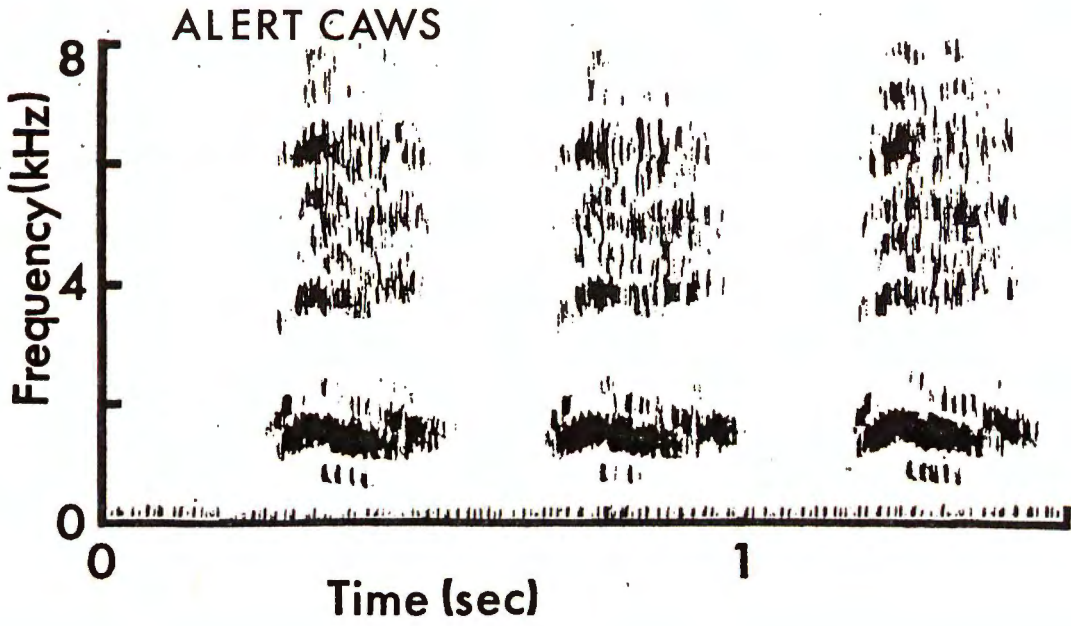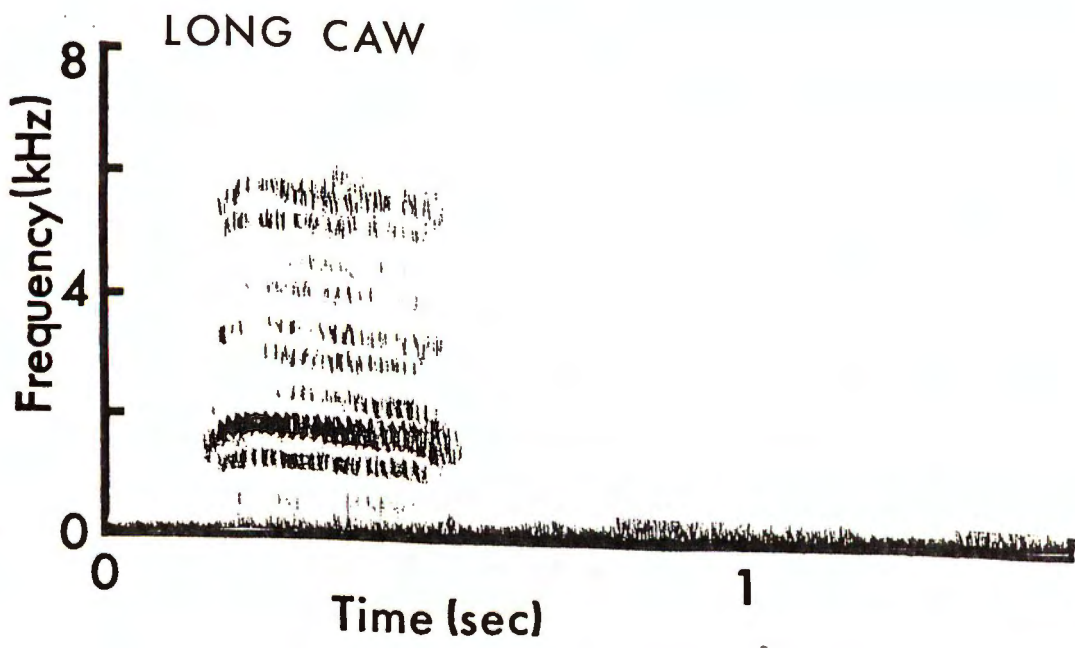Top, alert caws by RU.

Bottom, inflected alarm caws by RU.

ALERT CAWS

INFLECTED ALARM CAWS

Figure 6. Cawtype used in the study.
Long caws by RU.

LONG CAW

are of longer duration (about 450 msec) and with a longer
intercaw interval (about 250 msec). They are typically
given in sequences of 2-3 caws. Caw characteristics and
intercaw interval are variable among, but relatively
constant within individuals, while intersequence interval
varies with motivation.

Results of playback experiments

The numbers of mixed, alert, and long caws given before,
during, and after playback of the test caws are shown on
each histogram included in Figs. 7-10. Scream responses
were elicited only twice, and were lumped with mixed caw
responses on the basis of physical and functional
similarity. Only caws occurring 20-40 s after playback
onset were included in the post-playback time interval
indicated by the dashed line at 40 s.

Temporal response characteristic of each caw type

Mixed caws (Figs. 7-10) were elicited immediately upon
presentation of the playback, if elicited at all, and their
numbers declined progressively thereafter. Baseline
(pre-playback) levels of mixed caws were very low.

Alert caws (Figs. 7-10) were suppressed or remained at
baseline levels during the playback, while they usually
(except in Fig. 9) reached a high peak after playback.

Figure 7.   Responses to scream playbacks.

The pre-playback interval included in the
analysis (G-tests) described in the text is -60
to -0 s; the stippled during-playback interval,
0-20 s; and the post-playback interval, 20-40 s.
The 40-80 s interval is included in the graphs to
provide extra contextual information on caws
occurring later in time.   Numbers in each space
indicate the total number of caws for that
particular time interval (pre-, during-, or
post-playback) and were the same numbers entered
in the statistical analyses.   A bird-sequence is
defined as the record of caws occurring in the
sequential series of 10 s intervals from -60 to
80 s during a given playback trial, for a given
individual.   During any single playback trial,
all three receivers scored (G, P, and RU) could
potentially respond.   Since there were 36 trials
of each playback type (scream, mixed caw,
inflected alarm caw, alert caw), and 3 potential
respondents, a total of 108 bird-sequences was
potentially possible for each playback type/
response type combination.   The number given at
the top of each histogram shows the actual number
out of the potential 108.

SCREAM PLAYBACKS

MIXED CAW RESPONSES
23 bird-sequences

ALERT CAW RESPONSES
37 bird-sequences
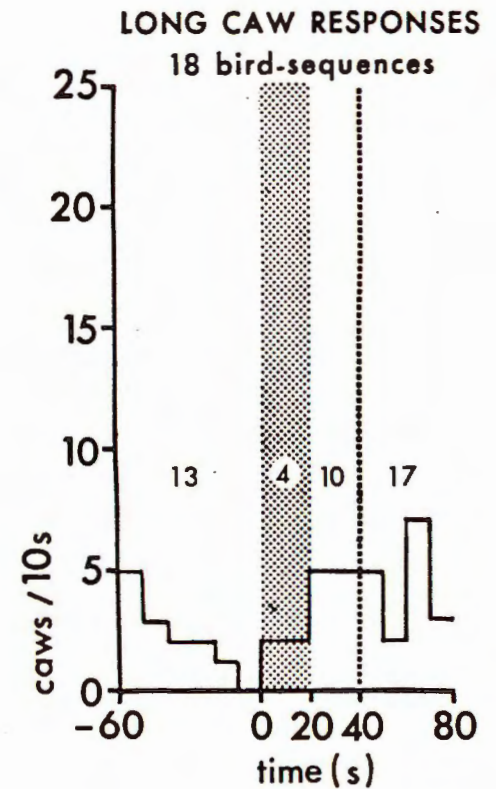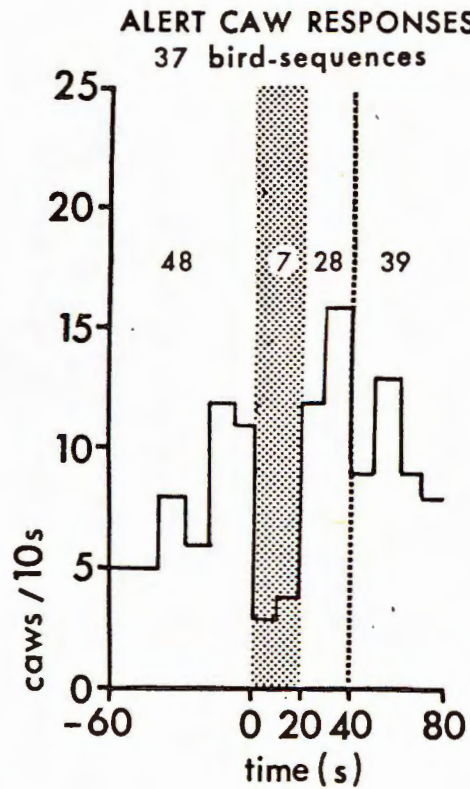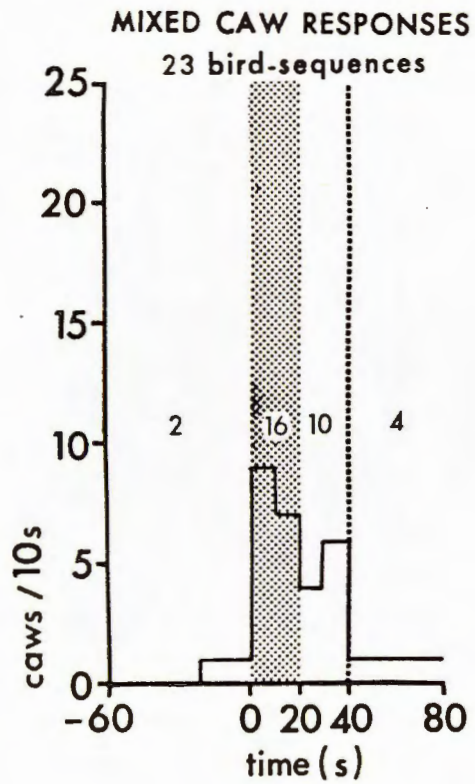
LONG CAW RESPONSES
18 bird-sequences

Figure 8.   Responses to mixed caw playbacks.

The pre-playback interval included in the analysis (G-tests) described in the text is -60 to -0 s; the stippled during-playback interval, 0-20 s; and the post-playback interval, 20-40 s. The 40-80 s interval is included in the graphs to provide extra contextual information on caws occurring later in time. Numbers in each space indicate the total number of caws for that particular time interval (pre-, during-, or post-playback) and were the same numbers entered in the statistical analyses. A bird-sequence is defined as the record of caws occurring in the sequential series of 10 s intervals from -60 to 80 s during a given playback trial, for a given individual. During any single playback trial, all three receivers scored (G, P, and RU) could potentially respond. Since there were 36 trials of each playback type (scream, mixed caw, inflected alarm caw, alert caw), and 3 potential respondents, a total of 108 bird-sequences was potentially possible for each playback type/ response type combination. The number given at the top of each histogram shows the actual number out of the potential 108.
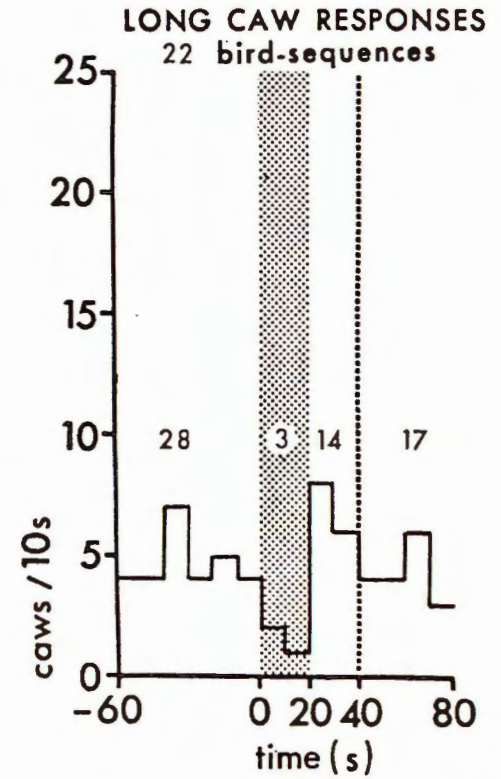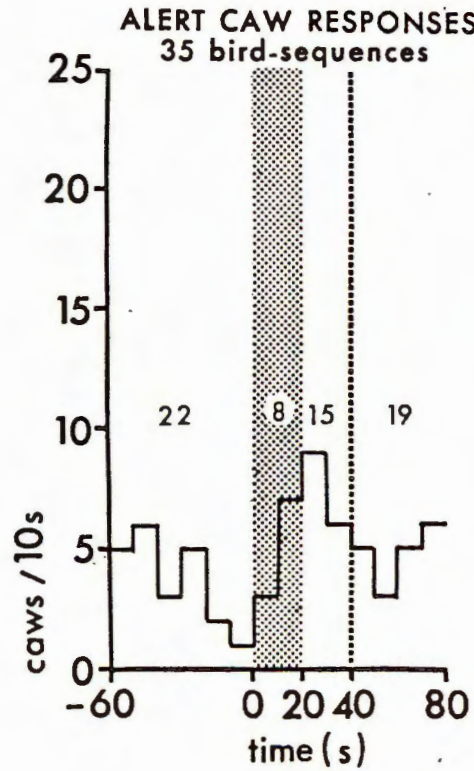
MIXED CAW PLAYBACKS

Figure 9. Responses to inflected alarm caw playbacks. The pre-playback interval included in the analysis (G-tests) described in the text is -60 to -0 s; the stippled during-playback interval, 0-20 s; and the post-playback interval, 20-40 s. The 40-80 s interval is included in the graphs to provide extra contextual information on caws occurring later in time. Numbers in each space indicate the total number of caws for that particular time interval (pre-, during-, or post-playback) and were the same numbers entered in the statistical analyses. A bird-sequence is defined as the record of caws occurring in the sequential series of 10 s intervals from -60 to 80 s during a given playback trial, for a given individual. During any single playback trial, all three receivers scored (G, P, and RU) could potentially respond. Since there were 36 trials of each playback type (scream, mixed caw, inflected alarm caw, alert caw), and 3 potential respondents, a total of 108 bird-sequences was potentially possible for each playback type/ response type combination. The number given at the top of each histogram shows the actual number out of the potential 108.

INFLECTED ALARM CAW PLAYBACKS

MIXED CAW RESPONSES
3 bird-sequences

ALERT CAW RESPONSES
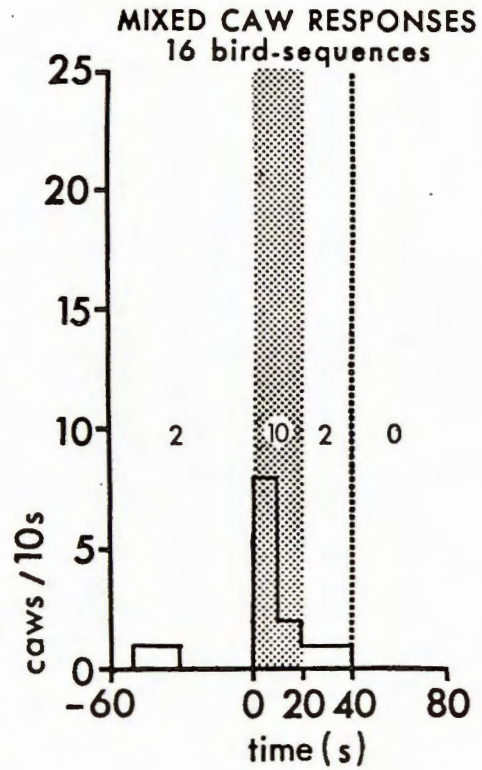38 bird-sequences

LONG CAW RESPONSES
23 bird-sequences

25a

Figure 10. Responses to alert caw playbacks.

The pre-playback interval included in the analysis (G-tests) described in the text is -60 to -0 s; the stippled during-playback interval, 0-20 s; and the post-playback interval, 20-40 s. The 40-80 s interval is included in the graphs to provide extra contextual information on caws occurring later in time. Numbers in each space indicate the total number of caws for that particular time interval (pre-, during-, or post-playback) and were the same numbers entered in the statistical analyses. A bird-sequence is defined as the record of caws occurring in the sequential series of 10 s intervals from -60 to 80 s during a given playback trial, for a given individual. During any single playback trial, all three receivers scored (G, P, and RU) could potentially respond. Since there were 36 trials of each playback type (scream, mixed caw, inflected alarm caw, alert caw), and 3 potential respondents, a total of 108 bird-sequences was potentially possible for each playback type/ response type combination. The number given at the top of each histogram shows the actual number out of the potential 108.
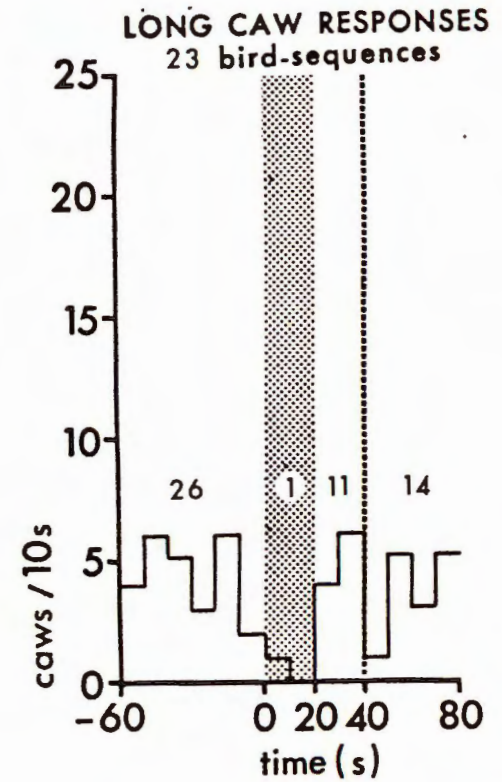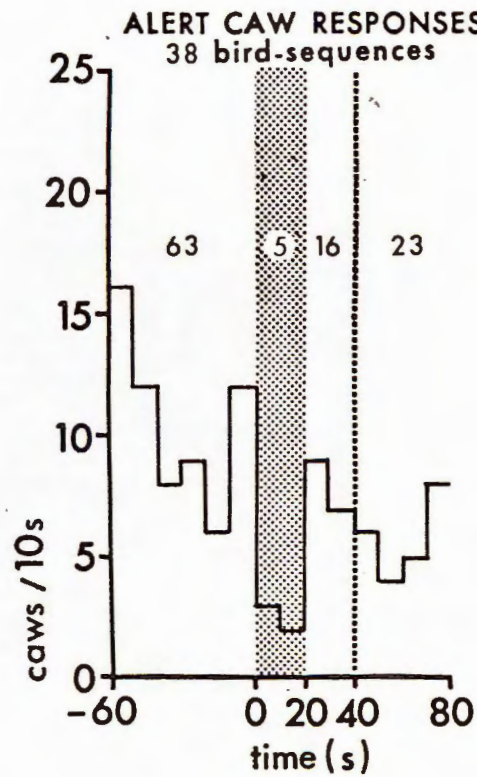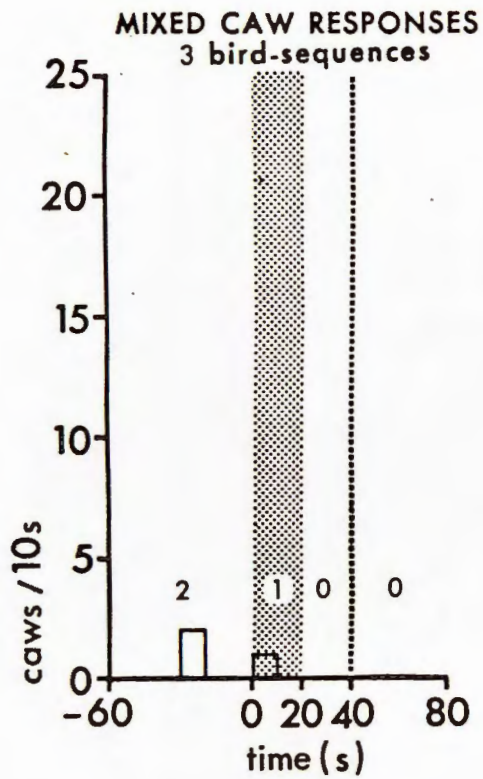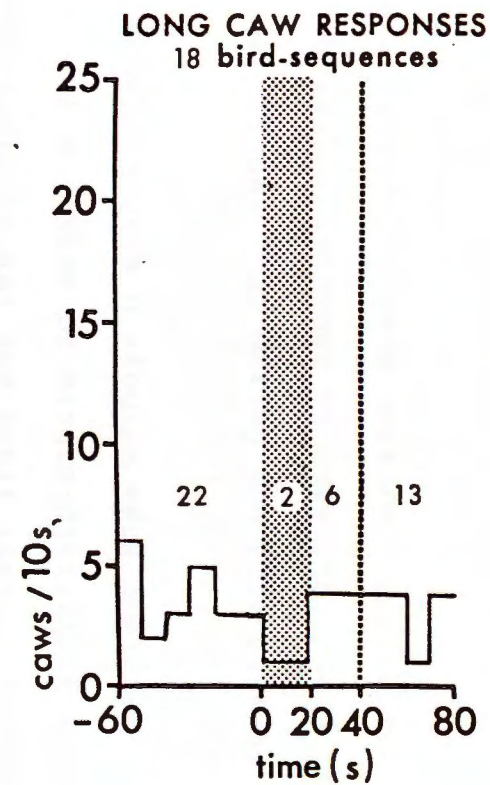
ALERT CAW PLAYBACKS

MIXED CAW RESPONSES
4 bird-sequences

ALERT CAW RESPONSES
53 bird-sequences

LONG CAW RESPONSES
18 bird-sequences
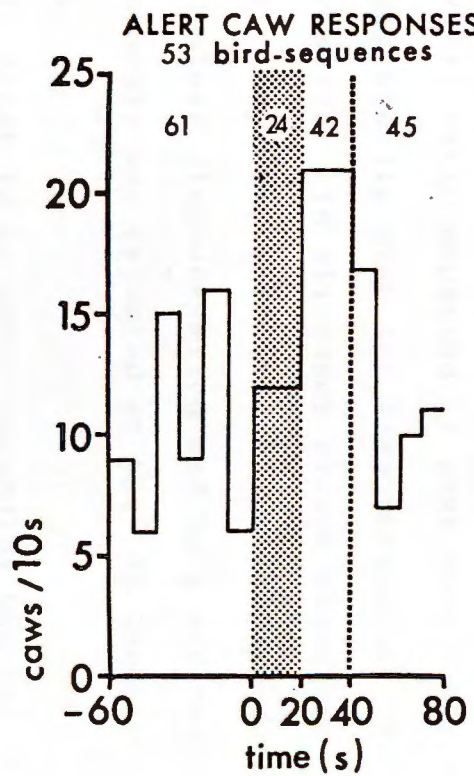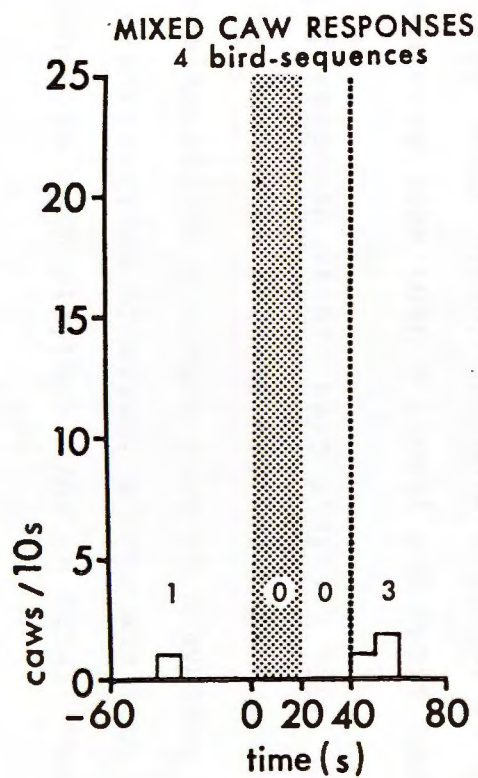
Long caws (Figs. 7-10) were uniformly suppressed during playback. They either returned to baseline levels (Figs. 9-10) or increased (Figs. 7-8) during the post-playback period.

The data shown in each histogram were analyzed statistically with a series of single-classification G goodness-of-fit tests (Sokal and Rohlf 1969). In each test, the observed ratio of caws distributed over the 60 s pre-, 20 s during-, and 20 s post-playback intervals were tested against the 3:1:1 ratio expected if caws were distributed proportionately equally over the time intervals. Table 2 shows these results: in all cases except mixed caw playback/alert response, inflected alarm playback/mixed caw response, and alert playback/mixed and long caw responses, the null hypothesis was rejected at the .05 level of significance.

A general caveat is in order regarding the reliability of some of the statistical results, since in some cases sample sizes were small ($n < 50$) and more than 20% of the expected values were less than 5 (Sokal and Rohlf 1969).

Patterns of response within each playback type

In order to determine whether different patterns of response were elicited by a single type of playback, I compared the distributions of mixed, alert, and long caws given in response to each playback type in turn. These

TABLE 2

Results of single-classification G goodness of fit tests for
caw distributions over the pre-, during-, and
post-playback intervals

Playback type

Response type		screams			mixed caws			alarm caws			alert caws		
		p	d	p	p	d	p	p	d	p	p	d	p
	mixed caws	2	16	10	2	10	2	--	--	--	--	--	--
			S			S							
	alert caws	48	7	28	22	8	15	63	5	16	61	24	42
			S			NS			S			S	
	long caws	13	4	10	28	3	14	26	1	11	22	2	6
			S			S			S			NS	

S indicates statistical significance, i.e., rejection of the null
hypothesis at α = .05; NS indicates acceptance. A dash indicates
sample size was too small to perform the test. p, d, p indicate
the 60 s pre-, the 20 s during-, and the 20 s post-playback intervals.

distributions within playback types were tested statistically by means of 4 two-way G tests of independence (Sokal and Rohlf 1969), the results of which are presented in Table 3.

Playbacks of screams elicited different patterns of response: distributions of mixed, alert, and long caws were significantly different (α = .05). Screams elicited mixed caws immediately, which then decreased after playback. Alert and long caws were suppressed, but reached a peak after playback. Their distributions were not significantly different.

Playbacks of mixed caws resulted in responses similar to those for screams. Mixed, alert, and long caw responses were significantly different when entered in a single analysis, but alert and long caw responses were not significantly different when tested without mixed caw responses. Mixed caw playbacks elicited mixed caws immediately. Alert caws were not suppressed though long caws were, and both reached a peak after playback.

Playbacks of inflected alarm caws elicited no mixed caws, and distributions of alert and long caws were not significantly different. Both were suppressed during playback and increased to baseline levels afterwards, though alert caws were sometimes somewhat suppressed over a longer post-playback period (Fig. 9).

TABLE 3

Results of two-way G tests of independence for numbers of caws over pre-, during-, and post-playback intervals for all types of response to a given playback type

Playback type

Response type	screams p d p			mixed caws p d p			alarm caws p d p			alert caws p d p		
mixed caws	2	16	10	2	10	2	--	--	--	--	--	--
alert caws	48	7	28	22	8	15	63	5	16	61	24	42
long caws	13	4	10	28	3	14	26	1	11	22	2	6
outcome	S			S			NS			S		

S indicates statistical significance, i.e., rejection of the null hypothesis at α = .05; NS indicates acceptance. A dash indicates sample size was too small to perform the test. p, d, p indicate the 60 s pre-, the 20 s during-, and the 20 s post playback intervals.

Playbacks of alert caws elicited no mixed caws, and elicited significantly different patterns of alert and long caw responses. Long caws were suppressed whereas alert caws were not; alert caws reached a high peak after playback, while long caws returned to baseline levels.

Patterns of response across playback types

To determine whether a single response pattern varied depending on the type of playback caw that elicited it, I compared the distributions of caws elicited by all playback types for each response type (mixed, alert, or long caws) in turn. These distributions across playback types were tested statistically with 3 two-way G tests of independence, the results of which are presented in Table 4.

Mixed caws were elicited only by scream or mixed caw playbacks, and not by inflected alarm or alert caw playbacks. The distributions of mixed caws elicited by scream and mixed caw playbacks were not significantly different, both including an immediate peak and then progressive decrease, but screams elicited mixed caws at a higher level over a longer time.

The distributions of alert caws in response to the 4 playback cawtypes were significantly different from each other. Alert caws were suppressed by screams or inflected alarm caws, but not by mixed caw or alert caw playbacks. Alert caws reached a high peak with respect to baseline

TABLE 4

Results of two-way G tests of independence for numbers of caws
over pre-, during, and post-playback intervals for
a given response to all playback types

Response type

	mixed caws			alert caws			long caws		
	p	d	p	p	d	p	p	d	p
screams	2	16	10	48	7	28	13	4	10
mixed caws	2	10	2	22	8	15	28	3	14
alarm caws	--	--	--	63	5	16	26	1	11
alert caws	--	--	--	61	24	42	22	2	6
outcome	NS			S			NS		

Playback type (row label)

S indicates statistical significance, i.e., rejection of
the null hypothesis at α = .05; NS indicates acceptance.
A dash indicates sample size was too small to perform
the test. p, d, p indicate the 60 s pre-, the 20 s
during-, and the 20 s post-playback intervals.

levels (=pre-playback) in response to scream, mixed caw, or alert caw playbacks, but barely returned to baseline levels in response to inflected alarm caws.

The distributions of long caws, elicited by the 4 playback types, were not significantly different from each other. Long caws were always suppressed and then returned to baseline levels, although in response to scream and mixed caw playbacks a post-playback peak was reached.

DISCUSSION

From the contexts in which the caws in this study
occurred, and from the responses to playbacks, some
conclusions can be drawn about the functions of these vocal
signals. Screams and mixed caws seemed to be used to
indicate immediate danger and to elicit mobbing behavior
from other crows within earshot. This interpretation is
supported in part by the fact that inflected alarm and alert
caw playbacks elicited negligible numbers of mixed caws.
Screams, associated with very intense mobbing behavior, were
a more potent signal than mixed caws: they elicited more
mixed caws, and suppressed alert caws to a greater degree
(the weak elicitation of alert responses during mixed caw
playbacks probably accounted for the non-significant results
of that particular single-classification goodness of fit
test). Inflected alarm caws seemed to be used only to
indicate flying raptors, some species of which are crow
predators, at a certain distance and altitude. Inflected
alarm caws elicited no mixed caws, screams, or other mobbing
behavior, and probably function to notify others of the
presence of an aerial predator. Parenthetically, it should
be noted that crows may sometimes rob raptors of their prey
(pers. obs.), and therefore the question of who is the
potential victim may be raised in some cases (Coombs 1978).
Long caws seemed to function as an "all clear" signal
because they were elicited in greater numbers after scream

and mixed caw playbacks; they probably also indicated "business as usual" and thus were suppressed in contexts involving immediate danger. Alert caws are probably multifunctional, since they occurred in a range of contexts including a few in which mixed caws may occur, and because they were suppressed by screams and inflected alarm caws but not by mixed caws and alert caws. Alert caws may function to indicate danger of less immediacy, "all clear," or "business as usual."

The types of information that might be carried by the various caws include those enumerated by Frankenberg (1981) for avian mobbing (e.g., screams and mixed caws) as well as other types encoded in caws not used during actual mobbing (e.g., inflected alarm, alert, and long caws). Screams, mixed caws, and inflected alarm caws all indicate that there is danger, while alert caws sometimes indicate danger. The type and/or immediacy of the danger can be indicated by the type of caw used, and the cessation of immediate danger can be indicated by long caws. Other birds are thus alerted to potential threats. Others can also find the vicinity of the predator: screams and mixed caws indicate the location of the mobbing assemblage around the predator; inflected alarm caws indicate an aerial predator within sight of the sender; alert caws indicate an occurrence at some distance from the sender. Information on the predator's movements can be carried by bouts of screams and mixed caws indicating waxing

and waning intensity of the mobbing, which is correlated with behavior of the predator (pers. obs; Frankenberg 1981). Further information on movement can be gained from listening to the vocalizations of various groups of crows in a large area: for instance, successive groups might give alert caws, mixed caws, and long caws in turn as the predator approaches, enters, and leaves their immediate vicinity. Information on the distance of the predator, and thus perhaps of the severity of the danger, may be had by the listener. Cultural transmission of predator recognition may also be effected (Curio, Ernst, and Vieth 1978). Finally, these caws give information to the predator so it knows that it has been discovered and is being watched.

In addressing the topic of the evolution of the common crow's vocal behavior in contexts associated with danger, it is important to consider (1) crow social organization; (2) design features of the communication system; and (3) current hypotheses on the evolution of avian mobbing in general.

Crows are monogamous and form life-long pair bonds (Good, 1952; Goodwin, 1976). The young remain with their parents as a family unit for months. Yearlings often return to associate with their parents and new siblings, as well as with other yearlings and unmated birds in their home area (Good 1952). Individual birds tend to return to traditional nest sites (Good 1952), feeding areas (Aldous 1944; Good 1952) and roost sites. In the spring and summer, families

stay together; in the fall and winter, families and individual crows join loose feeding flocks during the day and large communal roosts at night. At all seasons, crows participate in communal harassment of predators.

All the caws associated with contexts involving danger are long-distance broadcast vocalizations, and as such communicate the sender's message over a considerable area and distance. The use of vocal communication by crows thus provides a network allowing coordination of widely-scattered individuals or groups in communal action against serious threats, assessment of the nature and severity of the threat, and notification of return to the status quo. Presuming that such a system is adaptive, since behavior in contexts involving danger should be strongly influenced by natural selection, it is reasonable to speculate on the selective forces involved. Hypotheses about the adaptive significance of avian mobbing, reviewed by Curio (1978), provide a basis for this speculation. The various hypotheses presume individual selection and/or kin selection to be operating. Although my data do not allow discrimination among the following hypotheses, they point to design features of the crow vocal communication system which may be used as indirect evidence in support of all of the following hypotheses.

Since crows tend to feed, nest, and roost in traditional areas, individuals in an area would benefit from causing a

predator to leave the area either because it was stressed or molested by mobbers ("Move On" hypothesis, which suggests that mobbers benefit by driving the predator away, so it cannot obtain prey or knowledge of the locale), because it got no prey as a result of losing the advantage of attacking by surprise ("Perception Advertisement" hypothesis, which suggests that mobbers benefit if the predator gives up hunting because it realizes its quarry cannot be taken by surprise), or because it could not single out an individual from a group of mobbers ("Confusion Effect" and "Selfish Herd Effect" hypotheses, which suggest that mobbers benefit by joining a group, which may confuse the predator by unpredictable movements, or may simply reduce the risk to each individual member). Young or inexperienced birds might soon learn about particular dangers from experienced relatives or adults ("Cultural Transmission" hypothesis, tested by Curio, Ernst, and Vieth 1978, which suggests that birds learn to fear objects by seeing those objects mobbed by others; kin selection could act in such a case). Birds in an area are alerted and can be on guard ("Alerting Others" hypothesis, tested by Curio, Ernst, and Vieth 1978 and Frankenberg 1981, suggests that listeners can be warned, and thus helped, by mobbers). In such a case kin selection may be operating. "Aid a Distressed Relative" hypothesis suggests that mobbing may startle or confuse a predator, allowing its victim to escape and thus helping that victim.

Kin selection or reciprocal altruism (Rohwer, Fretwell, and Tuckfield 1971) might also act in this case, since many crows in an area may be closely related; Good (1952) found that 95% of the crows of all ages banded in a certain locale were retaken in the same area.

It is also possible that sources of selection which are unrelated to predation have to some degree shaped mobbing behavior in crows. Such selection could be related to social organization and social mechanisms which might integrate members of a population who, for instance, feed communally. In watching a large mobbing party of crows, I have often gotten the impression that there is a certain amount of purely social palaver, as well as choruses of caws and aerial acrobatics in excess of those strictly necessary to harass the predator. I have also observed large, early-morning mobs seem to become, after the disappearance of the predator, occasions for communal choruses of cawing sometimes heard before the birds disperse to feed.

It seems clear that the mobbing behavior of crows has been shaped by a variety of selective forces, and that no one hypothesis accounts entirely for all aspects of mobbing behavior. Detailed analysis of the vocalizations which are essential behavioral elements in particular contexts, here those involving danger, can thus contribute to our overall understanding of the ultimate functions of certain behaviors.

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    responses of male ovenbirds to recorded songs of
    neighboring and more distant individuals. Auk 76,
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INTRODUCTION

Several hypotheses, such as the selfish herd hypothesis (Hamilton 1971), have been proposed to explain the evolution of avian mobbing behavior (reviewed by Curio 1978 and discussed in Brown, in prep.). Some of these hypotheses invoke kin selection in accounting for selective advantages gained by the sender or receiver of information encoded in mobbing vocalizations. If relatives came to the aid of a mobber (Rohwer, Fretwell, and Tuckfield 1976), if individuals whose relatives were within hearing distance mobbed more strongly (Sherman 1977; Curio 1978), or if the mobber's kin learned to fear the specific features of predators (Curio 1978), selection for mobbing behavior might be presumed to take the form of kin selection.

This paper, a sequel to the preceding paper (Brown, in prep.) on functional interrelationships among mobbing and alarm calls of common crows (Corvus brachyrhynchos), examines the degree of social familiarity between sender and receiver as a variable affecting responses to those calls. I test the hypothesis that crows respond more strongly to the voices of well-known (kin) or familiar individuals than of unknown, anonymous crows. The outcome is relevant to the question of which types of selective forces may be inferred to have shaped mobbing behaviors.

MATERIALS AND METHODS

The subjects and methods used in this study are the same as those used in Part 1; therefore, I give only a brief summary here, noting differences in the data analysis, and refer the reader to Brown (in prep.) for a full description.

The subjects of this experiment were 7 tame captive common crows (Corvus brachyrhynchos) housed in 4 large outdoor aviaries in a rural area in Prince George's County, Maryland. Three of the birds (G, RU, and P) were siblings. G and RU were housed together, and P was housed alone at a short distance as described in Part 1. J and N were housed together adjacent to G and RU. BN and LN were housed together at a short distance from the other aviaries.

I prepared test tapes for playback experiments, and conducted experiments, as described in Part 1.

In analyzing the tape recorded responses to playback trials, I transcribed each track of each tape separately. Each single track carried the responses of birds in one aviary. I noted the type of vocalization given, the identity of the vocalizer, and the time with respect to playback onset for the 2 min previous to, the 20 s during, and the 2 min after playback. However, I ultimately used data for only the 1 min previous to, the 20 s during, and the 20 s post playback. I tallied three response types (mixed caws, alert caws, and long caws) separately for the four

separate types of test caws (screams, mixed caws, inflected alarm caws, and alert caws) played back. I used responses from only 3 of the receivers (G, RU, and P), all siblings, and combined the data from these birds.

For each type of response to each type of playback caw, I further subdivided the tallies on the basis of the relationship of the 3 sibling receivers to the sender whose voice was played back. The taped sender was classified either as a sibling (cage-mate or former cage-mate); a familiar bird caged within sight and hearing; an unknown, anonymous crow; or itself. Thus, G, P, and RU heard siblings or themselves when hearing the voices of G, P, and RU played back; heard familiar birds when hearing J's and BN's voices played back; and heard an unknown bird when an anonymous wild crow's voice was played back.

Single-classification G goodness-of-fit tests (Sokal and Rohlf 1969) were performed on the ratios of responses to sibling, familiar, and unknown crows. Tests were performed on these ratios for each type of response (mixed, alert, and long caws) to each type of test caw (screams, and mixed, inflected alarm, and alert caws) within each time interval (pre-, during-, and post-playback). The "self" category, i.e., responses by birds to their own taped voices, although not lumped with other categories, was not included in the analysis. I thought that the birds, although perhaps not recognizing their own voices, might be prompted to respond

simply because their companions, who recognized the voice, responded. If such were the case, responses in the "self" category would accurately reflect neither the birds' ability to recognize their own voices, nor natural situations in which birds were stimulated to respond because others responded.

<div align="center">RESULTS</div>

Vocalizations used in the study

Descriptions, sonagrams, and contextual information pertinent to the vocalizations included in this study may be found in Part 1 (Brown, in prep.).

However, several points are important to note here. First, each crow's voice was highly individualistic (Brown 1979), regardless of the type of caw being made, probably in much the same way that human voices are individually recognizable. Figs. 11 and 12 show examples of two cawtypes made by two different birds. I have learned to recognize individuals by their voices, and am convinced that the tame crows recognized each other's voices equally well, since they often answered each other differentially. For instance, if a cage-mate was temporarily removed, the remaining bird would fly continually about the aviary, cawing; upon hearing the voice of its companion, it would orient immediately in the direction of the sound and a volley of caws would be rapidly exchanged. Second, it is

Figure 11. Alert caws by two individual crows, illustrating

vocal differences which made possible recognition

by voice.
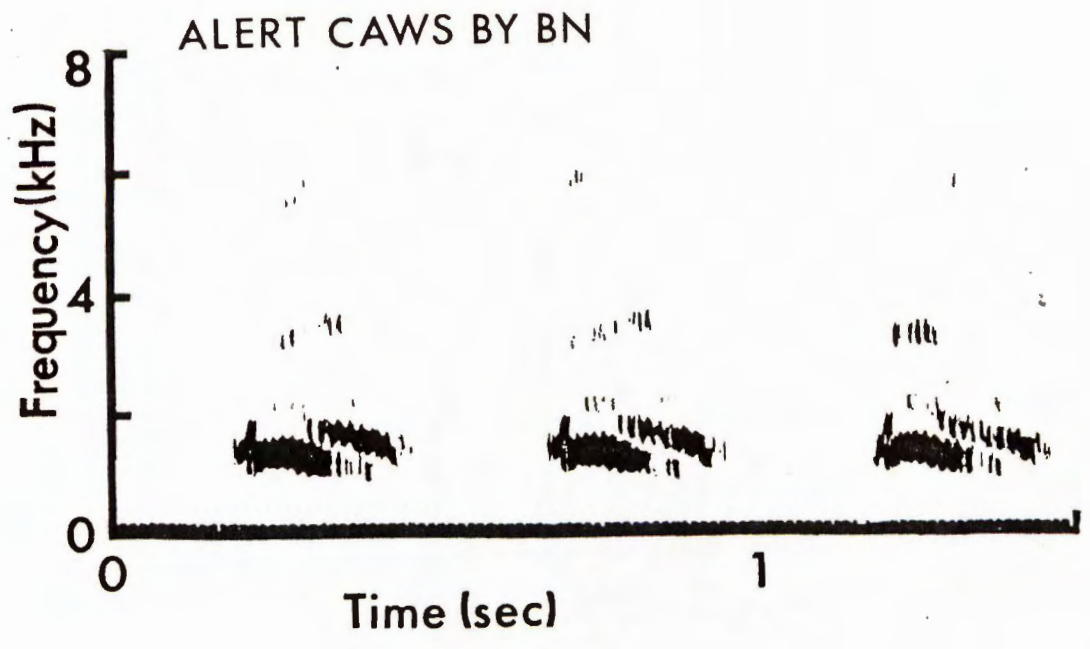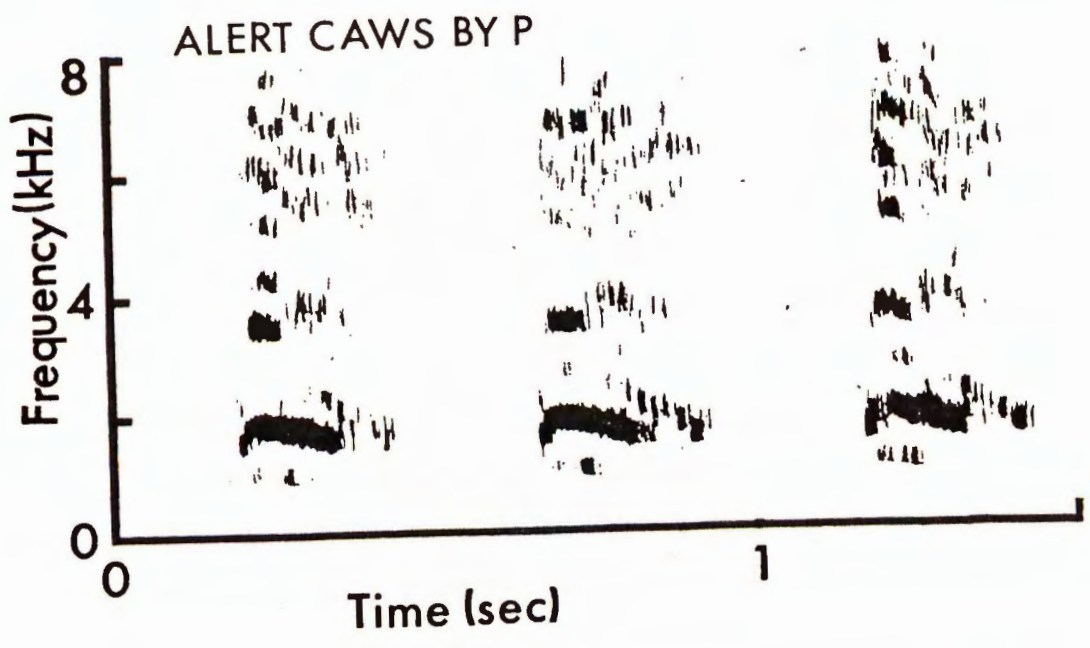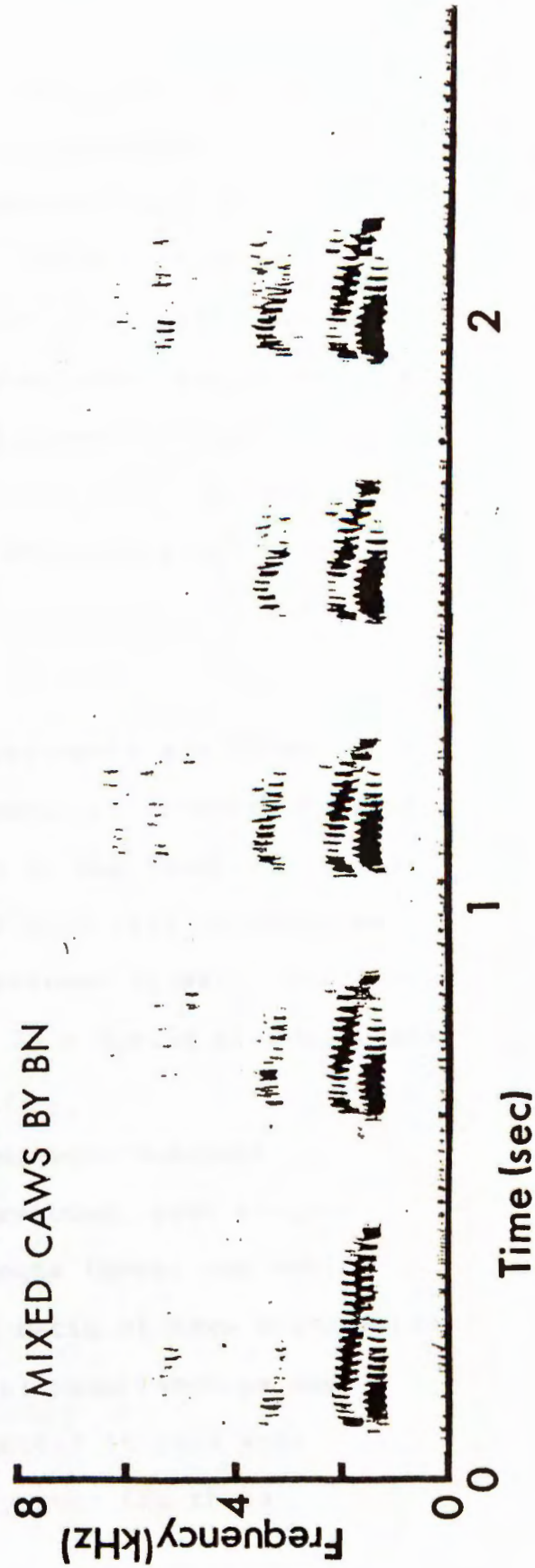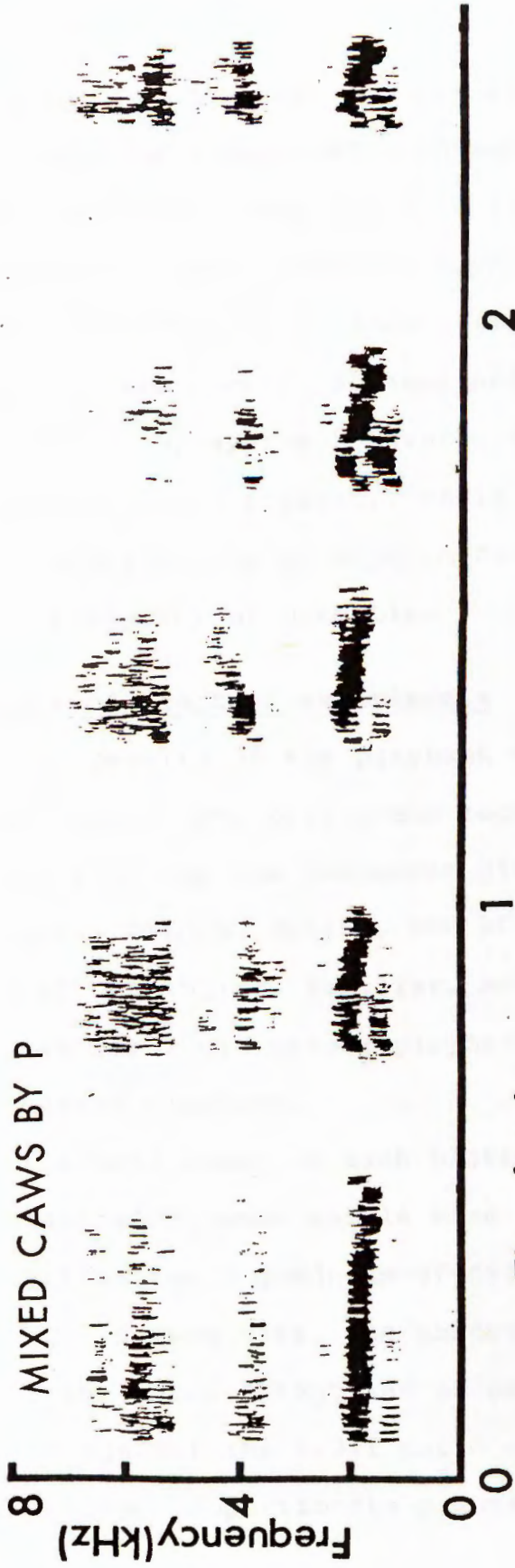
Top, P .

Bottom, BNC.

ALERT CAWS BY P

ALERT CAWS BY BN

Figure 12. Mixed caws by two individual crows, illustrating

vocal differences.

Top, P..

Bottom, BNC.

important to note that screams and mixed caws are the vocalizations associated with mobbing behavior; inflected alarm caws, with long intercaw intervals, might be considered "aerial predator warning calls." None of these calls are difficult to locate (Marler 1955), and none cause crows to take cover. Screams and mixed caws are frequently accompanied by approach toward, and often physical harassment of, a predator, while inflected alarm caws often cause crows to fly to a perch from which they can survey as much of the sky as possible.

Results of playback experiments

The results of the playback experiments are shown in Figs. 13-16. The histograms represent the numbers of mixed, alert, and long caw responses given by the receivers (3 siblings) before, during, and after each type of test caw uttered by sibling, familiar, and unknown crows. Caws were tallied for 1 min before playback, 20 s during playback, and 20 s after playback.

The data shown in each histogram were analyzed statistically, when sample size permitted, with single-classification G goodness-of-fit tests (Sokal and Rohlf 1969). In each test, the observed ratio of caws distributed among the three categories of social relationships was tested against the 2:2:1 ratio expected if caws were distributed proportionately equally over the three

Figure 13. Responses to different senders during scream
playbacks.

Numbers of caws given by the 3 sibling receivers
to each type of sender (S=sibling, F=familiar,
U=unknown) in the intervals pre (60 s), during
(20 s), and post (20 s) playback. Pre-playback
activity is adjusted to caws/20 s. The dashed
lines aid visual comparison of the proportional
number of caws given in response to each class of
sender, and represent an adjustment of the actual
2 sibling:2 familiar:1 unknown sender ratio to
2 sibling:2 familiar:2 unknown sender ratio.
This was done for heuristic purposes only; the
actual numbers entered in the statistical
analyses (G-tests) are indicated by solid lines.
ns = not significant (p > .05)
s = significant (p < .05)
nt = no test due to small sample size.

SCREAM PLAYBACKS

MIXED CAW RESPONSES

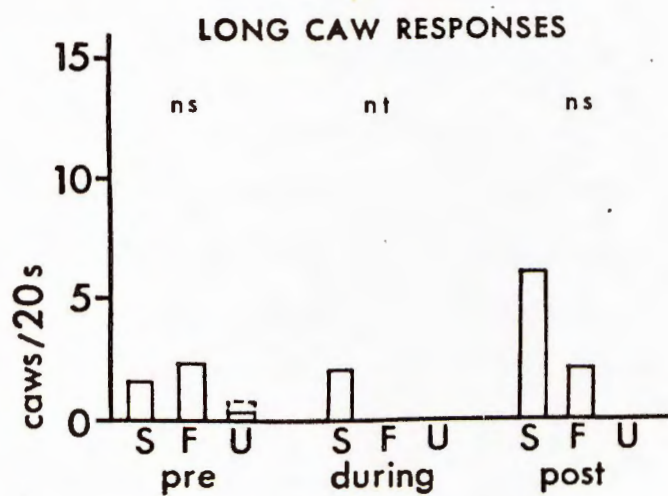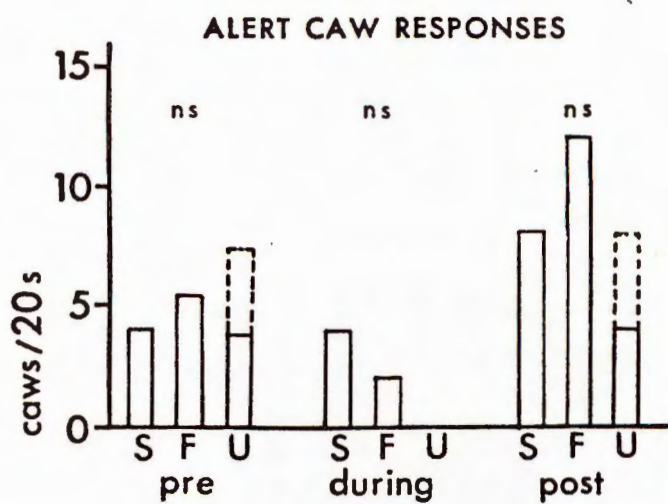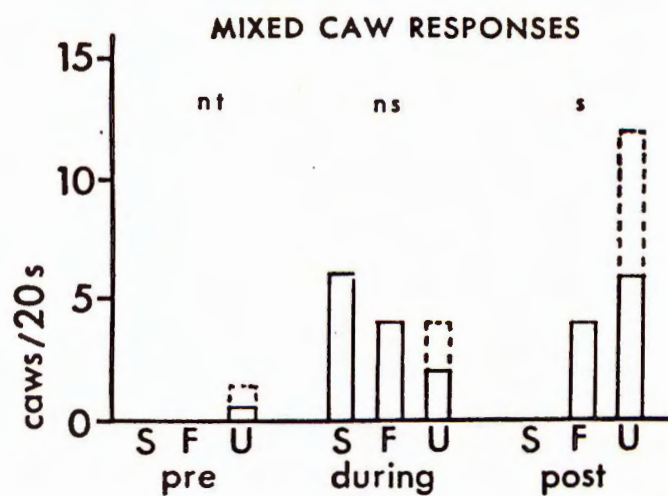ALERT CAW RESPONSES

LONG CAW RESPONSES

Figure 14. Responses to different senders during mixed caw
playbacks.

Numbers of caws given by the 3 sibling receivers
to each type of sender (S=sibling, F=familiar,
U=unknown) in the intervals before (60 s), during
(20 s), and post (20 s) playback. Pre-playback
activity is adjusted to caws/20 s. The dashed
lines aid visual comparison of the proportional
number of caws given in response to each class of
sender, and represent an adjustment of the actual
2 sibling:2 familiar:1 unknown sender ratio to
2 sibling:2 familiar:2 unknown sender ratio.
This was done for heuristic purposes only; the
actual numbers entered in the statistical
analyses (G-tests) are indicated by solid lines.
ns = not significant (p > .05)
s = significant (p < .05)
nt = no test due to small sample size.

MIXED CAW PLAYBACKS

MIXED CAW RESPONSES

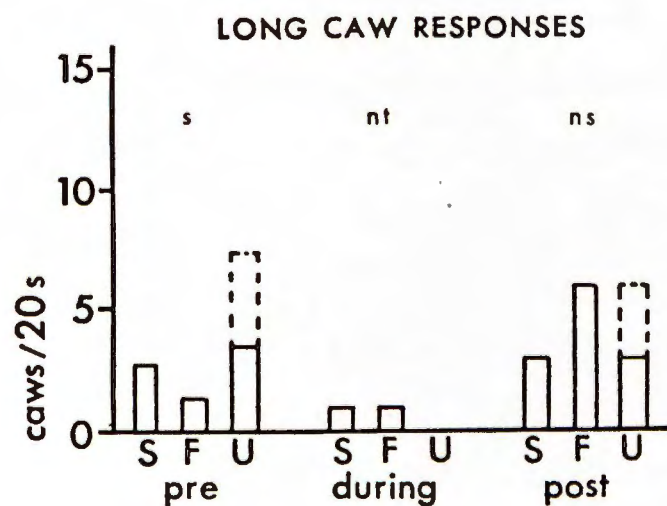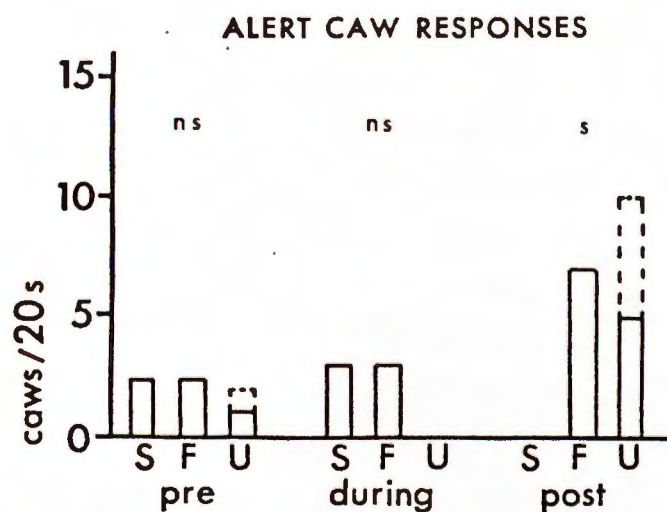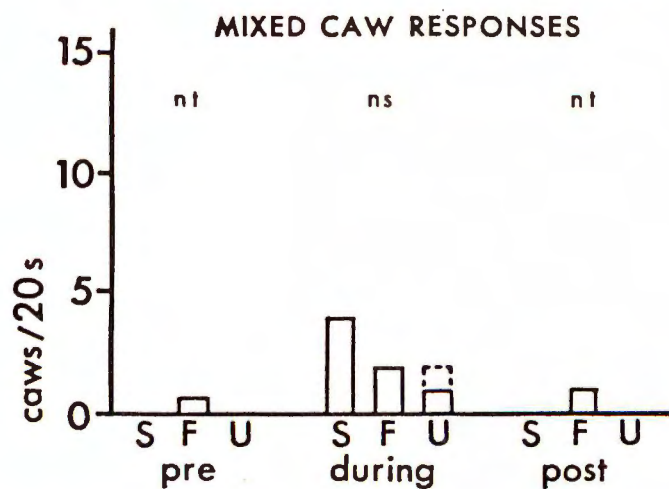ALERT CAW RESPONSES

LONG CAW RESPONSES

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Figure 15. Responses to different senders during selected
alarm caw playbacks.

Numbers of caws given by the 3 sibling receivers
to each type of sender (S=sibling, F=familiar,
U=unknown) in the intervals before (60 s), during
(20 s), and post (20 s) playback. Pre-playback
activity is adjusted to caws/20 s. The dashed
lines aid visual comparison of the proportional
number of caws given in response to each class of
sender, and represent an adjustment of the actual
2 sibling:2 familiar:1 unknown sender ratio to
2 sibling:2 familiar:2 unknown sender ratio.
This was done for heuristic purposes only; the
actual numbers entered in the statistical
analyses (G-tests) are indicated by solid lines.
ns = not significant ($p > .05$)
s = significant ($p < .05$)
nt = no test due to small sample size.

INFLECTED ALARM CAW PLAYBACKS

MIXED CAW RESPONSES

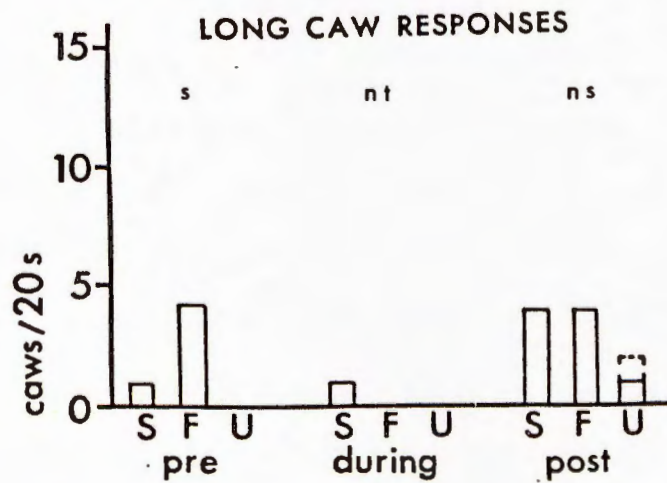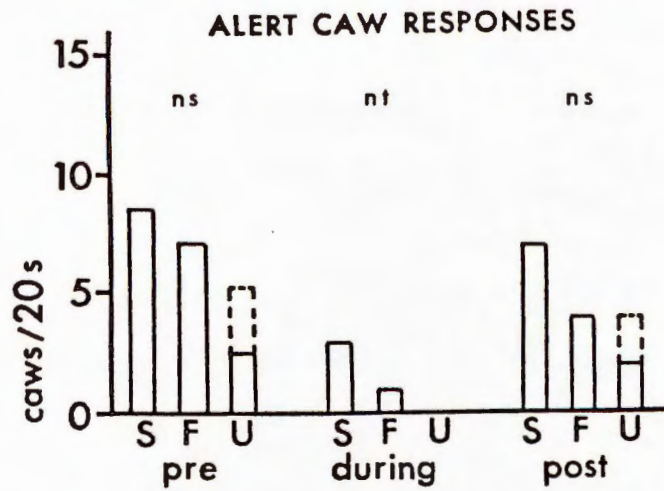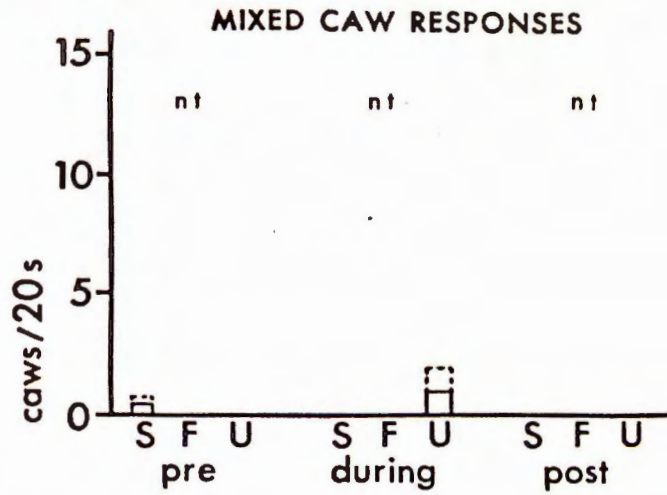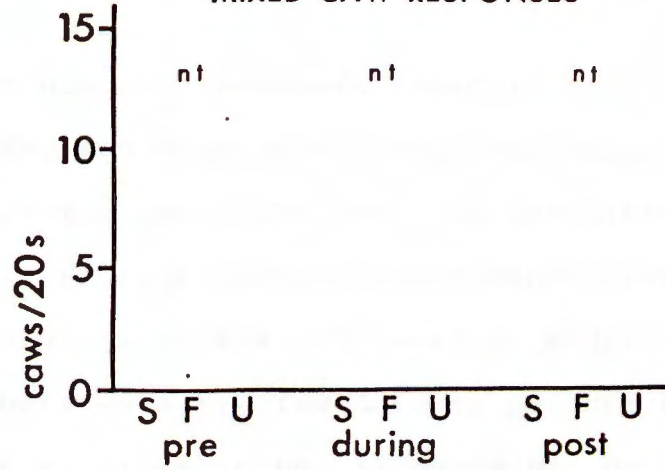**ALERT CAW RESPONSES**

LONG CAW RESPONSES

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Figure 16. Responses to different senders during alert caw
playbacks.

Numbers of caws given by the 3 sibling receivers
to each type of sender (S=sibling, F=familiar,
U=unknown) in the intervals before (60 s), during
(20 s), and post (20 s) playback. Pre-playback
activity is adjusted to caws/20 s. The dashed
lines aid visual comparison of the proportional
number of caws given in response to each class of
sender, and represent an adjustment of the actual
2 sibling:2 familiar:1 unknown sender ratio to
2 sibling:2 familiar:2 unknown sender ratio.
This was done for heuristic purposes only; the
actual numbers entered in the statistical
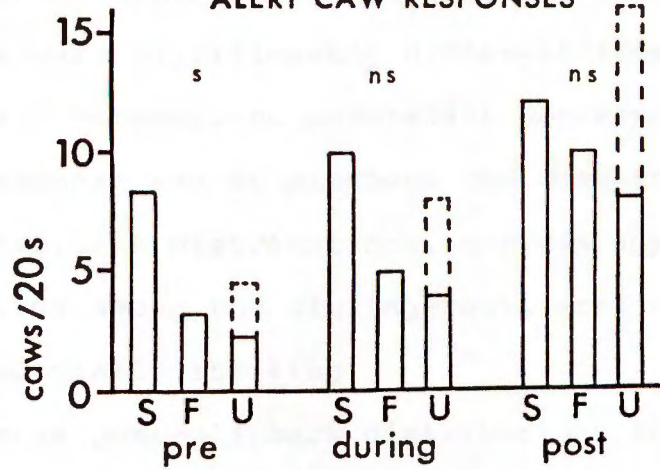analyses (G-tests) are indicated by solid lines.
ns = not significant ($p > .05$)
s = significant ($p < .05$)
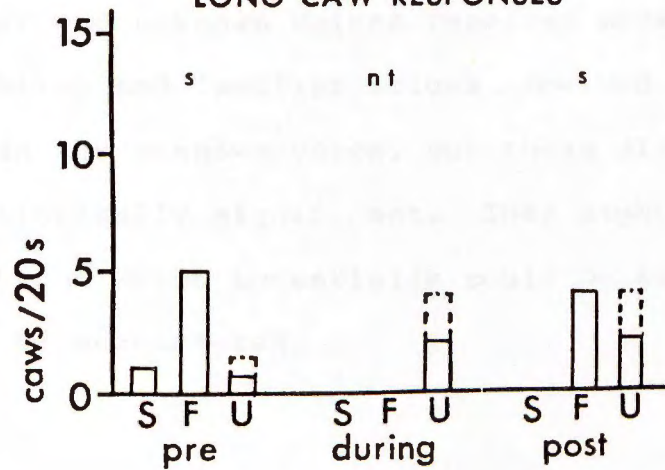nt = no test due to small sample size.

ALERT CAW PLAYBACKS

MIXED CAW RESPONSES

ALERT CAW RESPONSES

LONG CAW RESPONSES

categories, since the receivers heard recordings of two sibling and two familiar crows, but only one unknown crow. The results of the tests are shown on the histograms: "s" and "ns" indicate rejection and acceptance, respectively, of the null hypothesis at the .05 level of significance; "nt" means that there were too few data to perform a G test.

Of the 36 possible tests, 13 could not be performed because the sample sizes were too small. Of the remaining 23 tests, 4 pre-playback and 3 post-playback caw distributions were significantly different from expected distributions. However, no consistent patterns were evident: no type of response caw or playback caw consistently produced significant distributions, nor was any pattern of caw distribution among the sibling-familiar-unknown categories especially striking.

In the three post-playback distributions that showed a significant deviation from an expected distribution, sibling voices received fewer than the expected number of responses, while familiar and unknown voices received more. During playback, sibling and familiar voices received more responses than the unknown voice, but these distributions were not statistically significant. They might, at most, represent a trend which potentially could be enhanced were more data to be accumulated.

DISCUSSION

Given the results of the single-classification tests, there is no compelling evidence that crows respond to the voices of other crows from any particular social category more than another. A further indication that social relationship does not have a dramatic effect on responses in that the percentage of tests with significant results is about the same pre-playback and post-playback. Thus it is very possible that the factors responsible for significant pre-playback results could also be responsible for significant post-playback results. Had the percentage of significant post-playback tests been very high, it would have been more likely that social relationship had an effect.

The limitations of the data in this study are clearly evident. The results of the G tests must be interpreted with caution, since in most cases n<50 and more than 20% of the expected values are less than 5 (Sokal and Rohlf 1969). Further, the small sample sizes severely limited the choice of suitable statistical tests. For these reasons the data are inconclusive. More data would, at the least, allow a more convincing argument to be made. However, a word of caution is appropriate here: if the interval between trials would be shortened too much, habituation would be likely to occur; while if too many replicates were run, the temporal homogeneity of the experimental conditions would be lessened.

With more data there might still be no apparent effect of social relationship on response, but it would then be possible to make a more positive statement that such was the case. Alternatively, some of the "trends" in the present data, such as greater numbers of caws in response to siblings and familiar birds during playbacks, might be enhanced in a larger data set.

This study addresses hypotheses about the adaptive significance of mobbing by focusing on the question of which individuals respond to the mobbing (i.e., screams and mixed caws) of which others. This approach can give some indication of the type of selective forces which have resulted in benefits for the callers as well as for those who respond. In the present study, bearing in mind the limitations of the data, there is no particular support for the idea that kin (or birds among whom long-term bonds exist, since the study does not differentiate between the two) are responded to more strongly than others. Kin selection for soliciting aid from relatives (Sherman 1977; Rohwer, Fretwell, and Tuckfield 1976) is thus not likely to explain benefits to either the caller or responders. This evidence is in line with observations of mixed-species mobbing (Stefanski and Falls, 1972; Curio 1978; pers. obs.) which certainly do not suggest kin selection (Curio 1978). It might still be possible for kin selection, or reciprocal altruism (Trivers 1971) as suggested by Rohwer et al.

(1976), to work "blindly" if many birds in an area are related and/or if the species is sedentary, so that most conspecifics joining a mob would be relatives or long-term associates. There is evidence that this may the case in crows (Good 1952), but the species is partly migratory and it is not known how the winter influx of northern migrants is integrated into the more southern resident populations.

How, then, could selfish responders, who are not aiding kin, benefit? It has been suggested that predators may leave an area sooner, and return less often, if they get no prey (see Curio 1978 for review of this hypothesis). For individual crows, which feed, nest, and roost in particular areas as a matter of tradition, such benefits might be substantial. Risks of mobbing might also be relatively low for crows, which are large enough to inflict real damage and may attack predators. Further, the fact that other species are alerted to danger by crow mobbing may result in even less hunting success for predators. As an example, my success in shooting rats which entered the aviaries was greatly diminished after the rats, which were habituated to my presence, learned to correlate the screams of the crows upon seeing the gun, with impending danger. By joining a "selfish herd" (Hamilton 1971) of mobbers, the risk taken by each is reduced, and, as Curio (1978) suggests, it may be wiser for potential prey "to run a diminished risk immediately than the full risk unprepared" (p. 177). The

idea of Owens and Goss-Custard (1976) that loud, locatable alarm calls function in flock formation in species which are dispersed may also be applicable to crows.

Although the data presented here do not permit conclusive statements, the approach of looking at who responds to whom seems to be potentially fruitful. It might be useful to set up experiments in such a way that receivers could see and hear (Curio, Ernst, and Vieth 1978; Frankenberg 1981) birds of different social categories (well-known, familiar, unknown) mobbing, without themselves being able to see the mobbed object. It would have been advantageous, in my study, to lengthen the period of stimulus (playback) presentation during each trial. This adjustment would have resulted in more response vocalizations being given, and might have allowed differentiation of changes in response over the course of time. For instance, an immediate response might be given to well-known birds and a later response to unknown birds. Finally, it would be best to focus on mobbing vocalizations like screams and mixed caws in crows, which elicit immediate matching responses (Brown, in prep.), rather than "alarm" vocalizations which elicit neither immediate vocal responses nor approach to the source of the sound.

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in press   The role of song and vocal imitation in social
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            brachyrhynchos). Accepted by Z. Tierpsychol.

in press   Functional interrelationships among mobbing and alarm calls of common crows. Abstract accepted for XVIII International Ethological Conference, Brisbane 1983.

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