

ACOUSTIC RECOGNITION IN THE BELTED KINGFISHER: CARDIAC RESPONSE TO PLAYBACK VOCALIZATIONS¹

WM. JAMES DAVIS²

Department of Zoology, University of Texas at Austin, Austin, TX 78712

Abstract. The cardiac response (change in heartbeat) of adult, free-living birds was monitored to evaluate whether or not acoustic recognition occurs between mated kingfishers. Consistent differences in cardiac responses to playback of familiar vs. unfamiliar vocalizations were observed across all birds tested. The temporal patterning of the initial pulses of "approach calls," vocalizations emitted while birds approached their nests, was found to be less variable between calls of an individual than between calls sampled from different individuals. Statistical analysis of call parameters indicates that temporal patterning of the initial pulses could be used for individual recognition.

Key words: *Belted Kingfisher*, *Ceryle alcyon*, *acoustic recognition*, *vocalizations*, *cardiac responses*.

INTRODUCTION

Two persistent concerns of the ethologist have been to determine the function of communication signals and to determine how such signals encode information. Studies of acoustic recognition in birds have been particularly fruitful in deciphering how information is encoded (Beecher 1982; Emlen 1971, 1972; Falls 1983). To establish whether vocal recognition occurs in a particular species, researchers have provided circumstantial evidence from field observations, analyzed sound recordings, or conducted playback experiments, preferably with free-living birds (Beer 1970). Most playback experiments depend upon a difference in overt behavioral responses to show that birds can perceive differences in playback of different calls. For hole-nesting birds, overt behavior cannot be easily observed, so another technique is necessary. In the present study, I investigated acoustic recognition in the Belted Kingfisher (*Ceryle alcyon*), using an uncommon field technique of measuring heart rate for assessing behavioral responses of this hole-nesting species. In this paper, I present experimental evidence that individuals of this species use acoustic signals to discriminate between their mates and alien kingfishers.

The Belted Kingfisher usually nests in lone pairs along waterways that can provide both adequate food and a suitable nesting bank (Bent 1940, Davis 1982). Both sexes are vocal and overtly aggressive in defense of the breeding territory; males and females will respond aggressively to playbacks of an alien kingfisher's vocalization when played within their territory (Davis, unpubl. data). Furthermore, during nest

exchange the relieving bird will often sit outside the nest entrance and vocalize before entering, perhaps informing its mate that an exchange of incubation duties will follow. Since the kingfisher's nest is a deep burrow excavated in a vertical bank, incubating birds are visually isolated and must depend on vocal cues to be aware of their mate's presence. These facts suggest that mates should vocally recognize each other.

All signals within the Belted Kingfisher's vocal repertoire are comprised of broadband pulses with most of the sound energy below 8 kHz. When a kingfisher of either sex approaches or leaves its nest, it characteristically emits a short chatter (0.5 to 1.0 sec, see Fig. 1). Although the length and intensity of this "approach call" may vary, other parameters such as rate of pulse modulation and inter-pulse interval length seem relatively constant for calls of an individual. All analyses and playback experiments in this study use approach calls recorded primarily from kingfishers that were either coming to relieve their mates at the nest or to feed nestlings.

METHODS

In order to determine if kingfishers discriminate between calls of their mates and calls of other kingfishers, playback experiments were conducted at five nests along two streams in southern Ohio during May 1983. The two creeks, Indian and Beasley Fork, were similar in size and provided numerous exposed banks for nesting birds; a description of the habitats can be found in Davis (1982). As a measure of response to different calls, I monitored the heartbeat of incubating birds. Since the heart rate of vertebrates slows down when the animal becomes attentive to a stimulus (Dooling and Searcy 1980, Anthony and Graham 1983), this "orienting response" was used as a mea-

¹ Received 30 March 1985. Final acceptance 19 May 1986.

² Present address: Box 370, RR 1, Avon, MN 56310.

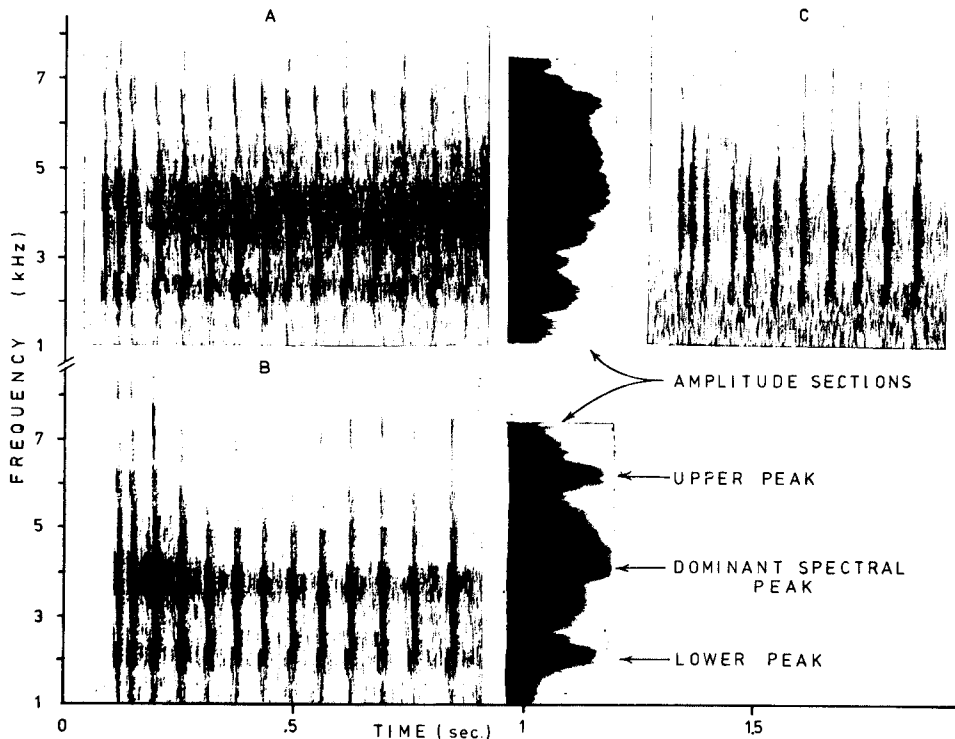


FIGURE 1. Three sonograms from three different kingfishers as they approached their nest during the incubation period or while feeding nestlings. To the right of sonograms A and B are amplitude cross sections which illustrate how sound energy is distributed across the frequency spectrum. Both cross sections were measured at the third pulse (syllable) from the left. Calls were recorded at varying distances from the microphone and the wide-band setting of the Sona-Graph was used.

sure of response to calls of mates and of alien birds.

I propose that the attention (reflected by changes in cardiac response) that a bird pays to a call of a conspecific individual will differ depending upon the bird's previous experience, i.e., a bird will either recognize a familiar call (of its mate), or the call will be unfamiliar (alien) to the bird. No assumptions were made concerning the effect that the different call types (sham, familiar, or unfamiliar) would have on cardiac output, therefore I used two-tailed criteria in the statistical tests ($\alpha = 0.05$). A consistent difference in response to each call type across subjects would be taken as evidence that individuals were discriminating between the three types. Furthermore, because previous analysis revealed no difference between acoustic structure or concomitant behavior of approach calls emitted by males or females (Davis 1985) data from the sexes were pooled for statistical analysis.

The monitoring device I used consisted of a stethoscope-like device constructed from a standard polyethylene petri dish (Fig. 2). This heart rate monitor (HRM) was inserted into the nest chamber, approximately 2 cm below the eggs. The floor of the nest is bare, sandy soil which is easily compacted over the HRM

(Fig. 2). Preliminary tests showed that the heartbeat of incubating birds was detected by the HRM while the heartbeat of young within the eggs was not. Laboratory trials were conducted to compare the output of the HRM with a standard EKG reading using a young pigeon placed in an artificial nest chamber with a bare sandy bottom. These trials indicated that heartbeat was detected by the HRM.

The experimental procedure was as follows: (1) a HRM was placed in each of five nests after laying had started (care was taken to minimize disturbance and in no case did an individual desert the nest after the HRM was inserted); (2) birds were captured in the nest and marked with lead-free paint on the tips of the rectrices. A spot of white paint was also placed on the crest of one individual at each nest (with the aid of a flashlight, this spot permitted identification of which bird was in the nest); and (3) over the period of incubation (average of 21 days, Davis 1980) each nest was visited at least four times to conduct a minimum of two playback series with the male and female. Testing started no sooner than the day after the HRM was placed in the nest and a minimum of four days elapsed between testing periods of each individual. Tests were conducted when a bird's mate was away (further

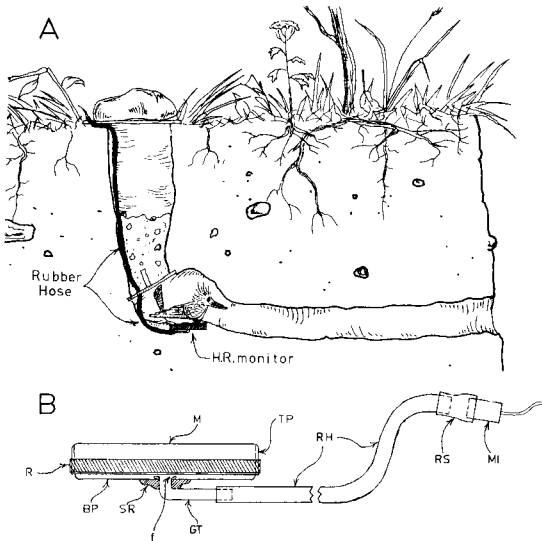


FIGURE 2. (A) Cross-section of a kingfisher's nest showing excavation of nest chamber and placement of the heart rate monitor (HRM). (B) Side view of the HRM used to detect the pulse of an incubating bird. BP—bottom of polyethylene petri dish (standard size); GT—0.64 cm glass tubing bent at 90° angle; f—flanged lip of tubing; M—thin rubber membrane (from a surgical glove) stretched over the cover (TP) of the petri dish and secured in place by a rubber band (R); MI—microphone; RH—rubber hose; RS—rubber sleeve connecting hose to microphone; and SR—silicon rubber cement. Three holes, not shown and ca. 2.5 cm diameter, were drilled in the cover (TP) before placement of the membrane (M). The cover (TP) and bottom (BP) of the dish were glued together to form an airtight seal.

than 100 m) from the nest entrance; a test was invalidated if the bird's mate flew into the vicinity of the nest and vocalized.

In each series, the bird's heartbeat was recorded with a microphone attached to the HRM and to a Uher Stereo 4200 tape recorder (record speed of 9.5 cm/sec). Each playback series consisted of seven periods. The first period was a 2-min control preceding any playback of previously recorded vocalizations. During the next six periods, heart rate was recorded during playback of two vocalizations selected from each of three categories. The categories were: (1) vocalizations of the bird's mate, (2) vocalizations from an unfamiliar kingfisher (conspecific individual greater than 16 km away) and (3) a vocalization from a Northern Flicker (*Colaptes auratus*), a common resident in the immediate nesting area. During each of the last six periods the heartbeat was recorded for 30 sec before stimulus presentation (from which a pre-stimulus baseline was calculated) and after stimulus presentation for a minimum of 3 min to assure that the heart rate had time to return to the pre-stimulus rate. A minimum of 5 min was allowed to elapse between playbacks. Before each

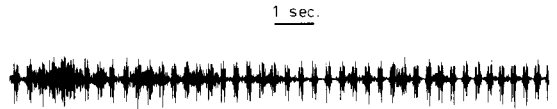


FIGURE 3. Output of the Gould recorder showing heart activity of a kingfisher before the start of a playback test (i.e., 2 min baseline). Approximately four cycles occur per sec; each cycle consists of the contraction of the atria and ventricles respectively. See text for details.

test the order of presentation of calls was randomly determined with each call category tested twice during a series (for a total of six periods). Different vocalizations were used for each of the two series performed on a given bird. The flicker's call was chosen since it is also comprised of a train of pulses similar to that of the kingfisher. Prior to each test, the unfamiliar kingfisher vocalization was randomly selected from a pool of six recordings. Calls from both sexes were included in this pool.

For each trial, I used one tape recorder for playing the vocalizations and a second for recording the bird's heartbeat. In the field, playback tapes were played from a Uher 4000 report tape player through a portable field speaker (Mineroff Electronics, Valley Stream, NY) which contained its own battery powered pre-amplifier. The playback speaker was positioned adjacent to nest entrance at least 10 min before the start of the control period, and sound pressure level of the first playback was set as close to 70 db SPL measured at 1 m from the speaker (re: 2×10^{-5} N/m) as possible (Realistic sound pressure meter; an SPL of 70 db was selected because on average the SPL of calls emitted by birds arriving in the vicinity of the nest was close to 70 db when measured at the entrance of the nest tunnel). Levels of all subsequent playbacks in a series were calibrated with the UV meter of the playback recorder.

The calls used for playback were recorded in the field with a Uher 4200 tape recorder using either a Dan Gibson Parabolic or Sennheiser directional microphone (ME 80 module). These calls were selected from a pool of 300 recorded vocalizations using the following criteria: (1) only vocalizations of birds arriving at the nest after a period of absence and showing no sign of alarm; (2) only recordings of marked birds of known identity; and (3) given that the above two criteria were met, recordings were selected that contained the least amount of background noise. Each recording was filtered through a Kron-Hite audio band-pass filter (24 db per octave) with cut-off frequencies of 1 kHz and 7 kHz (inspection of sonograms produced with a Kay Elemetrics Sona-Graph 6061B showed that little energy

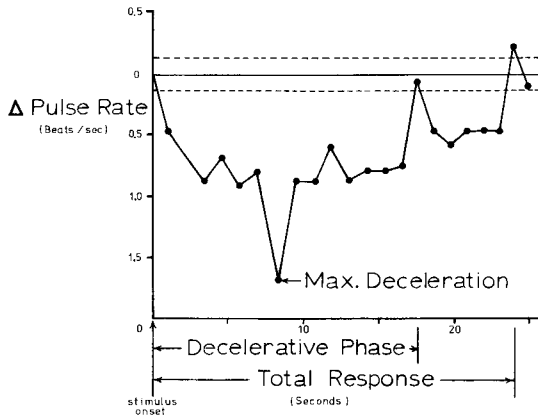


FIGURE 4. Time course of the change in heart rate of a typical adult bird listening to an unfamiliar vocalization played from outside its nest. The zero point on the Y-axis corresponds to the average (baseline) heart rate before stimulus presentation. The dashed lines show the 95% confidence interval above and below the baseline value. Change in heart rate is represented in beats/sec and time in sec from stimulus onset. Below the X-axis is shown both the decelerative phase and total response time. See text for definition of these time periods.

of the kingfisher's approach vocalization occurs below 1 kHz or above 7 kHz, while most of the background noise occurs below 1 kHz; see Fig. 1.)

Heartbeat recordings were filtered to eliminate unnecessary high and low frequencies (greater than 1 kHz and below 150 Hz) that were not part of the signal representing the beat of the bird's heart. The graphical representation (Fig. 3) of the temporal properties of the filtered signals was provided by a Gould recorder (model 2000s; paper speed = 5.0 cm/sec). The pattern representing the contractions of both the atria and the ventricles could be easily discerned on these graphs. Each graph was given a number corresponding to the order in which it was transcribed, and random with respect to the vocalization category used during the playback period in order to reduce experimenter bias during data transcription. To track the change in pulse rate, time elapsed was measured between every fifth ventricular contraction. Through this process, heart rate was calculated for the 30-sec period before onset of playback, as well as for a minimum of 2 min after onset of the playback of the different call categories. These data were subsequently sorted by call category and entered into a computer data file for analysis.

The following parameters (similar to those used by Dooling and Searcy, 1980) were determined: (1) Average baseline heart rate was calculated from the 30-sec period before stimulus onset. If this baseline value was significantly different (*t*-test, $P = 0.05$) from the value

calculated from the 2-min control period, then the data from that series was excluded from the analysis; (2) total response time, defined as the length of time it took the heart rate to return to its baseline value after playback of the stimulus; (3) the length of decelerative phase, defined as the length of time that the heart rate was below both the baseline average and baseline's lower 95% confidence interval (Fig. 4); and (4) the minimum heart rate that was recorded after stimulus onset. For each parameter, the data were divided into three groups corresponding to the type of vocalization used during the playback. Differential response of birds across the three vocalization categories (familiar, unfamiliar, and sham) and across the first and second trial series was evaluated by applying a two-way ANOVA (factorial design) to the data.

ANALYSIS OF VOCALIZATIONS

The next step was to quantify the acoustic parameters of vocalizations that may be used for recognition. To do this, I devised a computerized procedure which was regularly checked against measurements taken from sonograms produced on a Kay Elemetrics Sona-Graph (model 6061B). The following acoustic parameters were measured: (1) the total duration of the vocalization (sec); (2) the number of pulses per vocalization; (3) the inter-pulse interval length between each of the first five pulses, as measured from beginning of a pulse to the beginning of the next pulse (msec); (4) the location (Hz) of spectral peaks occurring in the following bandwidths, 1 to 2.5 kHz, 2.51 to 4.5 kHz, and 4.51 to 8 kHz (for each vocalization one peak generally occurred in each of the three bandwidths; Fig. 1); and (5) the pulse rates (number of pulses/sec) calculated over the entire vocalization (average PR) and over the first five pulses of the call (attack PR).

A vocalization from a pool of 300 was first filtered through two Kron-Hite filters with cut off levels set at 1 kHz and 7 kHz (roll-off of 48 db per octave). The filtered signal was then digitized (Digital equipment A/D converter; with a sampling rate of 16 kHz) and analyzed using a Fourier analysis (Digital Equipment program) to locate the spectral peaks (in Hz). In addition, the original filtered signal was also run through a RMS DC converter (custom built) and digitized. This second digitized signal, similar to the amplitude vs. time display of the Kay Elemetrics Sona-Graph, was analyzed by computer to determine interval lengths (to the nearest 0.5 msec).

Parameters of calls that vary significantly among individuals but not within calls of an individual would be useful as cues for indi-

TABLE 1. Summary of cardiac response data.

Response variable	Call type in trial 1			Call type in trial 2		
	Sham	Familiar	Unfamiliar	Sham	Familiar	Unfamiliar
Total resp. time (SE)	5.58* (1.11)	6.31 (1.92)	16.56 (2.84)	4.01 (0.85)	4.42 (1.09)	11.17 (1.89)
Length decel. phase (SE)	3.51 (0.99)	4.41 (1.50)	14.62 (2.49)	2.13 (0.43)	2.06 (0.66)	9.28 (1.58)
Statistical analysis:						
(two-way ANOVA)						
Across call types						
Total resp. time	$P = 0.01, F = 7.56, df(2, 10)$			$P = 0.048, F = 6.74, df(1, 10)$		
Decel. phase	$P = 0.003, F = 11.12, df(2, 10)$			$P = 0.048, F = 6.78, df(1, 10)$		

* Cell means ($n = 10$); units in seconds.

vidual recognition (Falls 1983, Moseley 1979). To assess variability, the data were analyzed using two statistical procedures. First the F statistic (ratio) was used to evaluate whether the variance of interval lengths and peak frequency values within vocalizations of an individual bird would be less than the variance across a randomly selected group of vocalizations from several birds in the same Ohio population (see Sokal and Rohlf 1981 for discussion of this test). The F ratio was calculated by dividing the sample variances of randomly selected vocalizations from eight birds by sample variances of eight calls from one individual (I used vocalizations recorded on separate days or vocalizations separated by periods of non-vocal behavior such as fishing, preening, or sitting quietly for more than 10 min).

DISCRIMINANT ANALYSIS

A discriminant analysis (Nie et al. 1975) was also conducted. Data from eight vocalizations from each of five birds (40 vocalizations) were used to formulate the regression equations describing each bird's vocal signature. The analysis then matched a second group of vocalizations with the correct bird (two new calls from four of the original five birds). The percent of correct matching is an indication of the reliability of distinguishing vocalizations based on the values of the parameters used in the anal-

TABLE 2. Statistical results of F test: comparing individual variation in selected parameters of Kingfisher vocalizations.

Parameter	Significance	F -ratio
1st interval	+	14.51 (0.001)
2nd interval	+	8.44 (0.006)
3rd interval	–	3.40 (0.064)
4th interval	–	1.16 (0.425)
Dom. freq. peak	–	0.67 (0.626)
High freq. peak	–	2.45 (0.179)
Call duration	–	1.30 (0.337)
Avg. pulse rate	–	5.89 (0.061)

+ Indicates significance at $P < 0.05$. P values are shown in parentheses.
– Nonsignificance $P > 0.05$.

ysis. A step-wise procedure was used to reduce the number of unnecessary parameters in the regression equation (SPSS, method option = minresid).

RESULTS

The cardiac response of adult birds to playback (Table 1) indicated that incubating birds could easily discriminate between calls emitted by their mates and calls emitted by a nonneighboring (unfamiliar) kingfisher. Both response measures, length of the decelerative phase and total response time were significantly greater when the bird heard an alien vocalization than when it heard a recording of its mate's call or that of a Northern Flicker (Table 1). Difference in response strength across trials was significant ($P = 0.048$) for both decelerative phase and total response time. On the other hand, there did not appear to be a difference in response between the flicker's and mate's vocalizations on either the first or second trial (difference in call means did not exceed the critical difference as determined by the Tukey-Kramer method for unplanned comparisons at $\alpha = 0.05$; see Sokal and Rohlf 1981). On four occasions during playback of the alien call, the playback series was stopped because the bird left the nest; on no occasion did a bird leave the nest during playback of either its mate's or the flicker's call. This observation also supports the hypothesis that a kingfisher can vocally discriminate between its mate and other birds.

ANALYSIS OF VOCALIZATIONS

The larger F values (Table 2) for the first and second inter-pulse intervals suggest that these properties were reliable indicators of which individual produced the call. The third interval may also be important although the F value did not reach significance at the 0.05 level. In contrast, the spectral peaks appear highly variable among calls of an individual. The lower spectral peak was not included in this analysis because few of these peaks were above the ambient background noise and they were difficult

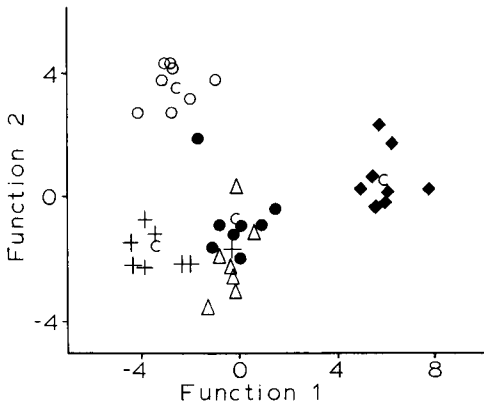


FIGURE 5. Plot of vocalizations in relation to the first two canonical discriminant functions. Vocalizations from different birds designated by different symbols (e.g., circles and triangles). The letter C designates the location of centroids from each group (i.e., all vocalizations from separate birds). This plot was generated using the SPSS by Nie et al. 1975.

to measure accurately. Neither the length of the call nor the pulse rate yielded F statistics large enough to consider them seriously as parameters useful in individual recognition.

The discriminant analysis (Fig. 5) uniquely described the 40 vocalizations using information on interval lengths (1 through 5) and location of spectral peaks (low, dom, high). The parameters important in predicting the correct bird were interval lengths 1, 2, and 3. On the other hand, the program determined, through a step-wise procedure, that data on spectral peak and interval lengths 4 and 5 added little predictive value to the regression equation and consequently this information was dropped from the analysis. Discriminant functions 1 and 2, which explain over 85% of the variance (Table 3), were strongly influenced by interval 1 (loading coefficient = 0.9274) and interval 2 (loading coefficient = 0.8381), respectively. These results indicated that initial inter-pulse intervals could provide a basis for identifying individuals.

A second part of the discriminant analysis, after the equations were generated, was to add data from new vocalizations and ask the program to correctly identify which birds produced them. Of eight vocalizations from four of the original five birds, the program correctly identified seven, and for the misidentified vocalization the program's second choice was the correct bird.

DISCUSSION

Results of this study provide experimental evidence that adult kingfishers do discriminate between one another on the basis of acoustic signals. In both sexes, kingfishers are aggres-

sive toward conspecific individuals (Davis 1982, 1985). Individual recognition may be one mechanism that reduces aggression levels between mated pairs permitting courtship and reproduction. In general, recognition by vocal cues is a common phenomenon in birds (Beer 1970, 1979; Falls 1983). Furthermore, acoustic recognition is likely the only means by which an individual kingfisher within the nest's subterranean chamber can identify a calling bird outside its nest.

VOCAL RECOGNITION AND SIGNAL FORM

Acoustic properties of a species' habitat may influence the evolution of signal form and subsequently, determine how information is encoded. For example, many species that reside in noisy environments, such as colonial seabirds, have vocalizations composed of a wave train of broadband pulses. Repetition of such pulses enables the signal to overcome the masking effect of the loud background noise with little distortion of the temporal pulse pattern (see Schleidt 1973). In seabirds such as gannets (White et al. 1970) and penguins (Joventin et al. 1979), the pattern of pulses has been shown to encode information used for recognition between mates.

The wave train of percussive sounds of kingfisher vocalizations may also be an adaptation to penetrate an excessively noisy background. Along streams, the sound of flowing water is a constant source of low frequency sound. Along my study streams, ripples are a primary source of noise (0.0 to ca. 1.5 kHz) and occur on the average every 20 to 30 m. Ripple noise could interfere with perception of vocalizations when the sender and receiver are greater than 20 m apart. Approach calls of the Belted Kingfisher are frequently emitted when the sender is more than 30 m from its nest. Transmission of spectral components higher than 1.5 kHz seems to be unaffected by stream noise although, frequency-dependent attenuation is greater with increasing frequency (Wiley and Richards 1983). I have determined from playback experiments that frequencies above 5 to 6 kHz can be significantly attenuated when broadcasted (at SPL of 100 db) over 30 m or when the signal travels through the nest tunnel (unpubl. data); on the other hand, the temporal patterning of pulses remained unaffected. These observations indicate that the spectral components of kingfisher calls are less reliable for encoding information concerning identity than the temporal patterning of the initial pulses. This conclusion is supported by the analysis of approach calls, which showed that spectral components are highly variable between calls of an individual, while inter-pulse intervals

TABLE 3. Summary of discriminant analysis.

Functions	% Variance explained	Cumulative percent	Loading coefficients			
			int1	int2	int3	int4
1	61.25	61.25	0.9274	-0.5940	-0.4551	0.3266
2	24.07	85.31	0.1185	0.8381	-0.1738	0.2356
3	14.60	99.92	0.5022	0.3310	0.6222	-0.8817
4	0.08	100.00	0.0638	-0.5110	0.6819	0.6854

Int1, int2, int3, and int4 designate pulse intervals 1 through 4.

between pulses 1 and 2, 2 and 3, and 3 and 4 are not.

It is assumed in most studies, that if vocal recognition occurs, then individuals are uniquely defined by their vocal signatures. Beecher's (1982) study, however, pointed out that the amount of information necessary to identify individuals differs depending on: the number of functions served by the signal, the number of individuals to be discriminated, and the number of acoustic properties of the signal that can be used to encode information. In order to address how much information is conveyed by a kingfisher's approach call, one must first ask how many unique signatures in the population can result by varying interval lengths alone. There may be a large number of combinations of unique beginnings if very small changes (less than 1 msec) in interval lengths can be perceived by kingfishers. But psycho-physiological data indicate that birds may not be able to perceive differences between interpulse intervals less than 10 to 20% in length or 2 to 3 msec (see Dooling 1983). I compared the difference in length between intervals 1 and 2, 2 and 3, and 3 and 4 of the 55 vocalizations from the five birds used in the discriminant analysis. Eighty percent of these comparisons showed differences of greater than 10% between lengths of adjacent interpulse intervals.

The issue, however, may not involve the ability to distinguish between separate intervals but instead involve the ability to discern a particular rhythm set up by the consistent relationship between the interval lengths. A visual inspection of spectrograms gives a crude indication of the rhythmic relationship between the initial pulses of a vocalization. In Figure 1, the temporal pattern formed by the first few pulses can be seen: in Figure 1a is shown a triplet followed by more evenly spaced pulses; in Figure 1b, a doublet followed by singles; and in Figure 1c, a triplet then doublet pattern can be seen. Theoretically, a large number of signatures are possible but from viewing over 300 sonograms, six patterns are most commonly observed. They are: (1) a triplet followed by single pulses; (2) a triplet followed by a doublet; (3) a doublet followed by

single pulses; (4) a doublet followed by a doublet; (5) all singles; and (6) a quadruplet followed by singles. The vocalizations that were most difficult to separate in the discriminant analysis (Fig. 5) were those that displayed the same rhythm; vocalizations represented by triangles and solid circles were both comprised of triplets followed by singles.

If birds have similar difficulties, then are six patterns sufficient to perfect vocal discrimination? Simply stated, from within the nest, a bird would have a one in six chance of misidentifying its mate (assuming that the six patterns are evenly distributed in the population at large). Outside the nest, visual information is also available to facilitate recognition. Most notable are differences in plumage coloration between the sexes. Outside the nest, plumage coloration would reduce to half the number of birds that could be confused as a bird's mate; if the intruding bird is the opposite sex, a kingfisher will still have a one in six chance of misidentifying the intruder as its mate. However, it may be that if the intruder is a neighbor, the kingfisher may have learned from previous encounters additional idiosyncrasies of its neighbor's call. Thus the estimate of one out of six is conservative, and is probably sufficient given the kingfisher's widely dispersed noncolonial nesting behavior.

ACKNOWLEDGMENTS

This study was supported by grants from Sigma Xi, Chapman Fund from the American Museum of Natural History, and a grant from the Cincinnati Museum of Natural History. I would like to thank Drs. Fred Wasserman, Mike Ryan, Linda Mealey, and Jill Trainer for reading the manuscript and providing valuable suggestions for improvements. Drs. Wes Thompson and George Pollak provided access to needed lab space and equipment for data analysis.

LITERATURE CITED

- ANTHONY, B. J., AND F. K. GRAHAM. 1983. Evidence for sensory-selective set in young infants. *Science* 220: 747-750.
- BEECHER, M. D. 1982. Signature system and kin recognition. *Am. Zool.* 22:477-490.
- BEER, C. G. 1970. Individual recognition of voice in the social behavior of birds, p. 24-27. *In* D. S. Lehrman, R. A. Hinde and E. Shaw [eds.], *Advances in the study of behavior*. Academic Press, New York.

- BEER, C. G. 1979. Vocal communication between laughing gull parents and chicks. *Behaviour* 70:118-146.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U.S. Nat. Mus. Bull. 176. Washington, DC.
- DAVIS, W. J. 1980. The belted kingfisher, *Megaceryle alcyon*: its ecology and territoriality. M.Sc.thesis. Univ. of Cincinnati, OH.
- DAVIS, W. J. 1982. Territory size in *Megaceryle alcyon* along a stream habitat. *Auk* 99:353-362.
- DAVIS, W. J. 1985. Acoustic signalling in the belted kingfisher, *Ceryle alcyon*. Ph.D.diss. The Univ. of Texas, Austin.
- DOOLING, R. J. 1983. Auditory perception in birds, p. 95-130. In D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds. Vol. 1: production, perception, and design features of sounds*. Academic Press, New York.
- DOOLING, R. J., AND M. H. SEARCY. 1980. Early perceptual selectivity in the swamp sparrow. *Dev. Psychobiol.* 13:499-506.
- EMLEN, S. T. 1971. The role of song in individual recognition in the Indigo Bunting. *Z. Tierpsychol.* 28: 241-246.
- EMLEN, S. T. 1972. An experimental analysis of bird song eliciting species recognition. *Behaviour* 41:130-171.
- FALLS, J. B. 1983. Individual recognition by sounds in birds, p. 237-278. In D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds. Vol. 2: song learning and its consequences*. Academic Press, New York.
- JOVENTIN, P., M. GUILLOTIN, AND A. CORNET. 1979. Le chant du Manchot empereur et sa signification adaptative. *Behaviour* 70:231-250.
- MOSELEY, L. J. 1979. Individual recognition in the Least Tern (*Sterna alifrons*). *Auk* 96:31-39.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. *Statistical package for the social sciences*. McGraw-Hill, New York.
- SCHLEIDT, W. M. 1973. Tonic communication: Continual effects of discrete signs in animal communication system. *J. Theor. Biol.* 42:359-386.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Freeman Publications, San Francisco.
- WHITE, S. J., R.E.C. WHITE, AND W. H. THORPE. 1970. Acoustic basis for individual recognition by voice in the Gannet. *Nature* 225:1156-1158.
- WILEY, R. H., AND D. G. RICHARDS. 1983. Adaptations for acoustic communication in birds: sound transmission and signal detection, p. 132-181. In D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds. Vol. 1: production, perception, and design features of sounds*. Academic Press, New York.