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VOCAL ADVERTISING AND SEX RECOGNITION IN EARED GREBES[1]

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Abstract. As a preliminary display of the *Discovery Ceremony,* male and female Eared Grebes (*Podiceps nigricollis*) advertise in bouts of 1–12 calls. Although superficially similar, female *Advertising* calls were significantly higher in frequency than male calls for all three frequency measures taken. Playback experiments demonstrated that courting males readily distinguished advertising calls of unpaired females from those of unpaired males. When the playback speed of the male calls was increased by 10%, courting males responded to them as though they were female calls, demonstrating that call frequency or duration cues play an important role in sex recognition. Since courting grebes already know the species and sex of their display partner upon hearing its initial, spontaneous advertising, the many elaborate and vigorous pair-formation displays of the *Discovery Ceremony* of grebes may be functioning in mate choice decisions at more subtle levels.

Key words: Podicipediformes; Eared Grebe; Podiceps nigricollis; *courtship; vocalization; sex recognition; mate choice.*

INTRODUCTION

During pair formation, many grebe species give conspicuous *Advertising* calls. The call was first described and named by Simmons (1954) in the territorial Great Crested Grebe (*Podiceps cristatus*), and was later described by Storer (1963) for a wide variety of grebes. In most colonial grebes, both sexes give advertising calls throughout the extended breeding season, but calls are especially frequent during pair formation. For many individuals, pair formation takes place shortly after arrival on the breeding grounds, when unpaired birds frequent the outer edges of incipient nesting colonies in search of potential mates. Advertising calls are most frequently given by lone individuals or by paired individuals separated from their mates. In all five colonial grebe species that we have studied, advertising bouts frequently provide a first contact between two separated birds. The call therefore provides an opportunity to test the vocal discrimination abilities of unpaired birds under natural field conditions. In a series of playback experiments on Western Grebes (*Aechmophorus occidentalis*), Nuechterlein (1981) concluded that the call fulfilled multiple functions including recognition of sex, pairing status, and individual identity. Females possessed advertising calls that were shorter and higher in frequency than males, but the Western Grebe studies did not examine whether these were characteristics important for sex recognition.

The advertising call of Eared Grebes (*Podiceps nigricollis*), is a clear, drawn-out "*oo-ink'-aa*" that is given in bouts of 1–12 calls spaced 0.3–0.6 sec apart (Fig. 1). During pair formation, lone males and females give call bouts regularly, either spontaneously or in response to calling by members of the opposite sex. Frequently, the call is used to initiate the *Discovery Ceremony* (Storer 1963), a series of elaborate, mutual pair-formation displays. Advertising therefore appears to serve as the first contact between potential mates. Although the call is superficially similar in males and females, responding birds appeared to be capable of discriminating the sex of calling individuals. In this study our major objectives were: (1) to describe any structural differences in the calls of males and females, and (2) to test what structural cues were used by courting males for sex recognition.

METHODS

Eared Grebe advertising bouts were recorded on a Sony TCM 5000 tape recorder using a small, floating blind disguised as a muskrat house. This blind consists of a cattail-camouflaged wire dome constructed over a doughnut-shaped plywood platform and truck inner tube. Clad in waders and surrounded by this apparatus, we could approach and move about slowly within a grebe colony without disturbing the courting birds. The

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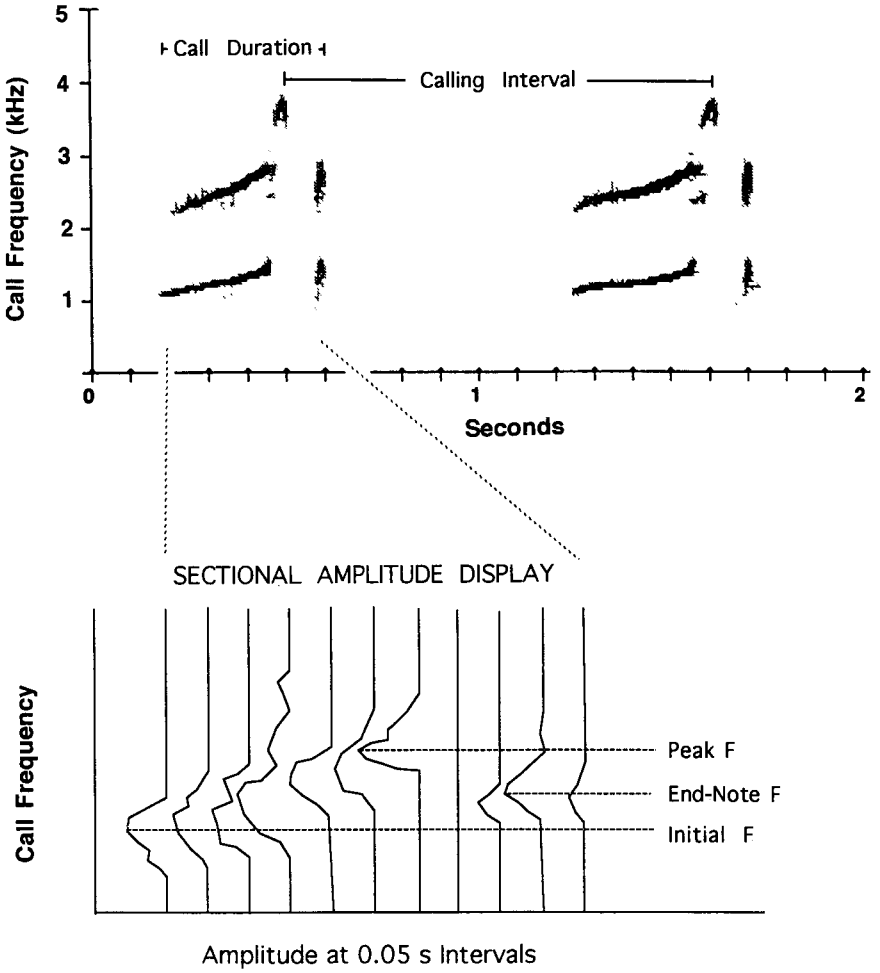

FIGURE 1. Two-call advertising bout given by a male Eared Grebe. From the sound spectrograms, we measured the interval between the repeated calls of a bout and overall call duration. Within a call, we measured the initial frequency of the long introductory note, the peak frequency of the call, and the maximum frequency of the short end-note.

floating platform supported both us and the recording or playback equipment.

Prior to hearing an individual advertise, all birds were sexed visually using bill size, which is greater in males for most or all grebe species (R. W. Storer, unpubl. data from museum collections). Only birds that could be easily sexed visually were included in the sample. Calls used in the analysis and playback experiments were recorded from early May to mid-June 1986–1988 from West Toqua Lake in Bigstone County, southern Minnesota, where we also live-captured and individually marked over 60 adults.

After identifying a bird's sex, we recorded several advertising bouts. Upon returning from the field, we analyzed structural differences between the advertising bouts of the courting males and females, using a Uniscan II real-time sound spectrograph. Calls within a given advertising bout usually were similar in structure, and we chose the second call of a bout for measurements. This allowed measurement of recorded advertising bouts for which the first call was either missed or partially cut off, which occurred frequently in the field recordings. On the advertising call sound spectrograms, we measured the interval between repetitions of the calls within a bout, call duration, initial frequency of the first note, the peak

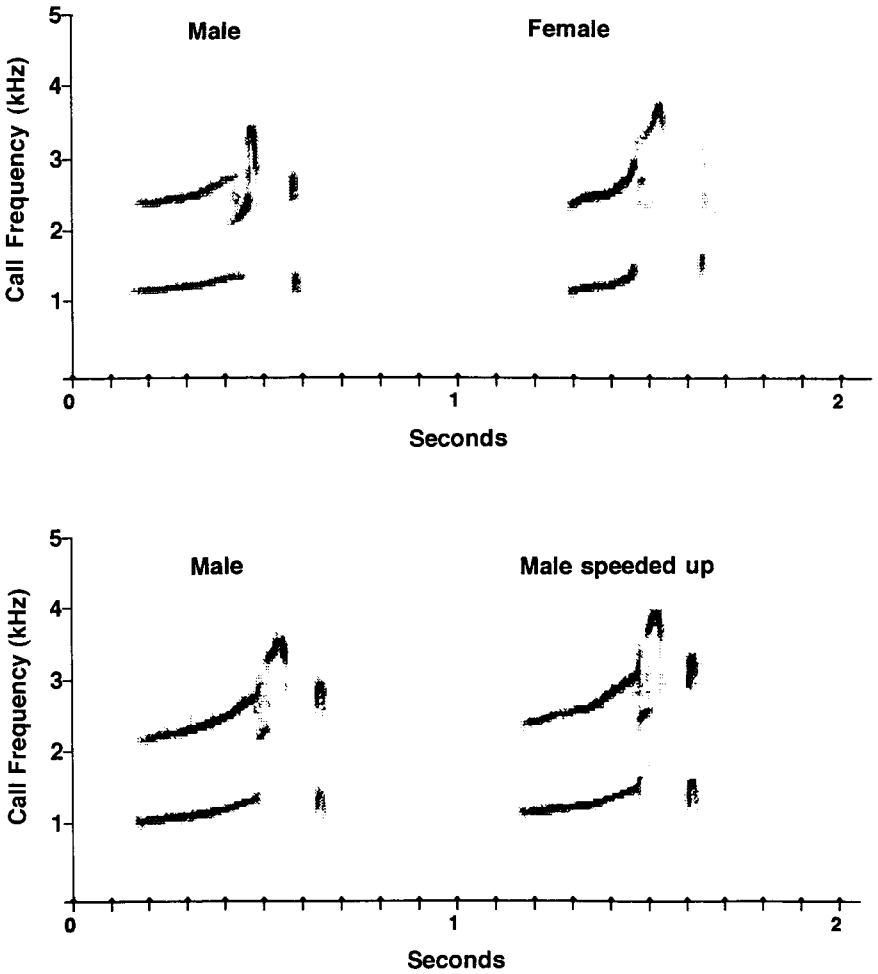

FIGURE 2. Advertising calls of female and male Eared Grebes. Experimental playbacks of male calls were played both at normal speed and at 110% of normal speed.

frequency of call, and the maximum frequency of the end-note. Precise frequencies for each call portion were measured directly from a digital read-out of the cross-sectional amplitude display, by examining the frequencies of the amplitude peaks (Fig. 1). Sex differences were tested using Student's *t* test (two-tailed).

Advertising bouts from this sample served as playbacks for the two sex discrimination experiments. Both playback experiments were performed in May 1989 near a colony at Cook's Creek in the Delta Marsh, on the south-central end of Lake Manitoba. We conducted the experiments only on actively courting males, defined as males observed to advertise or engage in other courtship activities (for descriptions of displays see McAllister 1958, Fjeldsa 1982) during the previous 5 min. Experiments were conducted by positioning the muskrat house blind near the edge of emergent beds and playing calls to males as they swam past and were moving away from the blind at 8–10 m. The order in which control and experimental calls were presented was pre-established by random draw. The particular call used in a playback trial was chosen from a pool of calls representing that variant-type. When a call was used, it was removed from the pool until all calls had been used, at which time the procedure was repeated. We used a new bird for each of the trials of an experiment and

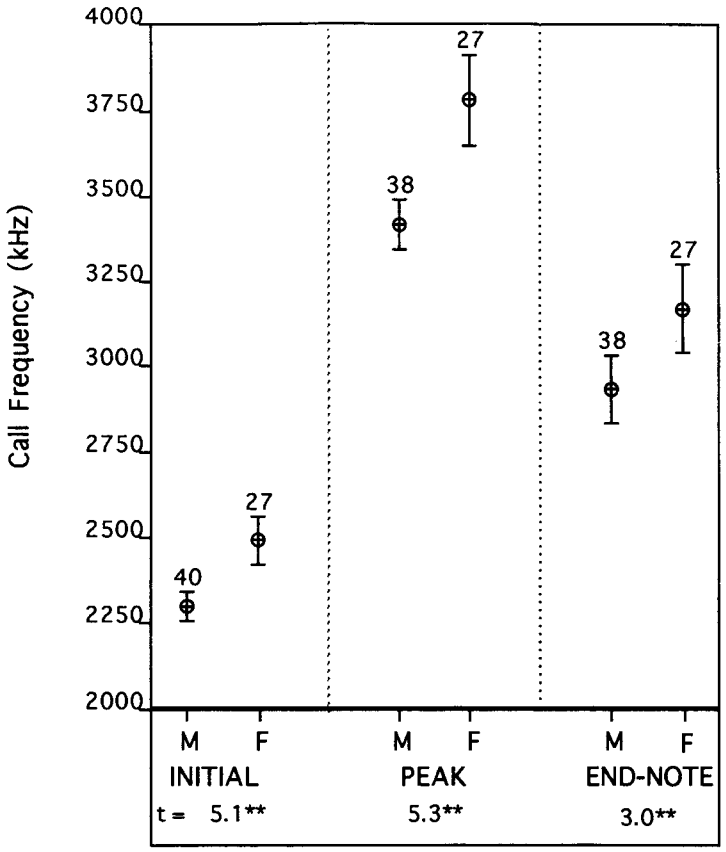

FIGURE 3. Sex differences for three advertising call frequency measurements. Calls of males (M) were significantly lower than those of females (F) for all frequency measures. Bars show mean ± 95% CI and sample sizes; differences between means were tested using Student's t (** = $P < 0.01$).

equalized the amplitude peaks of playback calls. Experiments were conducted only under calm wind conditions.

During each trial, we played the same call bout (three calls per bout) to a male three times, with an interval of at least 1 min between each playback. We recorded whether or not the following two positive and independent overt responses occurred within 10 sec of initiating a playback call bout: (1) TURNS/APPROACHES blind: bird turns the long axis of it body to face within 90 degrees of the blind's direction and begins to approach the blind, and (2) ADVERTISES: bird replies by giving an advertising call. A negative response was scored for the trial if the target bird did neither of the above within 10 sec. We also recorded any other courtship-related activities prior to and following the playback calls.

In the analysis, a bird was given a score of 1 for each positive response, such that a very responsive bird could score up to 6 points during its playback trial of three call bouts. This allowed us to rank the playback responses for each male on a 7-point scale (0–6) and thereby obtain a rank order for control and experimental playbacks.

Experiment 1 tested whether courting male Eared Grebes would distinguish, and approach, the calls of females versus males. The particular playback call used in a trial was randomly chosen from a pool of 24 available advertising bouts (12 male, 12 female), each of which was used once. Each advertising bout consisted of three calls given 0.5–1.5 sec apart, and had been recorded from a different courting bird. Data were analyzed using a Mann-Whitney U test (Zar 1974).

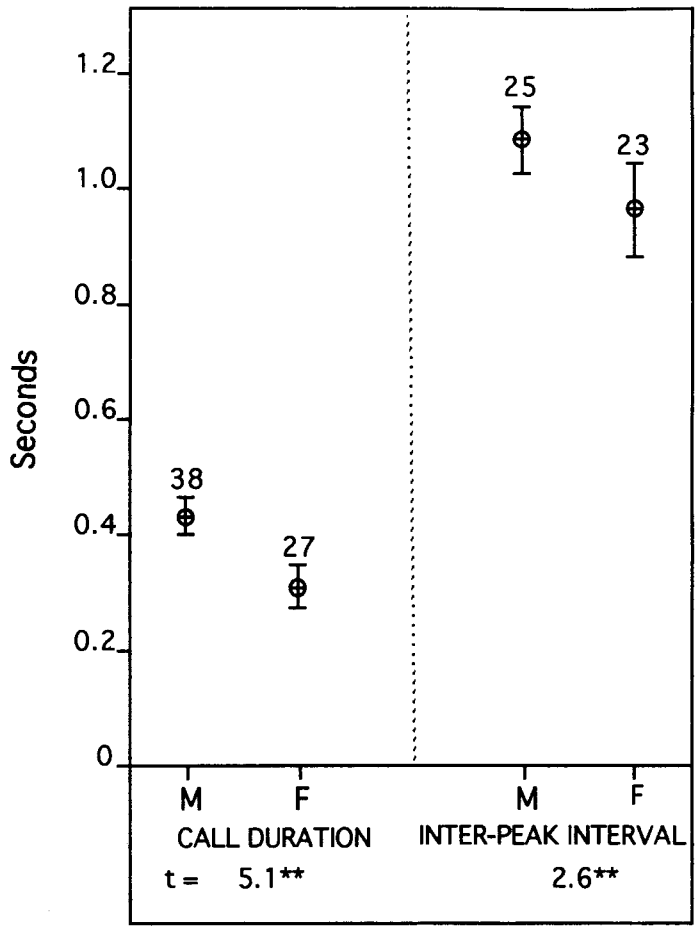

FIGURE 4. Sex differences for call duration measures. Calls of males (M) were significantly lower than those of females (F) for both measures. Bars show mean ± 95% CI and sample sizes; differences between means were tested using Student's t (* = $0.01 < P < 0.05$, ** = $P < 0.01$).

Experiment 2 was a follow-up experiment that examined the mechanism of vocal sex discrimination. (i.e., Whether courting males identified female advertising calls by using the cues of call frequency or length.) For control trials, we used 10 of the same male calls from Experiment 1; for experimental trials, we used the same 10 tapes played back at 110% of normal speed. The increased tape speed was chosen so that the frequency of the resulting playback calls fell within the range normally exhibited by females (Fig. 2). The order of presenting playbacks was predetermined by random draw from the 20 available calls. The experiment was then replicated using a separate random order. Data were analyzed using the Wilcoxon paired-sample test (Zar 1974).

RESULTS

SOUND SPECTROGRAM ANALYSIS

Female advertising calls were significantly higher in frequency than male calls for all three of the frequency measures taken (Fig. 3). Average duration of an individual female call also was significantly shorter than that of a male, and the calls within a bout were given at shorter intervals (Fig. 4). Stepwise discriminant analysis (SAS 1988) revealed that the most important sex discriminating variables were, in order, initial frequency, call duration, and peak frequency. Cross-validation procedures showed that, in combination, these three variables enabled correct sex determination for 82% of 62 calls tested.

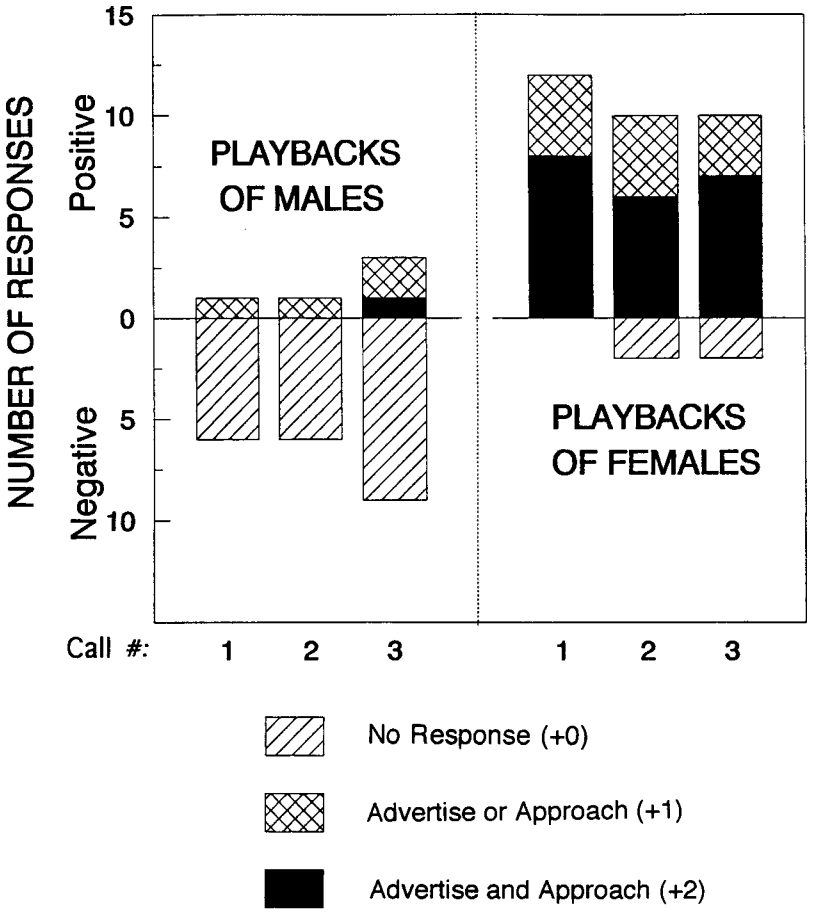

FIGURE 5. Sex Recognition Experiment: Distribution of response ratings for unpaired male (control) and unpaired female (experimental) advertising call playback trials. A maximum of 6 points was possible, which would indicate that the target bird approached (1 point) and advertised (1 point) within 10 seconds for all three playback calls.

EXPERIMENT 1: SEX RECOGNITION

Courting males readily distinguished advertising calls of unpaired females from those of unpaired males (Fig. 5). For statistical testing, the three playback responses for each individual were combined and this overall response was ranked by intensity. Courting male response ratings to male calls ranged from 0–2 points (median = 0), while ratings to female calls ranged from 3–6 points (median = 4). Mann-Whitney U analysis indicated a highly significant difference ($U = 144$, $P < 0.001$) between male responses to control versus experimental calls.

EXPERIMENT 2: MECHANISMS OF SEX DISCRIMINATION

Increasing the playback speed of male calls by 10% (Fig. 2) caused nearly a complete reversal in the responses from the courting males (Table 1). Again, males nearly ignored the male control calls, obtaining response ratings ranging from 0–1 for both repetitions of the experiment (median = 0, for both Experiments 2A and 2B, Table 1). When the same male calls were played at a faster speed, response ratings increased in 18 playback trials and remained the same in two trials. (For those two cases, neither the control nor experi-

TABLE 1. Sex Discrimination Mechanisms: Matched-pair response rankings for male advertising calls when played to courting male Eared Grebes at normal speed (control) and at 110% normal speed (experimental). Two repetitions of the experiment (2A and 2B) were conducted, using the same 10 calls presented in a different random order.

Playback #	Experiment 2A			Experiment 2B		
	Playback speed			Playback speed		
	Normal	110% Normal	Diff.	Normal	110% Normal	Diff.
1	1	3	+2	1	3	+2
2	1	5	+4	0	3	+3
3	0	5	+5	0	5	+5
4	0	4	+4	0	0	0
5	0	4	+4	0	4	+4
6	1	1	0	0	4	+4
7	0	1	+1	1	3	+2
8	0	4	+4	1	4	+3
9	0	3	+3	0	3	+3
10	1	3	+2	0	1	+1

Wilcoxon paired-sample:
Experiment 1: $t = 0$, $P < 0.001$.
Experiment 2: $t = 0$, $P < 0.001$.

mental variation of the call obtained response ratings greater than 1.) The difference (experimental − control) in response ratings for the trials ranged from 0 to +5 (median = +4). For both repetitions of the experiment, this increase in responsiveness was highly significant (Wilcoxon paired-sample analysis: Experiment 2A: $t = 0$, $P < 0.01$; Experiment 2B: $t = 0$, $P < 0.01$).

DISCUSSION

Spectrographic analysis of the advertising calls of Eared Grebes show that females give calls that are both higher in frequency and shorter in duration than those of males, which parallels differences that have been found in Western Grebes (Nuechterlein 1981), Hooded Grebes (*Podiceps gallardoi*) and Silvery Grebes (*P. occipitalis*) (Nuechterlein and Buitron, unpubl. data). This study is the first to demonstrate that courting male grebes rely on these cues for sex recognition. In these experiments, we did not attempt to determine whether frequency or duration cues were most important, since speeding up the male playbacks caused both measures to become more similar to female calls. Follow-up experiments with computer-altered calls could be used to examine these two parameters independently.

Species and sex recognition often have been described as two of the fundamental functions of courtship displays in birds. Our playback experiments, however, demonstrate that courting grebes already know the species and sex of their display partner upon hearing its initial, spontaneous advertising calls. Since these calls precede the elaborate visual displays of the Discovery Ceremony (Storer 1963, Nuechterlein and Storer 1982), the Discovery Ceremony itself may have little to do with species or sex recognition. Instead, the vigorous pair-formation displays of grebes may function in mate choice decisions at a more subtle level. Nuechterlein (1981) reached a similar conclusion for the *Rushing Ceremony* of Western Grebes (*Aechmophorus occidentalis*), and this may be true for the elaborate courtship displays of most grebe species.

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