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DO WOODPECKER DRUMS ENCODE INFORMATION FOR SPECIES RECOGNITION?[1]

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Abstract. We investigated whether woodpecker drums are exchanged interspecifically and attempted to ascertain the drum variables responsible for species recognition. Playback experiments were conducted on four woodpecker species (Nuttall's *Picoides nuttallii*, White-headed *P. albolarvatus*, Hairy *P. villosus*, and Downy *P. pubescens* Woodpeckers) comparing behavioral responses to sympatric hetero- and conspecific drums. There was a significant difference in behavioral responses to sympatric hetero- versus conspecific drums; individuals responded less intensely to drums of heterospecifics when drum cadences were dissimilar. Allopatric species drums with similar cadences were used to examine whether cadence was a variable that encodes species identity. There was no significant difference between responses to allopatric hetero- versus conspecific drums with a similar cadence, indicating that the drum's cadence encodes information for species recognition. Further playbacks eliminated drum duration and spectral properties as important variables for species recognition. Results suggest that if an individual drums at a similar cadence to a sympatric heterospecific, then their signal may elicit a conspecific response.

Key words: drumming, interspecific communication, nonvocal communication, species recognition, woodpeckers.

INTRODUCTION

Acoustic communication in birds normally occurs by the use of songs and calls. However, woodpeckers lack the ability to generate songs similar to those used by passerines (Brackenbury 1982). Along with a vocal repertoire of calls, woodpeckers employ a long-distance nonvocal acoustical signal aptly referred to as drumming. A woodpecker drum is a rapid, repetitive series of strikes with the bill on a substrate, not associated with foraging or cavity excavation (Bent 1939, Pynnönen 1939, Short 1974). Drumming is unusual in that a separate instrument in addition to the bird's bill is required to produce the signal (Skutch 1985).

Limited information is available concerning nonvocal acoustical signals in avian species (Prum 1998). As an instrumental signal, drumming has been noted to be a form of long-distance communication that may or may not elicit hetero- or conspecific responses (Crockett 1975, Duncan 1990). Functions attributed to drumming include territorial establishment, mate attraction, pair bond maintenance, and localization of individuals (Short 1982, Wilkins and Ritchison 1999). Given that many of these functions correspond to bird song, some researchers have concluded that drumming should have similar characteristics and have even postulated drumming to be the evolutionary counterpart to passerine song in woodpeckers (Pynnönen 1939, Lawrence 1967), although others disagree (Winkler and Short 1978).

Although there are several accounts of interspecific reaction to drumming, references have tended to consolidate the variety of responses as equivalent to responses given to conspecific drums (Lawrence 1967, Winkler and Short 1978). The problem with comparing woodpecker responses to drums stems from the lack of information on the function of the multiple signals woodpeckers use to communicate. There are three classes of calls (call notes, intimate calls, and rattle calls) which may be given in response to a drum, and it is unknown if these calls are equivalent responses to drumming alone.

There is no consensus as to whether drums encode species-specific information detectable by receivers. Four hypotheses have been suggested. First, drums are species-specific and not normally exchanged interspecifically (Perrins and Middleton 1985, Welty and Baptista 1988). Second, drums are not distinctive because other

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TABLE 1. Descriptive statistics of the drum variables (mean ± SD) for the playback tapes.

Playback signal	Cadence (strikes sec^{-1})	Duration (sec.)	No. strikes	Interstrike interval (sec.)
Nuttall's	20.8 ± 0.4	1.03 ± 0.1	21.5 ± 0.7	0.050 ± 0.001
''Slow'' Nuttall's[a]	17.1 ± 0.5	0.78 ± 0.2	13.1 ± 3.2	0.064 ± 0.001
Downy	15.8 ± 0.4	0.79 ± 0.4	12.5 ± 0.7	0.066 ± 0.002
Hairy	26.6 ± 0.5	0.83 ± 0.3	22.0 ± 7.1	0.039 ± 0.001
Northern Flicker	19.3 ± 1.2	0.99 ± 0.4	19.3 ± 7.8	0.055 ± 0.005
White-headed	20.1 ± 0.5	1.64 ± 0.2	33.0 ± 2.0	0.048 ± 0.001
Three-toed	15.3 ± 0.6	0.78 ± 0.1	12.0 ± 1.0	0.070 ± 0.007
Black-backed	15.6 ± 0.3	1.83 ± 0.1	28.5 ± 0.7	0.066 ± 0.002
Ladder-backed	31.1 ± 1.2	1.13 ± 0.1	35.0 ± 1.2	0.033 ± 0.001
Pulse tone 400 Hz	15.9	1.3	20	0.066
Nuttall's altered to Hairy	26.3	1.0	26	0.041
Hairy altered to Nuttall's	18.8	1.0	19	0.053

[a] Drums $>$ 2 SD below species average.

signals, perhaps rattle calls, are used for species identification (Short 1974, 1982, Winkler and Short 1978). Third, drums are fairly species-specific even to the human ear, but woodpeckers may react indiscriminately (Winkler et al. 1995). Fourth, drums are sympatrically, but not allopatrically, species-specific, with the drum cadence (in strikes sec^{-1}) as the predominant variable for species identification (Stark et al. 1998).

Two unresolved questions remain in the aforementioned hypotheses. First, whether responses to hetero- versus conspecific drums are different, and whether the variable(s) used by woodpeckers for species recognition are contained within the drum. We designed three experiments to resolve these questions. Experiment 1 established a method of scoring responses to drums, and experiment 2 compared behavioral responses to playbacks of sympatric hetero- versus conspecific drums. Experiment 3 compared behavioral responses to playbacks of allopatric heterospecific and computer-generated drums versus conspecific drums, to test possible variables used for species recognition.

METHODS

GENERAL PLAYBACK DESIGN

Populations in four regions of California, including the Los Padres, Sequoia, Sierra, and Inyo National Forests, were sampled during the 1993–1996 breeding seasons. Four species were studied using playbacks: Nuttall's (*Picoides nuttallii*), Hairy (*P. villosus*), Downy (*P. pubescens*), and White-headed Woodpeckers (*P. albolarvatus*). In addition, the drums from four other species were used as playback stimuli: Black-backed (*P. arcticus*), Three-toed (*P. tridactylus*), and Ladder-backed Woodpeckers (*P. scalaris*), and the Northern Flicker (*Colaptes auratus*). Determinations of sympatry were based on each species' breeding range within sampled areas. White-headed Woodpeckers could be considered marginally sympatric with Nuttall's and Downy Woodpeckers, but only during nonbreeding months (Beedy and Granholm 1985, Gaines 1988).

The following procedure was used for all playback trials: Subject birds were observed for a minimum of 5 min before each trial. Only individuals that were foraging, preening, or cavity-excavating, and within acoustical range were used. Playback experiments were conducted in a random, balanced, pairwise design (conspecific:heterospecific), with a minimum of 30 min between stimuli (based on log survivorship curves calculated for the maximum natural duration a bird remained responsive during drumming sequences, Dodenhoff 1996). Birds unresponsive to both stimuli were excluded from the analysis.

Drum variables for playback tapes were based on those reported by Stark et al. (1998), and included duration (sec), number of strikes per drum, cadence, and interstrike interval in one drum (interstrike interval, in seconds; Table 1). Tapes were generated by editing together field recordings and commercially available drums (Cornell Laboratory of Ornithology 1992a, 1992b), computer generated tones, and altered natural drums reset to specific cadences. Playback tapes were standardized for decibel level.

The results from the analysis of behavioral observations were used to construct a scoring method for comparing responses to playback signals for experiments 2 and 3. Although there are differences between calls and displays of woodpeckers, stereotypical behaviors are observed within the family Picidae (Winkler et al. 1995). Therefore, generalizations from observations of Nuttall's Woodpecker correlated with behaviors observed for other subject species. We used these results to rank the behavioral data appropriately concerning responsiveness to drum playbacks.

Behaviors observed more often during drumming sequences from experiment 1 were used to create a categorical scoring method similar to Emlen (1972) for experiments 2 and 3. Behaviors included alarm calls, approach, drumming, flights over the speaker, display, attack/supplant, and frozen antipredation posture. These behaviors composed the intensity scale. The intensity scale ranked the behavioral level achieved during each playback and ranged from 0–7 (low–high). Given the subjective nature of categorical scoring, we also employed a hybrid scale, which subdivided the intensity scale into differing levels of response (using frequency data), weighing each of the seven categories equally. Hybrid scores ranged from 0–14 (low–high). Behavioral responses were compared using two-tailed Wilcoxon signed-ranks tests. For the test to be able to detect significance at the $\alpha = 0.05$ level, n must be at least 6. If $n = 6$, then differences had to be of like sign (Sokal and Rohlf 1981).

EXPERIMENT 1: BEHAVIORAL SEQUENCE ANALYSIS

Since there were no previous measurements of drum responses for these species, we conducted a behavioral sequence analysis to categorize behavioral responses to drumming. Observations of Nuttall's Woodpeckers during natural and induced drumming sequences were made in the Los Padres National Forest, San Luis Obispo County, California during the 1993–1995 breeding seasons. Behaviors were identified according to previous descriptions (Short 1971, Winkler and Short 1978) and categorized for analysis. Behaviors for this analysis included foraging, flying or changing locations, intimate calls, preening, rattle calls, look around (with bill wave), call notes, agonistic attacks, and copulations. Behavioral transitions, defined as observable changes from one behavior to another, were noted for each individual during a drumming sequence (adapted from Halloran and Bekoff 1995). Behaviors that significantly preceded or followed drumming were determined by sequence analysis using a first-order Markov chain.

Independence between consecutive behaviors was tested using categorical modeling procedures (SAS Institute 1990), which used maximum likelihood values to estimate the G-test statistic and its associated χ^2 statistic (Sokal and Rohlf 1981). Data collection excluded the possibility of behaviors following themselves. Therefore, the ''expected'' values where the preceding and following behavior were the same were considered ''logical zeros,'' and the expected values were calculated using a log-linear model (Fagen and Young 1978). Significant differences were detected when the transformed frequency $|Y| > 1.08$.

To investigate which behaviors occurred more often during drumming sequences versus other activities, a comparison of the frequency of each behavior was conducted using a χ^2 analysis for contingency tables. Twelve different Nuttall's Woodpeckers were observed for 30–60 min each during the months of March and April, 1993, during non-drumming sequences. Behaviors observed were classified categorically and compared to the behaviors observed during the drumming sequences.

EXPERIMENT 2: SYMPATRIC SPECIES PLAYBACKS

Behavioral responses of the four subject species to sympatric hetero- and conspecific drums were compared. Trials with Nuttall's Woodpeckers included drums from three sympatric species (Downy and Hairy Woodpeckers, and Northern Flickers), and trials with Downy Woodpeckers included drums from three sympatric species (Nuttall's and Hairy Woodpeckers, and Northern Flickers). Northern Flicker drums used for playback were recorded from individuals sympatric with Nuttall's Woodpeckers. Hairy Woodpecker trials were conducted using the drums from two sympatric species (Nuttall's and Downy Woodpeckers), whereas White-headed Woodpecker trials consisted of drums from a single sympatric species (Hairy Woodpecker).

EXPERIMENT 3: ALLOPATRIC AND COMPUTER GENERATED PLAYBACKS

Behavioral responses of three subject species to allopatric hetero- and conspecific drums were compared. Trials with Nuttall's Woodpecker included four allopatric species drums, one with a similar cadence (White-headed Woodpecker) and three with different cadences (Ladder-backed, Black-backed, and Three-toed Woodpeckers). Trials with White-headed Woodpeckers included playbacks with Nuttall's Woodpeckers, whereas trials with Downy Woodpeckers included three allopatric species: two with similar cadences (Black-backed and Three-toed Woodpecker) and one with a dissimilar cadence (White-headed Woodpecker). Although Black-backed and Three-toed Woodpeckers' drums are similar in cadence to Downy Woodpeckers (Short 1982), they differ in the spacing pattern of individual strikes; Black-backed and Three-toed Woodpeckers increase cadence towards the end of their drum, whereas Downy Woodpeckers decrease (Stark et al. 1998). Also, the drum of Black-backed Woodpeckers is significantly longer than Downy Woodpecker drums (Stark et al. 1998).

Because behavioral responsiveness to allopatric drums may be observed, computer-generated drums were used to test whether drum cadence was the primary variable responsible for species recognition (as predicted by Stark et al. 1998). Two types of trials were conducted using computer-generated drums to test spectral properties. First, a 400-Hz tone was repeated to simulate a drumming Downy Woodpecker. Second, a Nuttall's Woodpecker strike was set at a cadence similar to a Hairy Woodpecker drum, and reciprocally, a Hairy Woodpecker strike was set at a cadence similar to a Nuttall's Woodpecker drum.

RESULTS

EXPERIMENT 1: BEHAVIORAL SEQUENCE ANALYSIS

Nuttall's Woodpeckers ($n = 68$ birds, with 574 transitions) were observed for the behavioral sequence analysis. The sample size was large enough for the χ^2 distribution to approximate the G distribution. Results of the categorical model implied a strong dependency between behaviors ($\chi^2_{29} = 190$, $P < 0.01$). Twelve Nuttall's Woodpeckers were used to analyze behavioral responses to drums by comparing each behavior's frequency of occurrence during drumming sequences to its occurrence during non-drumming sequences. The behaviors ‘‘preening’’ and ‘‘rattle call’’ were observed more often during drumming sequences ($\chi^2_9 = 183$, $P < 0.01$). Rattle calls have been noted to elicit drums, and are considered similar in function to drumming (Short 1971, Winkler and Short 1978). Although ‘‘look around with bill wave’’ did not always precede or follow drumming, it was observed more often during drumming sequences. Foraging was observed during both sequences more than expected. Previously, call notes have been considered a conspecific response to drumming (Short 1982, Kilham 1983). However, our analysis indicated call notes were observed frequently in non-drumming rather than drumming sequences. Furthermore, these call notes preceded foraging and were more often observed during non-drumming activities. Thus, call notes without supporting behaviors were not considered a response to drumming.

EXPERIMENTS 2 AND 3: RESPONSE TO PLAYBACKS

Individuals demonstrated a significant difference in the level of response between sympatric hetero- versus conspecific drums, except between Nuttall's Woodpecker and the Northern Flicker (Table 2). Furthermore, both Downy and Nuttall's Woodpeckers were similar in their responses to the Nuttall's playback tape generated from an individual greater than 2 standard deviations below the mean cadence for Nuttall's Woodpeckers (‘‘slow’’ Nuttall's, Stark 1996).

Responses to conspecific drums were not significantly different from responses to allopatric species, provided the drum cadences of the two species were comparable. Conversely, responses to allopatric species with dissimilar cadences were of significantly lower intensity. The results for the hybrid scale were similar to those for the intensity scale (Table 2), except for a marginal difference in the Hairy versus Ladder-backed Woodpecker comparison; there was a significant difference for the intensity scale but a nonsignificant difference for the hybrid scale (Table 2). Hairy Woodpeckers responded to Ladder-backed Woodpecker drums, but less intensely than to a conspecific signal (although the hybrid scale score approached significance). The results from playbacks with computer-generated signals indicated no significant difference between the re-

TABLE 2. Wilcoxon signed-ranks test results for comparisons of responses to sympatric, allopatric, and computer-generated drum signals versus the conspecific signal. Nonsignificant results indicate no significant differences in responses to conspecific and heterospecific signals. Listed are *P*-values (*n* birds). Int = Intensity scale; Hyb = Hybrid scale; see Methods for a description of the two scales.

		Species			
Playback signal	Scale	Nuttall's	Downy	Hairy	White-headed
Nuttall's	Int		0.01 (8)	0.04 (9)	0.58 (10)
	Hyb		0.01 (8)	0.02 (9)	0.61 (10)
''Slow'' Nuttall's[a]	Int	0.23 (9)	1.00 (9)		
	Hyb	0.17 (9)	0.83 (9)		
Downy	Int	0.01 (29)		0.01 (11)	
	Hyb	0.01 (29)		0.01 (11)	
Hairy	Int	0.01 (20)	0.01 (11)		0.02 (7)
	Hyb	0.01 (20)	0.01 (11)		0.02 (7)
Northern Flicker	Int	0.16 (18)	0.04 (6)		
	Hyb	0.29 (18)	0.04 (6)		
White-headed	Int	0.40 (19)	0.02 (8)		
	Hyb	0.08 (19)	0.02 (8)		
Three-toed	Int	0.03 (11)	0.18 (13)		
	Hyb	0.01 (11)	0.23 (13)		
Black-backed	Int	0.03 (13)	1.00 (12)		
	Hyb	0.01 (13)	0.55 (12)		
Ladder-backed	Int	0.04 (6)		0.04 (13)	
	Hyb	0.04 (6)		0.06 (13)	
Pulse tone 400 Hz	Int		0.06 (7)		
	Hyb		0.06 (7)		
Nuttall's altered to Hairy	Int			1.00 (7)	
	Hyb			0.89 (7)	
Hairy altered to Nuttall's	Int	0.28 (8)			
	Hyb	0.25 (8)			

[a] Drums more than 2 SD below species average.

sponses of woodpeckers to these signals versus conspecific drums.

DISCUSSION

Although most researchers agree drums have species-typical characteristics (Short 1982, Kilham 1983, Winkler et al. 1995), it was unknown whether observed interspecific responses to drums were predictable. Previous studies included multiple responses as equivalent indications of species recognition (Short 1982, Winkler et al. 1995), which implied ambiguity within the drum, but did not indicate the absence of discrimination. Individuals may respond to a heterospecific drum, but those responses can differ from responses to conspecific drums, which could indicate discrimination between stimuli. Results from the playbacks of the ''slow'' Nuttall's stimulus to Nuttall's and Downy Woodpeckers indicated that interspecific behavioral responses to drums can occur naturally between sympatric species, if the drum cadences overlap. These results differ from Duncan (1990), because Duncan's comparisons did not include reciprocal playbacks with species sharing similar cadences.

Our results between species that share similar cadences indicated interspecific responses may occur between sympatric species. The responses by Nuttall's Woodpeckers to the drums of Northern Flickers were similar to responses elicited by a conspecific drum. Thus, interspecific responses may occur between these sympatric species. Individual drums of both species often have a similar drum cadence, and were predicted to have reciprocal heterospecific ambiguity in their drum (Stark et al. 1998). Despite this prediction, we did not observe interspecific responses to natural (i.e., non-playback) drums between individuals of these species over the course of this study. We attributed the lack of interspecific response to observations of restricted drumming by Northern Flickers. Northern Flickers within the study areas drummed for a few weeks during the breeding season, usually when Nuttall's Woodpeckers were unresponsive to drums. This may indicate a shift between species in the timing of drumming during the breeding season; species with similar drums could reduce ambiguity through temporal separation and maintain species distinctiveness (Stacier et al. 1996).

Allopatric playbacks followed the same pattern as observed in sympatric playbacks: drums of species with similar cadences elicited behavioral responses equivalent to conspecific signals, whereas those with dissimilar cadences did not. This indicates that drum cadence is one variable that encodes species identity. Playback trials with Downy Woodpeckers tested whether the variables ''interstrike interval'' and ''duration'' were used to encode species identity. Downy Woodpeckers responded similarly to conspecific, Black-backed and Three-toed Woodpecker drums, which indicated that drum duration and interstrike interval were not used by Downy Woodpeckers to differentiate between these species. This is similar to the finding that, for many passerines, signal duration is usually not a species-typical variable (Becker 1982). However, because heterospecific drums used as playbacks were no shorter than Downy Woodpecker drums, our test does not eliminate the possibility of a minimum duration required for species recognition. Shorter song durations may elicit less intense responses, and minimum durations are required for species recognition for passerines (Becker 1982).

Our results also eliminated the interstrike interval differences in drumming as a characteristic responsible for species recognition in Downy Woodpeckers. Kaiser (1990) suggested that the spacing pattern within unmodulated drums was related to the woodpecker's foraging method. In ''wood-pecking'' species the rhythm accelerates, whereas ''gleaners'' slow down toward the end or the rhythm and amplitude of their drums remain uniform (Winkler et al. 1995). Although Kaiser's hypothesis was based on small sample sizes, it suggested that the spacing pattern within a drum may be controlled by the musculature used for foraging. Thus, this variable would have a greater likelihood of overlapping with a sympatric species with a similar foraging strategy. Given the high degree of overlap between the foraging strategies of many sympatric woodpeckers, the interstrike interval of a drum may not be a reliable indicator of species identity. However, these results cannot exclude the possibility that either interstrike interval or duration encodes species identity for Downy Woodpeckers that are sympatric with Black-backed or Three-toed Woodpeckers.

Computer-generated drums tested whether spectral properties were important in species identification. Results from trials with Nuttall's, Hairy, and Downy Woodpeckers indicated that spectral properties of a drum were not characteristics responsible for species recognition. Instead, the spectral properties generated in drumming have been noted to depend on the drumming substrate selected (Eberhardt 1997). Furthermore, differential signal attenuation of frequencies through an environment may make the spectral properties of a drum a poor variable for species-specificity and signaler identification (Wiley and Richards 1982). However, these spectral properties may be important in other aspects of communication, including ranging (Morton 1986, Naugib 1995, 1998).

In summary, our results support the conclusion that the drum's cadence encodes species identity of the signaler, and that receivers perceive these differences within the acoustical environment. Individual woodpeckers did not react indiscriminately to drums. Responses to heterospecific drums with dissimilar cadences were less intense and did not include vocalizations or behaviors observed during playbacks with conspecific drums. Sympatric woodpecker drums are not usually exchanged interspecifically, but interspecific responses may result if individuals from different species have an overlapping drum cadence. However, due to the amount of overlap between species, both sympatric and allopatric, we conclude drums are not species specific. The lack of signal specificity does not prevent the encoding of species identity. For example, differential timing of drumming between species within a breeding season could result in a lack of selection pressure on drums to significantly diverge. This may allow a few sympatric species to utilize similar cadences to encode species identity without resulting in ambiguity between species. Nonetheless, given the similarities between allopatric species, it is unknown whether the trend of signal divergence observed in this study is applicable across broad geographic ranges or under differing acoustical environments. Clearly, considerable research still needs to be done in the area of avian mechanical acoustical signals, including woodpecker drums.

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