A QUANTITATIVE ANALYSIS OF WOODPECKER DRUMMING[1]

ROBERT D. STARK[2], DANIELLE J. DODENHOFF[2] AND ERIC V. JOHNSON

Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407

Abstract. The drumming patterns of 11 species of California woodpeckers were analyzed to determine if this long-distance signal is species-specific. Analyses for differences in the drum signal by sex, region, and playback initiation was performed on 5 of the 11 species. Nuttall's Woodpecker (*Picoides nuttallii*), White-headed Woodpecker (*P. albolarvatus*), Downy Woodpecker (*P. pubescens*), and Hairy Woodpecker (*P. villosus*) showed no significant difference in the drum signal for the above categories. Northern Flickers (*Colaptes auratus*) showed a significant difference in region and sex. Species discrimination showed signal overlap between Nuttall's and White-headed Woodpeckers, and between Hairy and Ladder-backed Woodpeckers (*P. scalaris*), and also between Northern Flicker and Hairy, Nuttall's, and White-headed Woodpeckers. Signal analysis of only syntopic species decreased misclassification and posterior probability error rates indicating syntopic, but not allotopic, signal specificity. Stepwise discrimination indicated cadence as the predominant variable for separation of species. Hairy and Downy Woodpeckers were not reciprocally misclassified, nor were Nuttall's and Ladder-backed, indicating drumming is a diagnostic indicator between these phenotypically similar species. We hypothesize that modulation of the drum in sapsucker species could minimize signal equivocation between syntopic woodpecker species with a matching introductory cadence. Signal equivocation between Northern Flickers and syntopic species is postulated as a possible selective pressure favoring the diagnostic long call prevalent in the species, rather than drumming.

Key words: discriminant analysis, drumming, Picidae, song, woodpeckers.

INTRODUCTION

Although analysis of passerine bird song has been extensively treated in the scientific literature, relatively little information is available on drumming, the postulated evolutionary counterpart to song in woodpeckers (Pynnönen 1939, Lawrence 1967). As an instrumental signal, a drum is a form of long distance communication which may or may not elicit heterospecific or conspecific responses (Crockett 1975, Winkler and Short 1978). Drumming has been documented to have the function of mate attraction and territorial announcement (Kilham 1959, Lawrence 1967, Winkler and Short 1978).

A woodpecker drum is a rapid, repetitive series of strikes with the bill on a substrate, not associated with feeding or cavity excavation (Short 1974, 1982, Winkler and Short 1978, Kilham 1983). Each single strike of the bill in drumming is herein referred to as a beat. A drumming bout is a series of drums by an individual over time which can be terminated by a number of factors, resulting in varying bout

lengths depending upon the species (Dodenhoff 1996). Drumming may be species-specific (Lawrence 1967, Perrins and Middleton 1989), diagnostic in some species (Short 1982), or too ambiguous for species recognition (Short 1971, Winkler et al. 1995). Winkler and Short (1978) attribute variation observed in drumming to numerous sources, including motivational context and geographic location. Few published studies give quantitative values for any variables associated with drumming (Short 1971, 1974, 1982, Winkler 1971, Winkler and Short 1978), although some drums are defined, using as variables: cadence (beats sec^{-1}), length of the drum (sec), and the number of beats drum^{-1}. However, none of the authors presented a statistical analysis of the drum signal.

The number of possible variables within a single drum is relatively low. Four parameters of a drum are available for statistical analysis: length (in sec), number of beats in a drum, cadence (beats sec^{-1}), and the spacing of beats within a single drum (interval between beats). Energetic considerations would dictate that stereotypes in one (or some combination) of these parameters should minimize the drum signal's equivocation (i.e., loss of signal from signaler's perspective), maximizing the efficiency and information con-

[2] Present address: Department of Zoology, The Ohio State University, Columbus, OH 43210, e-mail: stark.47@postbox.acs.ohio-state.edu

tent of the long distance signal, because ambiguity at the receiver's end should be minimal (Wilson 1975). Therefore, drumming should be species-specific.

Problems arise with this reasoning when drumming is considered over a broad geographic scale. There are currently 214 species of woodpeckers recognized world-wide, classified into 27 genera within three subfamilies (Winkler et al. 1995), most of which are known to drum. It is unlikely that the four variables available in a drum could account for a wide enough variety of drumming patterns for each species to have its own unique pattern. However, only syntopic species (closely related species occupying the same habitat) must compete with one another for space within their acoustical environment, and only syntopic species must differentiate communication signals. Therefore, natural selection should favor those species whose drums minimize this equivocation, as their signals would elicit responses only from direct competitors.

Conversely, due to the limited number of variables within a drum, it is reasonable to expect that the drumming patterns of allotopic species might be highly similar as selection pressures to minimize equivocation are not present. Given that those species with similar variables in drumming should rarely or never contact one another during the breeding season, such similarity would not be a problem; drumming could serve as a behavioral isolating mechanism between species.

To test the hypothesis of species specificity in the drum signal, we collected and analyzed the recordings of the drumming patterns of 11 species of syntopic and allotopic California-occurring woodpeckers. The species recorded included Nuttall's Woodpecker (*Picoides nuttallii*), White-headed Woodpecker (*P. albolarvatus*), Hairy Woodpecker (*P. villosus*), Downy Woodpecker (*P. pubescens*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Dryocopus pileatus*), Acorn Woodpecker (*Melanerpes formicivorus*), Black-backed Woodpecker (*P. arcticus*), Red-breasted Sapsucker (*Sphyrapicus ruber*), Williamson's Sapsucker (*S. thyroideus*), and Ladder-backed Woodpecker (*P. scalaris*).

METHODS

During the breeding seasons of 1983-1986 and 1993-1995, drums of 223 individuals from 11 species were recorded, with a total of 3,347 individual drums (1983-1986 recordings of 19 individuals collected by L. Morton [unpubl.] were used in this study only when positive identification of the bird [sex and species] was specified on the original recordings). In 1993 and 1994, recordings were made using a Uher 4000 SC reel-to-reel recorder with an AKG CE-8 directional microphone and AKG SE5-10 amplifier. In 1995, recording equipment was a Marantz PMD 222 professional cassette recorder with an Audio-Technica 815R microphone connected to a Whirlwind Phantom power source.

Recordings in California were made in San Luis Obispo County, Yosemite National Park, Kings Canyon National Park, Sequoia National Forest, Joshua Tree National Park, and Los Padres National Forest (Mt. Abel). Information about recorded individuals included species, sex, date, time, location, general weather conditions, and whether the drum was natural or was initiated using playbacks.

Drums for playback were taken from published recordings (Cornell 1992a, 1992b) and recordings made during the course of this study. Drums were edited together to imitate a drumming woodpecker. Multiple replicates of a single individual were avoided by using numerous recording sites and by noting plumage variations. To maintain accuracy in relation to tape speed, a C note (514 Hz) from a tuning fork was recorded at various tape positions and analyzed to detect fluctuations. Recordings from the field were digitized using SoundEdit (Farallon Computing Inc., Emeryville, California), producing a sonogram of each drum.

Statistical tests used for drumming analysis included a multivariate analysis of variance to test for variation between species, region, sex, and initiated versus natural drums, and four quadratic mahalanobis stepwise discriminant analyses for reclassification and grouping of the species (all species together, desert species, oak woodland species, and coniferous forest species) based upon the four drum variables. In the sapsuckers, there was a fifth parameter (termed "group") used to determine whether the introductory grouping of beats matched the cadence of the overall drum in either syntopic *Picoides* or *Dryocopus* species. To control for individual variation in drumming, the means for each drum variable per individual were used. As patterns within a single drum (increased or decreased cadence) are directly linked to the length of the

TABLE 1. Means (± SD) for each drum variable for each woodpecker species recorded during this study.

Species	Length[a]	Cadence[b]	N. beats[c]	Space[d]	Group[e]	n indi- viduals	n drums
Nuttall's	1.0 ± 0.2	20.6 ± 1.0	19.8 ± 3.8	0.050 ± 0.002	—	67	1,149
White-headed	0.9 ± 0.2	19.7 ± 1.3	18.4 ± 4.8	0.053 ± 0.004	—	32	377
Hairy	1.0 ± 0.1	26.1 ± 1.1	24.9 ± 3.7	0.040 ± 0.002	—	44	750
Downy	0.8 ± 0.2	17.1 ± 1.3	12.7 ± 2.8	0.064 ± 0.005	—	31	695
Northern Flicker	1.1 ± 0.3	22.3 ± 1.7	25.2 ± 5.8	0.047 ± 0.004	—	15	109
Pileated	1.7 ± 0.3	14.2 ± 0.4	23.8 ± 4.1	0.074 ± 0.004	—	5	45
Acorn[f]	0.7 ± 0.1	17.3 ± 0.6	11.3 ± 1.5	0.065 ± 0.003	—	2	127
Black-backed	1.9 ± 0.4	16.3 ± 0.6	30.9 ± 6.0	0.064 ± 0.003	—	9	35
Ladder-backed	0.9 ± 0.1	28.3 ± 2.0	26.6 ± 4.5	0.036 ± 0.003	—	6	120
Red-breasted	1.5 ± 0.5	12.6 ± 2.5	17.7 ± 4.7	0.094 ± 0.026	21.7 ± 2.8	10	65
Williamson's	1.4 ± 0.7	10.4 ± 3.5	16.7 ± 6.6	0.094 ± 0.026	25.6 ± 0.2	2	4

[a] Length: mean length of the drum (sec).
[b] Cadence: mean beats sec^{-1}.
[c] N. beats: mean number of beats contained within one drum.
[d] Space: average spacing between beats within one drum.
[e] Group: introductory grouping of beats (in beats sec^{-1}) in those species with a modulated drum cadence.
[f] Acorn Woodpecker: two populations, sampled twice.

drum, a contingency table was created from a random subset of drums ($n = 50$) for each species. Categorization of spacing patterns was conducted only on species with unmodulated drums.

RESULTS

Descriptive statistics of the drum variables for each species are listed in Table 1. Of the species recorded, five species were analyzed for differences in drums based upon categories (sex, region, initiated vs. natural drums, and the interactions of sex with initiated vs. natural drums): Nuttall's, White-headed, Hairy, and Downy Woodpeckers, and Northern Flickers. Multivariate analysis of variance to test for the overall effect of each test variable in relation to species demonstrated no significant difference in Nuttall's, White-headed, Hairy, and Downy Woodpeckers for any of the test variables in relation to each category. No region category was tested for Nuttall's, as drums of only two individuals were collected outside San Luis Obispo County. Initiation of drumming by playbacks had no effect on drumming parameters; natural and initiated drums were statistically indistinguishable. White-headed, Hairy, and Downy Woodpeckers showed no regional differences (dialects) between drumming sites sampled in California (all $P > 0.30$). There was a significant difference in the region category for Northern Flickers ($P = 0.02$), which was due to differences in cadence and spacing within a drum from two individuals from one region.

The results of the MANOVA testing drum variables indicated significant differences within the 11 species sampled (Wilks' lambda $F_{50,961} = 51.6$, $P \leq 0.001$). All species were analyzed to test for classification based upon the drum variables regardless of whether the species were syntopic or allotopic. Error counts estimated the percent misclassification of individuals from each species reclassified into each successive species based upon all five drum variables. Specifically, the Northern Flicker had high misclassification with Nuttall's (33.3%) and Hairy (13.3%) Woodpeckers. White-headed Woodpeckers overlapped with Nuttall's (62.5%) and Downy (12.5%) Woodpeckers. Conversely, 10.5% of the Nuttall's and 12.9% of the Downys were reclassified as White-headed Woodpeckers. Fifty percent of the Ladder-backed Woodpeckers were reclassified as Hairy Woodpeckers, resulting in an overall error count estimate of 21.8% for the reclassification matrix. Given the high misclassification percentage of allotopic species, coupled with the lack of plasticity in drum variables found in the previous analysis, species were separated and reanalyzed by syntopic relationships, based upon the habitats in which these species were found: desert, oak woodland, and coniferous forest.

Classification of syntopic desert species were based upon research by Short (1971), and included the Northern Flicker, Ladder-backed and Nuttall's Woodpecker. Reclassification error counts dropped significantly; 40% of Northern Flickers were reclassified as Nuttall's, resulting in an overall error count estimate of 9.1%. Syntopic oak woodland species included Northern Flicker, Acorn, Nuttall's, Hairy, and Downy

Woodpeckers. Notable reclassifications included only the Northern Flickers being redistributed as Nuttall's (40.0%) and Hairy (13.3%) Woodpeckers based upon drum variables. The overall error count estimate was 8.7%. Syntopic coniferous forest species included the Northern Flicker, Pileated, Black-backed, White-headed, and Hairy Woodpeckers, and Red-breasted and William-son's Sapsuckers. Again, error resulted from Northern Flickers being redistributed as White-headed and Hairy Woodpeckers (20.0% and 13.3%, respectively). The overall error count estimate dropped to 6.8%.

Posterior probability error rates for all species were tabulated as to the accuracy of the posterior probability equation in relation to misclassification of species membership. When all species were considered together, White-headed and Ladder-backed Woodpeckers had high probabilities of error (57.9% and 50.9%, respectively), as did Northern Flickers (47.1%), although most other species fell well under 6% error. It is interesting to note a 4.2% chance of a given species being classified into Hairy Woodpeckers, which was greater than the probability of a Hairy being reclassified into another species. High error rates in Northern Flickers, and White-headed and Ladder-backed Woodpeckers showed that there was considerable overlap in drumming variables of these species when analyzed together. Once separated by habitat, error rate estimates in White-headed Woodpeckers decreased to 6.3%, while Ladder-backed woodpeckers decreased to 0%. Northern Flicker's error rate estimates remained high (ranging from 21.7–38%) once separated by habitat, but still decreased from the original analysis. Posterior probability error rates were 14.3% for all species, 9% for desert species, 7.2% for oak woodland species, and 3.2% for coniferous forest species.

The stepwise portion of the discriminant analysis evaluated each drum variable for its effect on discriminating species from one another. In each case, stepwise discrimination of variables indicated cadence (beats sec^{-1}) as the predominant variable for the separation of species. All of the drum variables were required for species differentiation when all species and coniferous forest species were analyzed. Oak woodland and desert species did not include sapsuckers, so introductory grouping was not required for discriminating species. Furthermore, desert species did not require the mean spacing of the beats within a drum, which indicated the spacing variable was not a good indicator for differentiation.

A contingency table was used to test for independence between spacing of beats within a drum versus species, the null hypothesis being independence of the variables. The spacing between beats varied with species ($\chi^2_{16} = 26.3$, $P < 0.001$). Nuttall's, Acorn, Pileated, and Black-backed Woodpeckers all increased in drum cadence within one drum. Northern Flicker's drum remained relatively constant throughout, rarely increasing or decreasing in cadence. Downy and Ladder-backed Woodpeckers' cadences decreased throughout one drum, however, Hairy and White-headed Woodpeckers did not have any specific pattern associated with their drumming beyond what would be expected by chance.

DISCUSSION

Within-species analyses demonstrated that the drums of male and female Nuttall's, White-headed, Hairy, and Downy Woodpeckers were statistically indistinguishable, indicating the drum signal was not influenced by the sex of the drummer. Furthermore, analysis of natural and initiated drums had no effect on an individual's drum parameters, which suggested that mimicry was not occurring. Therefore, the variables of drumming may be directly affiliated to the morphological constraints of the woodpeckers. Regional analysis of Hairy, Downy, and White-headed Woodpeckers revealed little plasticity in drumming throughout California. Values obtained in this study compare favorably to previous studies (Short 1982), denoting that drumming may be uniform throughout a larger geographic region. There was no evidence the drum signal changed throughout the breeding season.

Patterns of drumming variability were different for Northern Flickers; drumming differed significantly between coniferous forests and oak woodlands in multivariate tests of cadence and spacing. Northern Flickers in coniferous forests consistently drummed faster than those in oak woodlands, with little variation within each population. However, only 2 of the 15 individuals sampled were from oak woodland areas, and such a small sample size precludes a definitive conclusion. Further research is needed to determine whether a drumming dialect occurs in Northern Flickers.

Analysis of all species redistributed by the discriminant function demonstrated that drumming is not species-specific; notable misclassifications occurred between Nuttall's and White-headed Woodpeckers, and between Ladder-backed and Hairy Woodpeckers. The overall error count was 21.8%, whereas the posterior error rate was 14.3%, which indicated poor separation and high overlap of species based upon selected drum parameters. However, reanalysis of the drum signal using syntopic species indicated signal specificity within their acoustical environment based upon a combination of drum variables. This interaction was clearly illustrated between the allotopic White-headed and Nuttall's Woodpeckers, and between Hairy and Ladder-backed Woodpeckers. These species' couplets have similar drum parameters, but due to allotopic distributions within study areas, each species' drum was diagnostic within its restricted acoustical environment.

Syntopic posterior probability error rates for desert species totaled 7.2%; thus prediction of species membership by drum alone in desert habitats within California is fairly precise (92.8%). Recordings of desert species' drums where species coexist were not made during the course of this study. Therefore, it is possible that drums of these three species are different in their drum variables in areas where they occur syntopically. However, drums recorded during this study do compare favorably to drums from Nuttall's Woodpeckers recorded in Baja California by Short (1971). This would suggest that there is little plasticity in the drums of Nuttall's Woodpecker throughout habitats in the Southwest.

Posterior probability error rates were even lower in habitats which contained a greater variety of species within California. Oak woodland species could be classified by drum alone with 94% accuracy, whereas coniferous forest species' drums were diagnostic 96.8%. In every habitat, it was the drum of Northern Flickers which increased the posterior error rate and increased the probability of overall species misidentification. Therefore, posterior probability error rates for each species demonstrated that drumming in woodpeckers is syntopically, but not allotopically, species-specific.

It is significant to note that Downy and Hairy Woodpeckers were never misclassified into one another, and that the drumming of Downy (17.1 ± 1.3 beats sec^{-1}) was significantly slower than that of Hairy Woodpeckers (26.1 ± 1.1 beats sec^{-1}). This is contrary to the report of Short (1982) and other researchers, which describe drumming in Hairy Woodpeckers as variable and at times indistinguishable from that of Downy Woodpeckers (Lawrence 1967, Short 1971, Kilham 1983). Drumming in these species is exactly opposite to that reported by Bent (1939), who described the Downy Woodpecker as having the faster cadence. However, these authors primarily relied upon eastern representatives of these species, whereas this study examined western species. Although there was no evidence for differences between woodpecker drums over a small geographic region, differences between this study and eastern studies may indicate geographic variation in drumming. Furthermore, the drumming of Nuttall's Woodpecker (20.6 ± 1.0 beats sec^{-1}) was significantly slower than that of the Ladder-backed Woodpecker (28.3 ± 2.0 beats sec^{-1}). Drumming could potentially act as a behavioral isolating mechanism between these phenotypically similar species. However, hybridization studies on Nuttall's and Ladder-backed Woodpeckers may indicate drumming is not a premating isolating mechanism between these species (Short 1971).

The stepwise portion of the discriminant function indicated cadence as the primary variable in drumming for separation of species, although the other variables selected were necessary for separation depending upon habitat. This would indicate that these variables were secondarily necessary for species identification. Therefore, nonmechanical portions of the signal also may be important in species identification. For example, woodpeckers may emphasize certain frequency components of the signal which could cause a particular portion or phrase to be species-specific. However, the frequency (Hz) of the signal would depend upon the resonance of the substrate selected, and different frequencies attenuate differently over distance (Brenowitz 1981, Wiley and Richards 1982, Dabelsteen et al. 1993).

Woodpeckers could control for basal frequency through selection of substrate. However, this was not the case for a study on Yellow-bellied Sapsuckers (S. varius), which determined that the peak power and longest lasting frequency was not significantly different between drum, nest, and food trees (Eberhardt 1997). There was a tendency for drum substrates to produce lower

sounds than nest or food substrates which may indicate a tendency for selection of substrate which would generate longer wavelengths for increased distance in signaling. Signal frequency is probably not a constant variable required for long distance communication, although it may have other functions such as individual identification (Wiley and Richards 1982). This component of the signal was not tested in this study, but was investigated by behavioral studies (Dodenhoff 1996).

The patterns in spacing of beats within an unmodulated drum are usually perceived as a tonal quality within the drum, often described as "bouncy" or "more rapid at end" (Lawrence 1967, Kilham 1983). However, long distance signals often encode species specificity temporally (Becker 1982), with harmonics and tonality considered relatively unimportant. We believe the spacing characteristics within a drum may contain species information, but due to the difficulty of dealing with this type of data in a discriminate function, analysis of this parameter was left to behavioral experimentation (Dodenhoff 1996).

Spacing patterns of beats within a modulated drum may be diagnostic in some species (Campephilus and Sphyrapicus) due to a spaced cadence in drum taps (Short 1982). Both sapsuckers examined in this study modulated the cadence of their drums, which was diagnostic within their habitat. The introductory cadence (group) of the drum of Red-breasted Sapsuckers overlapped the overall cadence of White-headed Woodpeckers, whereas the Williamson's Sapsucker group overlapped the Hairy Woodpecker, with all four species being syntopic. This may result in signal equivocation remaining between those species with a similar introductory cadence (Kreutzer 1990). Further research is needed concerning minimum drum signal length that initiates a behavioral response in picids.

We postulate the modulation of the cadence of sapsuckers may have arisen from acoustical competition due to high signal overlap with heterospecific noncompetitors. Theoretically, if the introductory grouping matched the cadence of another syntopic species, then natural selection should favor a signal which decreased equivocation over time. Modulation of the drum to a broken cadence is a possible means to increase signal specificity without requiring major changes in musculature or structural morphology, unlike an increased cadence. Although difficult to prove, the resulting specificity should increase the organism's fitness, eliciting responses only from conspecifics in an acoustically complex environment.

In contrast, high signal equivocation indicated that drumming in Northern Flickers should tend to elicit a response from heterospecific and conspecific individuals. Northern Flickers had the highest degree of misclassification of any species studied, being classified into species whose cadence was both faster (Hairy Woodpecker) and slower (Nuttall's and White-headed Woodpeckers) than itself. The classification error rate of Northern Flickers was higher in oak woodlands (53.3%) than in coniferous forests (33.3%), which followed the observation that drumming in Northern Flickers was more common at higher elevations. However, Northern Flickers have developed the use of a "long call" which is highly diagnostic as a species-specific signal even at extremely long ranges, and usually accompanies drumming bouts (Moore 1995).

Short (1971) suggested that long calls may have been favored within environments which lacked suitable substrate for drumming. The Northern Flickers within this study were recorded drumming on wood, aluminum roofs and chimney covers, plastic light housings, and even a glass light covering, yet drums recorded from these substrates were within species parameters, indicating the drum signal (with the exception of basal frequency) is not affected by variable substrate. Therefore, we postulate that signal equivocation in Northern Flicker's drums with syntopic woodpeckers may favor this highly diagnostic call in environments with available substrate. Because flickers occur across North America, and eastern birds call more often than western counterparts (Johnson, pers. observ.), it would be instructive to look at eastern flickers' equivocation with syntopics.

This study was intended to be a preliminary investigation to determine whether drums were species-specific. Although drums are species-specific syntopically, the geographic ranges sampled were limited. Regions where two species with similar drum parameters co-occur should be sampled to determine whether temporal spacing of individual beats encodes species-specific information. Another aspect of drumming not analyzed by this study was the

occurrence of temporal differences in drumming for each species. Many of the species recorded were observed drumming during similar times of the year, with the notable exception of Northern Flickers. This may indicate a way for species with similar heterospecific drums to avoid signal equivocation through temporal stratification of reproductive cycles, rather than signal modification. Therefore, we suggest further investigation of species-specific components which incorporate experimentation from a signal receiver perspective.

ACKNOWLEDGMENTS

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