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SEASONAL VARIATION IN ACOUSTIC SIGNALS OF PILEATED WOODPECKERS

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ABSTRACT.—We used remote recorders to document temporal variation in acoustic signals of a population of Pileated Woodpeckers (*Dryocopus pileatus*) along the Choctawhatchee River in the Florida Panhandle, sampling seven different locations for 24 hrs once a week between mid January and mid April 2006. We found significant seasonal variation in the drumming behavior and vocal behavior of Pileated Woodpeckers. Drumming behavior peaked in mid March, just prior to onset of breeding activities. The three primary long-distance Pileated Woodpecker vocalizations, the *cackle* call, the *wuk* series call, and the *wok* call had similar patterns of seasonal variation. All four acoustic signals declined to low levels by early April when birds were nesting. The seasonal pattern of variation for all four Pileated Woodpecker acoustic signals had a similar pattern to that observed for song in many temperate passerines, and support the hypothesis that woodpecker calls and drumming displays are the functional counterparts to passerine song. *Received 17 September 2007. Accepted 27 January 2008.*

The long-range acoustic signals of many territorial birds function in both territory defense and mate attraction (Catchpole and Slater 1995). Comparatively little research has been conducted on acoustic communication in woodpeckers (Piciformes) (Stark et al. 1998). The functions of the majority of acoustic signals used by woodpeckers are not fully understood, and seasonal patterns of variation in their acoustic behavior have yet to be investigated. A clear understanding of seasonal variation in woodpecker acoustic signals may increase our understanding of the function of their calling and drumming behavior.

Woodpecker vocalizations remain virtually unstudied, although woodpecker mechanical sounds have received modest attention (Stark et al. 1998). All woodpeckers produce nonvocal acoustic signals referred to as ''drumming'' and these far-carrying sounds are thought to function in long distance communication (Dodenhoff et al. 2001). A woodpecker drum consists of a repetitive series of strikes by the bird's bill against an external substrate, and is distinguished as not being associated with foraging or cavity excavation (Bent 1939, Pynnönen 1939, Short 1974). Woodpecker drumming is postulated to be the evolutionary counterpart to song (Pynnönen 1939, Lawrence 1967), replacing the complex vocalizations used by passerines for long-distance communication (Dodenhoff et al. 2001). Several hypotheses for the function of drumming have been proposed; the best supported include territory announcement and maintenance, mate attraction, pair bond maintenance, and individual localization (Short 1982, Wilkins and Ritchison 1999).

Pileated Woodpeckers (*Dryocopus pileatus*) are sexually dimorphic, monogamous, nonmigratory woodpeckers that inhabit deciduous and coniferous forests from southern Canada through the western, midwest, and eastern United States (Bent 1939, Bull and Jackson 1995). The ecology of Pileated Woodpeckers has been studied in greater detail than many other woodpecker species, perhaps owing to their majestic appearance, large size, and wide distribution. The basic characteristics of Pileated Woodpecker drums have been described (Bull and Jackson 1995, Stark et al. 1998), although a detailed study of variation in drumming behavior over time has not been previously conducted. Additionally, there are discrepancies regarding vocalizations, especially concerning terminology and function (Humphrey 1946, Kilham 1959).

We recorded the acoustic signals of a population of Pileated Woodpeckers along the Choctawhatchee River in the Florida panhandle over a 4-month period. Our objective was to examine seasonal patterns in the acoustic behavior of this species to better understand the possible functions of both vocal and nonvocal acoustic communication in woodpeckers. We predicted that acoustic signals of Pileated Woodpeckers would show a peak in activity at the start of the breeding season, sim-

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ilar to the documented pattern of seasonal variation in singing behavior of many songbirds (e.g., Catchpole 1973, Amrhein et al. 2004).

METHODS

Field Techniques.—We studied Pileated Woodpeckers in a plot of mature bottomland forest along the Choctawhatchee River in the Florida Panhandle (30° 3′ N, 85° 5′ W), during a bioacoustic search for Ivory-billed Woodpeckers (*Campephilus principalis*) (Hill et al. 2006). We placed seven automated ''listening stations'' throughout our study site in January 2006. Each listening station consisted of a Sennheiser ME-62 omni-directional microphone and K6 power module connected to a Marantz PMD-670 solid-state digital recorder powered by a sealed lead-acid battery. The microphones were shielded in protective rain guards made from polyvinyl chloride (PVC) tubing and were attached to the top of a 3-m wooden stake via a 30-cm shelf bracket. Wooden stakes were attached to small trees in an effort to capture sound from all directions and minimize any sound shadow resulting from the tree trunk. All visible materials were camouflaged with spray paint to minimize the influence of their presence on the behavior of resident birds. Each of the seven listening stations recorded 24-hr MP3 files at 44.1 kHz, 16 bit, 160 kbps onto Hitachi 3GB microdrive cards. Memory cards and batteries were changed daily by quietly paddling or hiking to the site. Full details of the recording apparatus and sampling regime are given in Hill et al. (2006).

We selected recordings from 14 dates between 20 January and 20 April 2006 (specific recording dates: 20, 27 Jan; 3, 10, 16, 22, 28 Feb; 7, 14, 22, 28 Mar; and 5, 14, 20 Apr). We used recordings from seven distinct areas on each of the 14 dates which yielded 98 24-hr recordings. The recordings analyzed were selected from days with no precipitation and little to no wind to ensure consistency in recording conditions. Files were scanned using Syrinx-PC sound analysis software (John Burt, Seattle, WA, USA) and acoustic signals of interest were annotated using Syrinx-PC's time and frequency cursors.

The seven recording units were separated by a distance of 766.4 ± 83.2 m ($\bar{x}$ ± SE) between the seven microphones. The territory size of Pileated Woodpeckers has not been carefully described, but reported breeding densities in bottomland forests of the southern United States are one pair/14–43 ha (Tanner 1942, Dennis 1951, Carter 1967). Consequently, we assume that each one of the seven recording units was recording different individuals.

We collected direct observations of birds on the Choctawhatchee River to assess the timing of Pileated Woodpecker breeding behavior. A team of field technicians searching for Ivory-billed Woodpeckers from January to May 2006 and 2007 documented any Pileated Woodpecker breeding behavior observed. We also referred to published records of the timing of Pileated Woodpecker breeding. We collected average daily temperature data throughout the recording period from www.accuweather.com.

Definition of Drums and Vocalizations.—The Pileated Woodpecker drum pattern is a tattoo of 11–30 beats lasting ~3 sec and trailing off in amplitude towards the end (Kilham 1959; Fig. 1A). Birds also produce a quieter ''drum-tapping'' which is a slow, close-range communication that can be heard during times of feeding, courtship, and upon agreement regarding the location of a nest hole (Kilham 1959). Many other woodpecker species present at our study site engaged in similar forms of drum-tapping, and we omitted drum-tapping given the difficultly in accurately distinguishing between Pileated Woodpecker and heterospecific tapping without visual identification.

Pileated Woodpecker vocalizations have been described by several authors, notably Kilham (1959) and Short (1982), although terminology is inconsistent across authors. Kilham (1959) described five basic calls while Short described three. However, across all descriptions, Pileated Woodpecker vocalizations are simple acoustic signals, consisting of 1–2 syllables given individually or in series (Bull and Jackson 1995). We examined temporal patterns in the three most common long-distance Pileated Woodpecker vocalizations: (1) the *cackle* (also referred to as a fast *wuk* series call), (2) the *wuk* series call, and (3) the *wok* call (also referred to as the *waa* call). The *cackle* call (Fig. 1B) consists of rapid series

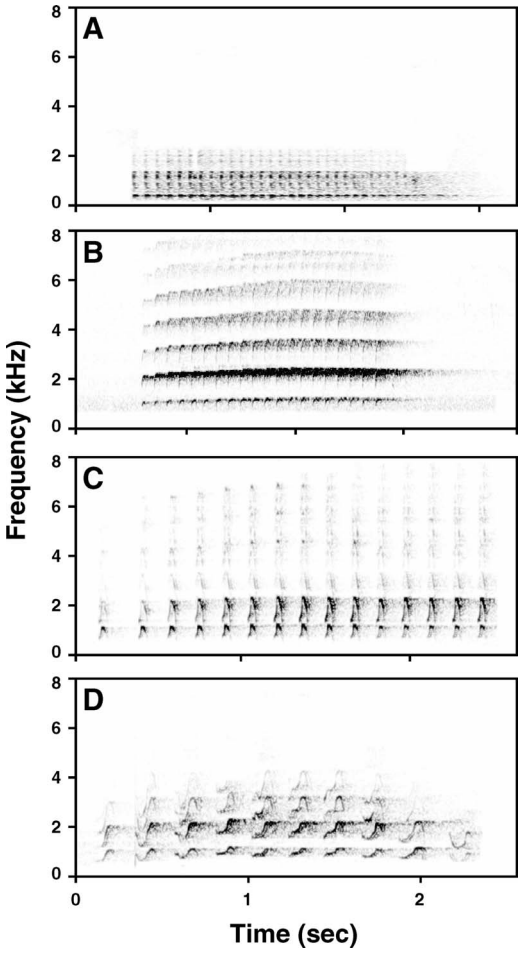

FIG. 1. Sound spectrograms of four primary long-distance acoustic signals of Pileated Woodpeckers sampled with automated recorders in the Choctawhatchee River bottomland forests in Florida: (A) drumming, (B) the *cackle* call, (C) the *wuk* series call, and (D) the *wok* call.

of notes that rise and then fall in pitch. Capable of transmitting over long distances, it is thought to be used in territorial assertion, distant interactions, and as a copulation readiness signal (Short 1982). The *wuk* series call (Fig. 1C) described by Short (1982), is a much longer series of spaced-out notes. Some authors categorize the *cackle* call as a fast version of the *wuk* series call, but we distinguish the *wuk* as the substantially slower, drawn-out calls. The *wuk* series is used in situations of agitation or alarm (Bull and Jackson 1995). The *wok* call (Fig. 1D) described by Short (1982), is a lower amplitude vocalization generally given in a series of eight notes, at a rate of ~3 notes/sec. It is used during interactions between birds and appears to be synonymous with Kilham's (1959) ''high call''.

Statistical Analysis.—We applied repeated measures ANOVA using SPSS 14 to analyze temporal patterns in each of the four Pileated Woodpecker acoustic signals (SPSS Inc., Chicago, IL, USA). The within-subjects factor for each acoustic signal was the week number (14 levels), and the between-subjects factor was the recording location (7 levels). Values for each acoustic signal were calculated as the mean frequency of occurrence per hour across all daylight hours. Results are given as means ± SE and all tests are two-tailed.

RESULTS

Pileated Woodpeckers in the Choctawhatchee River bottomlands demonstrated significant seasonal variation in all four of this species' long-range acoustic signals. Drum production remained low throughout January and February, increased in early March, peaked in late March, and decreased to the January and February level by the beginning of April (ANOVA: $F = 2.49$, $P = 0.007$; Fig. 2A). The frequency of occurrence of the *cackle* call increased from the end of January to a peak in mid March, followed by a decrease which continued into mid April (ANOVA: $F = 4.50$, $P < 0.001$; Fig. 2B). The *wuk* series call exhibited substantial variation from week to week, but it followed an oscillating pattern which peaked in late March, before decreasing substantially in April (ANOVA: $F = 2.58$, $P = 0.005$; Fig. 2C). The *wok* call at all times of year was less frequent than all other call types (Fig. 2). There was an increase in the frequency of occurrence for the *wok* call from January to mid March; after this date the *wok* call was not detected again until early April when levels increased once again, albeit at a low level (ANOVA: $F = 2.70$, $P = 0.003$; Fig. 2D).

Pileated Woodpeckers were abundant at the study site and were encountered daily throughout the period from January to April. Pileated Woodpecker breeding activities were observed on four occasions; (1) one pair of birds excavated a cavity between 20 and 23 March (cavity excavation is believed to last

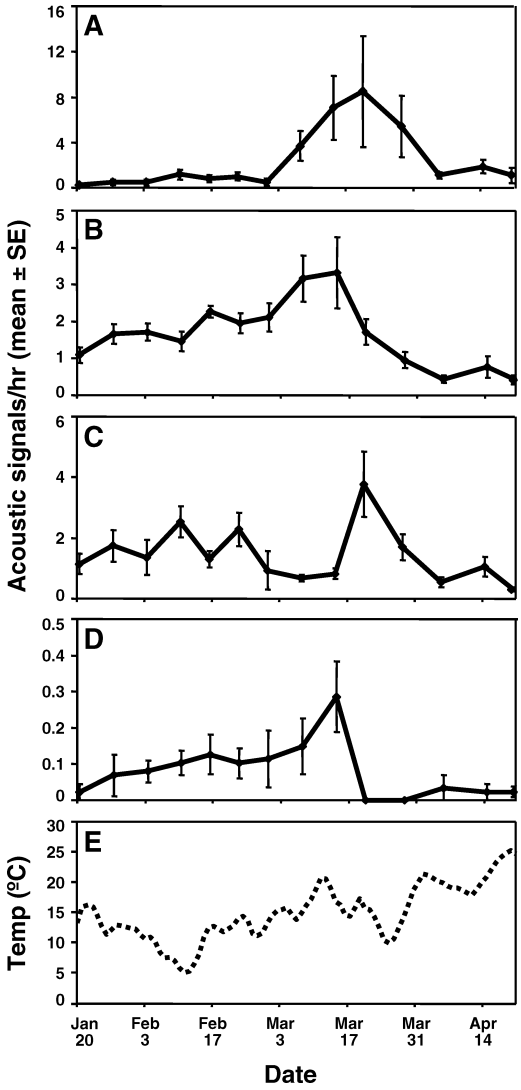

FIG. 2. Seasonal variation in frequency of recording the four primary long-distance acoustic signals of Pileated Woodpeckers in the Choctawhatchee River bottomland forests in Florida: (A) drumming, (B) the *cackle* call, (C) the *wuk* series call, and (D) the *wok* call. Seasonal variation in temperature (E) shows a gradually increasing mean temperature across the recording period.

~3–6 weeks); (2 and 3) two different nests were found, both with incubating parents, on 3 and 5 May (incubation is believed to last 18 days, suggesting eggs in these nests were laid in Apr); and (4) for a fourth pair fledglings were observed in early May (suggesting eggs were laid in late Mar or early Apr). This period of nesting and egg laying activity in late March and April corresponds to a period when the temperature on the Choctawhatchee River was beginning to increase (Fig. 2E).

DISCUSSION

Our recordings from the bottomland forests along the Choctawhatchee River in the Florida Panhandle revealed significant seasonal variation in the acoustic behavior of Pileated Woodpeckers. All four of the Pileated Woodpecker's long-distance acoustic signals reached a peak in mid March. Pileated Woodpeckers in Florida commenced breeding in mid March; other studies have found that egg laying occurs between 17 March and 25 May in Florida (Bent 1939, Stevenson and Anderson 1994). Our observations confirmed that mid March and early April mark the beginning of the breeding period for the Choctawhatchee Pileated Woodpecker population. Our results support the prediction that acoustic signals peak in activity at the start of the breeding season. The pattern we observed for all four Pileated Woodpecker acoustic signals corresponds to the pattern of seasonal variation documented for the singing behavior of many songbirds (e.g., Catchpole 1973, Amrhein et al. 2004).

All four of the long-range signals of Pileated Woodpeckers that we studied were given at low levels throughout late January and February. Pileated Woodpecker pairs are territorial at all times of the year (Hoyt 1957, Bull and Jackson 1995) and this early winter period corresponds with pre-breeding activities when males and females have not yet started excavating nest cavities. The *wuk* series call followed a non-linear pattern during this period of low vocal activity, which may be related to the proposed function of this call. This acoustic signal is thought to be given as an alarm call or when a bird is agitated (Bull and Jackson 1995). The stochastic pattern of variation we observed for the *wuk* series call likely relates to the stochastic nature of threats that may have elicited alarm. Both the *cackle* call and *wok* call increased in frequency in early March, reaching their peak in mid March. Both the drum and the *wuk* series call reached their maximum the following week. Drumming is believed to function in territorial announcement (Lawrence 1967); this maximum

presumably occurred because adults were actively defending their territory and nest site at the time of intensified courtship and egg laying. A decrease occurred in the production of all four acoustic signals in late March. Egg-laying has been documented to occur in Florida between 17 March and 25 May (Bent 1939), and this minimum in acoustic signal production may have occurred because females were incubating their clutches; high levels of calling may increase birds' conspicuousness and reveal the location of their nest hole to predators.

The drum display, *cackle* call, and the *wok* call had a similar pattern of seasonal variation, suggesting that all three signals have roles of increased importance during the breeding season. The drum and *cackle* call of the Pileated Woodpecker have both been proposed to function in territorial advertisement; both males and females have been observed to respond to territorial intrusion by drumming and calling (Mellen et al. 1992). Pileated Woodpecker pairs defend territories all year, but do not defend their territories as vigorously during the non-breeding season in the fall and winter; during this time territorial intrusion by floaters is generally tolerated (Bull and Jackson 1995). The seasonal patterns we observed in both the drum and *cackle* calls of Pileated Woodpeckers in northern Florida reflect this increase in territorial aggression with hourly rates starting low during the pre-breeding season in January and mid February before peaking during the onset of breeding in mid March. The *wok* call is usually given in interactions between individuals, which should similarly reach a maximum during the period of affiliation associated with the start of the breeding season. Understanding how these vocalizations vary across the breeding season has important implications for survey techniques (Selmi and Boulinier 2003); our data show that Pileated Woodpeckers should be most readily detectable early in the breeding season.

Woodpecker drumming has long been postulated to be the functional counterpart to passerine song (Pynnönen 1939, Lawrence 1967). Our analyses reveal a pattern of seasonal variation in drumming behavior, as well as calling behavior, that supports this hypothesis. Drumming has received modest attention in the literature (Stark et al. 1998, Dodenhoff et al. 2001), but more quantitative work is needed to clarify possible functions.

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