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Vocal behavior of Great Curassows, a vulnerable Neotropical bird

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ABSTRACT. The Cracidae rank among the most threatened families of Neotropical birds, and studies of their vocal behavior may help guide conservation and monitoring efforts. We describe the vocal behavior of Great Curassows (*Crax rubra*), a little-studied Cracid species currently listed as vulnerable. From 2008 to 2010, we recorded curassows in northwest Costa Rica using both handheld and automated digital recorders. Analysis of recordings revealed that Great Curassows had a repertoire of five call types. *Yip* and *bark* calls are sex-specific alarm calls of short duration (0.12 and 0.08 s, respectively). The descending whistle is a longer duration alarm call (2.18 s) produced primarily by males. The *snarl* is a short call (0.67 s) associated with a threat display produced by adults with dependent young. The *boom* call was the most common Great Curassow vocalization, and was given only by males. *Boom* calls are long (8.86 s), low-frequency (<150 Hz), multisyllable calls comprised of four stereotyped phrases. Great Curassows often uttered *boom* calls well before dawn, with a peak in activity at dawn and the hours following. Males produced bouts of repeated *boom* calls that lasted an average of 35 min, but sometimes continued for more than 5 h. *Boom* calls were given from February to June, with a peak in late April and early May when breeding begins. Discriminant analysis of *boom* calls of birds from 10 different locations revealed interindividual variation in call structure that may be useful for bioacoustic monitoring of individuals. Our results suggest that automated recorders might provide a way to monitor the abundance of male curassows because their *boom* calls are given frequently during the period from February to June and can be detected at distances up to 250 m.

RESUMEN. **Conducta vocal de *Crax rubra*, una especie Neotropical vulnerable**
Los crácidos se encuentran entre las familias de aves Neotropicales más amenazadas, y estudios de su conducta vocal puede ayudar a proveer guías para su conservación y monitorear los esfuerzos de estas. Describimos la conducta vocal de *Crax rubra*, una especie pobremente estudiada, actualmente considerada vulnerable. De 2008 al 2010, grabamos la vocalización de esta especie en el noroeste de Costa Rica, utilizando grabadoras manuales y digitales. El análisis de las grabaciones reveló que el ave tiene un repertorio de cinco tipos de llamadas. Las llamadas "yip" y "bark", especificas al sexo, son de alarma y de poca duración (0.12 y 0.08 seg, respectivamente). El silbido descendente es una llamada de alarma de mayor duración (2.18 seg) que es producidas principalmente por los machos. El "snarl" es una llamada corta asociada con una conducta de amenaza producida por adultos con pichones. El "boom" resultó ser la vocalización más común del ave, y fue producida únicamente por los machos. Esta llamada es larga (8.86 seg) y de baja frecuencia (<150 Hz), y las multisílabas fueron parte de cuatro frases estereotipadas. Las aves estudiadas exhibieron los "booms" mucho antes del amanecer, con un pico de actividad, al amanecer y en las horas subsiguientes. Los machos produjeron episodios de "booms" repetidos que duraron un promedio de 35 minutos, pero en ocasiones prosiguieron por más de cinco horas. Escuchamos "booms" de febrero a junio con un pico tarde en abril y principios de mayo, cuando comienza la época de reproducción. Un análisis de discriminación de los "boom" de aves de 10 localidades diferentes, reveló variación interindividual en la estructura de la llamada, que pudiera ser de utilidad para el monitoreo bioacústico de individuos. Nuestros resultados sugieren, que grabaciones automáticas pudieran proveer una forma de monitorear la abundancia de machos, debido a que sus llamadas (boom) se dan con frecuencia durante el periodo de febrero a junio y pueden ser detectadas hasta 250 m de distancia.

Key words: boom call, Cracidae, curassow, near infrasound, vocal activity, vocal repertoire

Understanding the context of bird calls and patterns of diel and seasonal variation in vocal output can help ornithologists and conservation biologists plan surveys and develop effective management and monitoring strategies. Great Curassows (*Crax rubra*) are considered a high conservation priority and have been designated as Vulnerable by the International Union for the Conservation of Nature, with an estimated 10 000 to 60 000 birds remaining in the wild (BirdLife International 2010). Great Curassows produce a variety of different sounds, from

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extremely low-frequency vocalizations to high-frequency alarm calls (Brooks and Strahl 2000). In this study, we provide a detailed account of the vocal behavior of this vulnerable tropical species using autonomous recordings as well as opportunistic focal recordings and field observations of calling birds.

Several previous accounts provide information about Great Curassow vocalizations, but these accounts are largely anecdotal and present incomplete descriptions that lack fine structural analysis or quantification. Stiles and Skutch (1989) indicated that the vocal repertoire includes "a high-pitched yipping like a small dog"; "a thin high-pitched usually descending whistle"; and "a deep, low, resonant, ventriloquial *hummm.*" We refer to the deep *hummm* as the *boom* call, the high-pitched whistle as the descending whistle, and two variants of the yipping sound as the *yip* call and the *bark* call. Russell (1964) described an encounter where a female defending young produced an additional vocalization: a "loud mammallike snarl" (cited in Delacour and Amadon 1973) that we refer to as the *snarl* call. Many accounts mention "*hoots*", "*grunts*", and "*moos*" that may refer to distant *boom* calls. In addition, various accounts have described short vocalizations that sound like "*pitt witt*" or "*puit's*" (González-García et al. 2001) or "*whip!*" calls (Jones and Gardner 2003) that may refer to variants of the *bark* or *yip* calls. To date, no formal nomenclature for the different call types has been established, making it difficult to determine how many call types comprise the vocal repertoire of Great Curassows. Additionally, little is known about how vocal output varies with time of day or time of year, and the possible functions of the calls have not been carefully investigated.

We analyzed recordings of birds in the Guanacaste Conservation Area in Costa Rica to provide the first quantitative description of the vocal repertoire of Great Curassows. Based on the existing literature and our own recordings and observations, we determined that Great Curassows have five call types and we provide fine structural measurements for each. We quantify diel and seasonal patterns of variation in *boom* call output, and also investigate the possibility of discriminating between individuals using structural differences in *boom* calls. Lastly, we report the results of a playback study to provide insight into the function of two curassow vocalizations.

METHODS

We recorded Great Curassows in Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica (10°40'N, 85°30'W). This area is recognized as a world heritage site by the United Nations Educational Scientific and Cultural Organization (UNESCO) and protects one of the largest remaining stands of tropical dry forest. We obtained recordings of curassows from March to June 2008 and from February to June 2010, corresponding to the late dry season and early wet season (Topp and Mennill 2008). Great Curassows are relatively common in the mature forested areas of the Guanacaste Conservation Area (Woodcock 2010), but are easily frightened by humans and difficult to observe. We supplemented our field recordings with observations of Great Curassow vocal behavior collected when conducting studies on other species from 2002 to 2010. We encountered curassows at least weekly during these studies; we noted any vocalizations, recorded them if possible, and documented any associated behaviors and the apparent context of calling (e.g., body postures, whether the animal retreated from the observer, and whether conspecific birds were present). We attempted to quantify behaviors when possible, but we include some anecdotal, qualitative observations that provide some perspective to curassow vocal behavior.

We recorded curassows using automated recorders. In 2008, we used automated recorders consisting of omnidirectional microphones (Model ME62/K6, Sennheiser; frequency response = 40 Hz – 20 kHz), and digital recorders (Model PMD670, Marantz) powered by sealed lead-acid batteries. Sounds were recorded as continuous 24-h recordings as 16-bit, 160-kbps MP3 audio files at a sampling frequency of 44.1 kHz (recordings were converted to WAV audio files for analysis). A detailed description of the recording devices used in 2008 is available in Hill et al. (2006). Two identical automated recorders were used in 2008 and were moved to different locations after each day of recording. In 2010, our automated recorders consisted of programmable autonomous recorders (Model SM2; Wildlife Acoustics, Concord, MA) with built-in omnidirectional microphones (frequency response = 20 Hz – 20 kHz). Sounds were recorded from 05:00 to 09:00 each morning as 16-bit, 320-kbps WAV audio files at a sampling frequency of 22.05 kHz. Four identical recorders were used in 2010 and were moved to different locations after each day of recording. During both 2008 and 2010, automated recording devices were placed at 30 different locations where we had observed Great Curassows. Recording sites were spread across a section of forest approximately 20 km^2 in area (5 × 4 km); adjacent recording sites were separated by a mean distance of 279 ± 21 (SE) m. To complement automated recordings, birds were recorded opportunistically around the study site using digital recorders (Model PMD-660; Marantz, Kanagawa, Japan) with directional microphones (Model ME-66/K6 or MKH70; Sennheiser, Wedemark, Germany; frequency response = 40 Hz – 20 kHz and 50 Hz – 20 kHz, respectively; recording format: 16 bit, 320 kbps, WAV audio files at a sampling frequency of 44.1 kHz). The *snarl* vocalization and one example of the *bark* vocalization were recorded using the internal microphone of a video camera (Model HDR-XR101; Sony, Tokyo, Japan).

We visualized recordings using Syrinx-PC sound analysis software (J. Burt, Seattle, WA). To analyze diel variation in use of *boom* calls, we visualized recordings as sound spectrograms, manually scanned through recordings, and annotated all calls in the 24-h recordings (N = 30 24-h recordings collected from 5 March to 25 April 2008). We determined the time each call was uttered by comparison to a Global Positioning System (GPS) time signal stated by the recordist at the start of each recording. To analyze seasonal variation in vocal behavior, we counted all calls in a 1-h period (05:00 – 06:00) from recordings collected between 22 February and 27 June 2008 and 2010 (N = 147 1-h recordings). This 1-h time interval was chosen because analysis of diel variation indicated that Great Curassows were most vocally active during this time (see Results). We calculated the average vocal output for two periods in each month: the first 15 days, and from the 16th to the last day of the month. When multiple individuals vocalized simultaneously in autonomous recordings, we distinguished individuals based on relative amplitude and only analyzed the vocalizations of the closer individual.

We analyzed the fine structure of calls using Audition software (Adobe Systems, San Jose, CA). For these analyses, Audition provided an approximate time resolution of 0.01 s and an approximate frequency resolution of 5 Hz (transform type = Blackman, transform size = 4096 Hz). Prior to analysis, we isolated calls from longer recordings and normalized calls to -3 dB in Audition. Occasionally, we used the lasso selection and amplify tools of Audition to "spot filter" a recording to remove low-frequency background noise so the curassow vocalizations were the loudest component of the recording. Calls chosen for fine structural analysis were the clearest (i.e., little background noise and no overlapping conspecific or heterospecific vocalizations) and easiest to measure. All vocalizations analyzed were from our recordings in Santa Rosa National Park, except for female *bark* calls. Although we heard these calls on several occasions, we only recorded this call once, so we supplemented our recording with two tracks from the Cornell Lab of Ornithology Macaulay Library of Natural Sounds (track 74016 of a bird recorded in Mexico and track 103331 of a bird recorded in Costa Rica). For analyses of the fine structure of *boom* calls, we measured the duration and frequency components of 10 calls from each of 10 individuals recorded in different parts of our study site. For analyses of the fine structure of the other types of calls, we measured all recordings of *yip* calls (9.2 ± 0.6 [SE] calls per individual from 5 individuals), *bark* calls (7.7 ± 1.2 calls per individual from 3 individuals, including tracks from the Macaulay Library), descending whistles (6.0 ± 1.6 calls per individual from 6 individuals), and *snarl* calls (4 calls from 1 individual). The descending whistle has pronounced harmonics (see Fig. 1D) and we report structural details of the fundamental frequency. For all calls except *snarl* calls, we first calculated mean values for each individual and then the mean across all individuals.

Playback study. We conducted a playback study from 22 to 27 February 2010 to help elucidate the function of *boom* and *yip* calls. We selected these two calls because they appear to be the most common calls for this species. We conducted 14 trials at Sector Santa Rosa and one trial at Sector Pitilla (~25 km northwest of Sector Santa Rosa within the Guanacaste Conservation Area). Playback sites were selected based on where Great Curassows

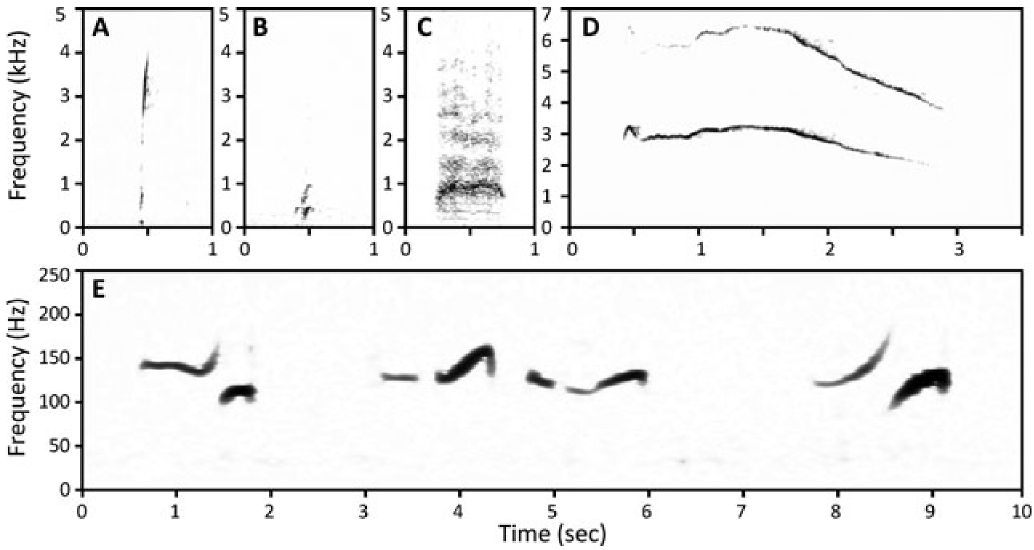

Fig. 1. Sound spectrograms showing the five call types produced by Great Curassows recorded in Costa Rica: male *yip* call (A), female *bark* call (B), *snarl* call (C), descending whistle (D), and male *boom* call (E). Note that frequency is expressed in kHz for A through D, and in Hz for E.

had been observed previously, and were at least 500 m apart. We conducted 14 trials between 05:00 and 11:00 and one trial at 15:45. Playback equipment consisted of a speaker (Sony SRS-77G; frequency response = 80 Hz – 20 kHz) connected to a digital playback device (Apple iPod) operated by an observer approximately 24 m from the speaker. All trials involved playback of both *boom* and *yip* calls. *Boom* call stimuli consisted of a 10-min loop of a single *boom* call presented at a natural rate of one call every 10 s. *Yip* call stimuli consisted of a 10-min loop of four *yip* calls repeated in succession, presented at a rate of one call every 2.5 s. Because *boom* calls are longer in duration than *yip* calls (see Results), this rate of presentation allowed us to keep the amount of vocal output consistent across the two playback treatments. The first 10-min playback stimulus was followed by a 10-min period of silence, and this was repeated for the second playback stimulus (each trial lasted 40 min). Order of stimulus presentation was alternated across the 15 trials. We normalized stimuli and broadcast them at the same amplitude across all trials at a level comparable to birds heard in the field. To minimize the effects of pseudoreplication, *boom* and *yip* calls recorded from three different individuals were used alternately across playback sessions. We noted whether or not a curassow was seen or heard during each trial, and what type of behavior the bird(s) exhibited. Thick vegetation made visual detection challenging, but we attempted to place the speaker so we could see any responding birds at least 10 m on either side.

Statistical methods. We conducted a canonical discriminant function analysis to determine if fine-structural differences in *boom* calls could be used to distinguish individuals. The discriminant analysis was constructed based on data from the first day of recording at 10 locations in Sector Santa Rosa in 2008. Curassows were not individually marked, so we used calls recorded at 10 different locations and assumed that birds recorded at each location were different individuals (mean ± SE distance between adjacent recording sites in this analysis = 488 ± 111; range = 281–1420 m). We isolated 10 *boom* calls from each location and used 12 fine-structural measures (see Table 1) to construct discriminant functions. We constructed the discriminant functions using a randomly selected subset of 70% of the 100 measured *boom* calls; we report factor loadings for these data. To cross-validate the discriminant analysis and determine if discriminant analysis could predict the correct recording location based on

Table 1. Characteristics of the four phrases of Great Curassow *boom* calls (N = 10 calls per individual from 10 individuals).

Variable	Mean ± SE
Total duration	8.86 ± 0.09 s
Phrase 1 duration	1.26 ± 0.02 s
Phrase 1 frequency of maximum amplitude	110 ± 1 Hz
Interval between phrase 1 and 2	3.15 ± 0.03 s
Phrase 2 duration	0.63 ± 0.01 s
Phrase 2 frequency of maximum amplitude	141 ± 2 Hz
Interval between phrase 2 and 3	0.97 ± 0.02 s
Phrase 3 duration	1.33 ± 0.02 s
Phrase 3 frequency of maximum amplitude	124 ± 2 Hz
Interval between phrase 3 and 4	3.28 ± 0.08 s
Phrase 4 duration	1.50 ± 0.04 s
Phrase 4 frequency of maximum amplitude	126 ± 1 Hz

the structural measures, we then tested our ability to correctly identify the location using the remaining 30% of the data; we report identification accuracy as the percentage of these calls assigned to the correct location. We also conducted a second cross-validation where we tested our ability to correctly identify the location of the calling individuals using recordings collected on a second day of recording at the same site. We had clear recordings collected on a second day for five of the 10 locations.

Descriptive statistics are presented as means ± SE. All analyses were conducted using JMP 8.0 (SAS Institute, Cary, NC).

RESULTS

Description of vocalizations and vocal behavior. Great Curassows have a vocal repertoire of five call types, including *yip* calls (Fig. 1A), *bark* calls (Fig. 1B), *snarl* calls (Fig. 1C), descending whistles (Fig. 1D), and *boom* calls (Fig. 1E). The *yip* call is a short duration call (0.12 ± 0.04 s) with a mean frequency of maximum amplitude of 3071 ± 68 Hz (Fig. 1A; N = 9.2 ± 0.6 calls per individual from 5 individuals). We often detected this vocalization when a male curassow encountered a human observer, typically while the bird retreated on foot away from the observer, suggesting that it serves as an alarm call (as argued by previous authors; Stiles and Skutch 1989). Males usually produced *yip* calls repeatedly and while displaying erect crest feathers.

The *bark* call is also a short duration call (0.08 ± 0.01 s), lower in frequency than the *yip* call, with a mean frequency of maximum amplitude of 610 ± 123 Hz (Fig. 1B; N = 7.7 ± 1.2 calls per individual from 3 individuals). It appears to be given only by females in the same context as the male *yip* call. We detected *bark* calls, usually given repeatedly, while birds were perched in a tree or after birds detected a human observer and retreated on foot (also reported by previous authors; Delacour and Amadon 1973).

The *snarl* call is a harsh, noisy vocalization (Fig. 1C) with a mean duration of 0.67 ± 0.07 s (N = 4 calls recorded from one female). The *snarl* was recorded only once, produced as part of an apparent threat display by an adult female accompanied by a young bird (matching a description by Russell [1964]). As the two birds fled from a human observer, the adult fanned its rectrices while the young bird attempted to hide beneath the adult's tail. When the young bird paused, the adult female moved toward the observer, puffed up her feathers, and produced four loud *snarl* calls in succession. The *snarl* was preceded and followed by *bark* calls. The adult retreated from the observer in a direction opposite to the young bird, as if to lead the human away from the young bird.

The descending whistle is a long, tonal vocalization with a mean duration of 2.18 ± 0.05 s and a mean frequency of maximum amplitude of 3074 ± 67 Hz (Fig. 1D; N = 6.0 ± 1.6 calls per individual from 6 individuals). The call ascends to a maximum frequency of 3233 ± 108 Hz and then descends to a minimum frequency of 2196 ± 88 Hz. It typically began with a short, low volume note before the long whistled section (as in Fig. 1D) and was sometimes preceded by a few low volume, short duration, high-pitched tonal sounds that we considered part of the descending whistle call. The descending whistle also appears to communicate alarm (also suggested by previous authors; Delacour and Amadon 1973). We heard this call on more than 10 occasions when males were escaping on foot after detecting a human observer, but, on three occasions, we heard this call while males were perched on a branch in the canopy. On five occasions, the descending whistle call was given by a male that had been giving *boom* calls near a female prior to detecting a human observer.

The *boom* call is a complex, low-frequency vocalization given only by males (Delacour and Amadon 1973, this study; Fig. 1E; $N = 10$ calls per individual from 10 individuals). *Boom* calls averaged 8.86 ± 0.09 s in duration and consisted of four phrases that varied slightly in duration and frequency (Table 1). The first phrase had the lowest mean frequency of maximum amplitude (110 ± 1 Hz) and the second phrase had the highest mean frequency of maximum amplitude (141 ± 2 Hz). The fourth phrase was consistently the loudest part of *boom* calls and was often the only audible component of the call in the field or when listening to recordings of distant individuals (SB and DJM, pers. observ.). The transmission distance of boom calls appears to be greater than that of other Great Curassow vocalizations; we detected the fourth phrase of the *boom* call at a distance greater than 250 m (distance estimate based on GPS coordinates collected after hearing a bird and approaching, until the male was observed calling from a perch; the other phrases became audible only when moving closer to the calling male). Unlike the *yip*, *bark*, *snarl*, and descending whistle calls, *boom* calls were regularly produced independently of encounters with human observers, as was evident in our automated recordings.

Great Curassows produced *boom* calls both from perches in the canopy and on the ground. Males gave *boom* calls repeatedly during extended periods of calling (average bout length: 34.5 ± 4.3 min with 121 ± 17 *boom* calls per bout; $N =$ 24-h recordings from 30 locations). The longest bouts often persist for many hours (average maximum bout length: 107.2 ± 12.3 min with 421 ± 54 *boom* calls per bout; $N =$ 24-h recordings from 30 locations); our longest recorded bout featured a bird that boomed continuously for 5 h and 32 min. The highest call output by a Great Curassow in our 1-h recording dataset was 260 *boom* calls per hour. During bouts of calling, Great Curassows produced calls with a mean inter-call interval of 15.4 ± 0.1 s ($N =$ 24-h recordings from 30 locations).

Although difficult to hear, spectrograms often showed distant individuals giving *boom* calls at the same time as the bird near the microphone. We found evidence of a second bird calling in the distance in 19 of 30 day-long recordings (with distant birds calling for an average of $16 \pm 3\%$ of the total time that the focal bird was calling). In nine of 30 day-long recordings, we found evidence of a third bird calling in the distance (with the third bird calling for an average of $2.6 \pm 1.5\%$ of the total time that the other two birds were calling).

Great Curassows adopt an unusual body posture when producing *boom* calls. Calling males flatten their bodies, lower their necks, bring their heads close to their shoulders, and droop their wings to their sides so that they almost touch the ground or perch. Before uttering the first note of a *boom* call, males rapidly bow their head to the ground and throw it back between their shoulders. They hold this pose for the duration of the call.

Diel and seasonal variation in boom calls. Great Curassows produced *boom* calls between approximately 01:30 and 17:00, with a peak at approximately 05:00 (Fig. 2). Curassows often produced bouts of *boom* calls before dawn. Five of 30 day-long recordings included bouts of *boom* calls starting two or more hours before dawn, and 16 of 30 day-long recordings included bouts of *boom* calls starting 1 h before dawn (dawn occurs at ~05:00 at this site). On average, the first call was given at 03:45 (range = 01:04 – 06:45; $N = 30$ day-long recordings). The *boom* call was the only curassow vocalization detected at night. Curassows produced *boom* calls between 05:00 and 06:00 during all months we recorded them (February – June), but we found significant variation in *boom* call output across the sampling period (Kruskal-Wallis test, $K = 23.4$, $P = 0.003$), with the highest levels in late April and early May (Fig. 3).

Individual distinctiveness of boom calls. Discriminant analysis distinguished between the calls recorded at 10 different locations based on 12 fine-structural variables (Table 1). Subsequent cross-validation assigned calls to the correct recording location with 83.3% accuracy, significantly higher than expected by chance (10% expected by chance based on $N = 10$ recording locations; binomial test, $P<0.0001$). Based on our assumption that individuals recorded at each location were different birds, this suggests that *boom* calls are individually distinct. Variables that contributed most strongly to the first canonical axis in this discrimination were frequency of maximum amplitude

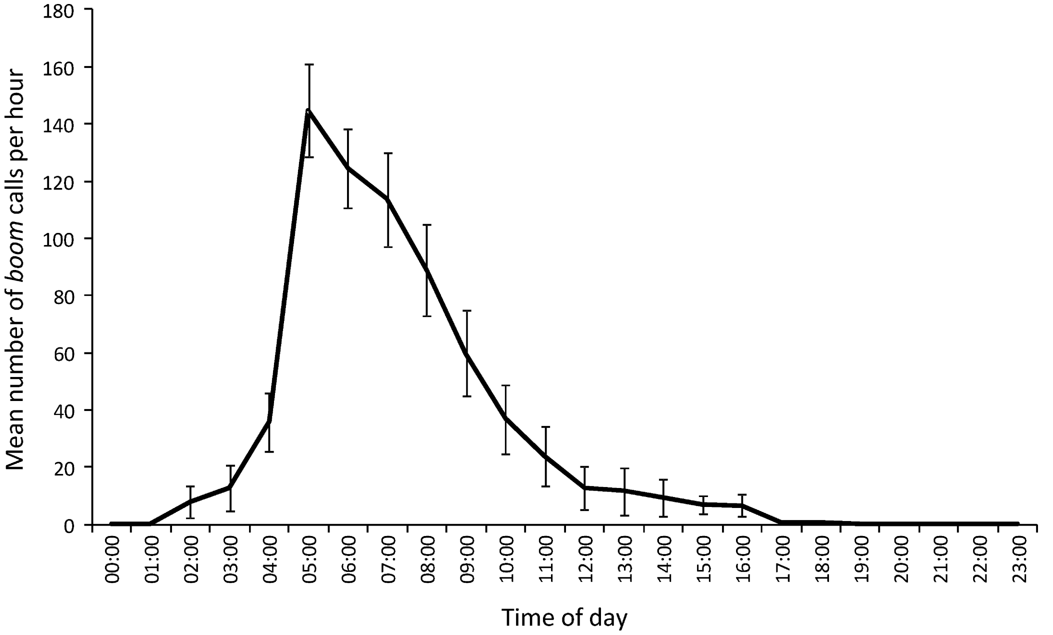

Fig. 2. Diel variation in the *boom*-call output of Great Curassows in Costa Rica. *Boom* calling begins several hours before dawn, peaks at dawn and the hours following dawn, and continues at lower rates into the late afternoon ($N = 30$ day-long recordings). Dawn occurs shortly after 05:00 at this site. Whiskers show standard errors for each 1 h time bin.

of the first, second, and third phrases, as well as the duration of the fourth phrase. Variables that contributed to the second canonical axis were the frequency of maximum amplitude of the first phrase, the duration of the second and fourth phrases, and the interval between the third and fourth phrases.

We performed a second cross-validation using 10 songs from locations where we recorded *boom* calls on subsequent days. This analysis assigned calls to the correct recording location with 48% accuracy, significantly higher than expected by chance (20% expected by chance based on $N = 5$ recording locations; binomial test, $P < 0.0001$), suggesting that the individually distinct characteristics in *boom* calls persist across different recording sessions.

Playback study. Great Curassows responded to playback during two of 15 trials (13.3%); no curassows responded during the other 13 trials. The two trials that elicited responses started at 05:47 and 07:43. During these two trials, birds approached the speaker during playback of *boom* calls (the *boom* call stimulus was the first stimulus presented during both trials), but did not respond during playback of *yip* calls. During one trial, a male and female flew toward the speaker 5 min after the start of playback. These birds perched approximately 10 m from the speaker and gave repeated *yip* and *bark* calls while oriented toward the speaker. Both birds retreated to a distance >100 m during the silent period after the *boom* call playback, joining another pair of curassows that had approached the area, possibly in response to playback. No birds returned to the speaker during the subsequent *yip*-call trial. During the second trial, a male was heard *boom* calling in the distance prior to the start of playback. Within a minute of starting the playback trial, a male, possibly the one that had been *boom* calling, quickly passed within 5 m of the speaker and disappeared from sight. Several minutes later, the male reemerged from the forest within 5 m of the speaker again, and walked silently past the loudspeaker while displaying erect crest feathers before disappearing into the forest. A minute after the last *boom* call was played, the male reemerged a third time, walked past the loudspeaker, and again disappeared into the forest. We assume that all three sightings were of the same male. Descending whistles were heard

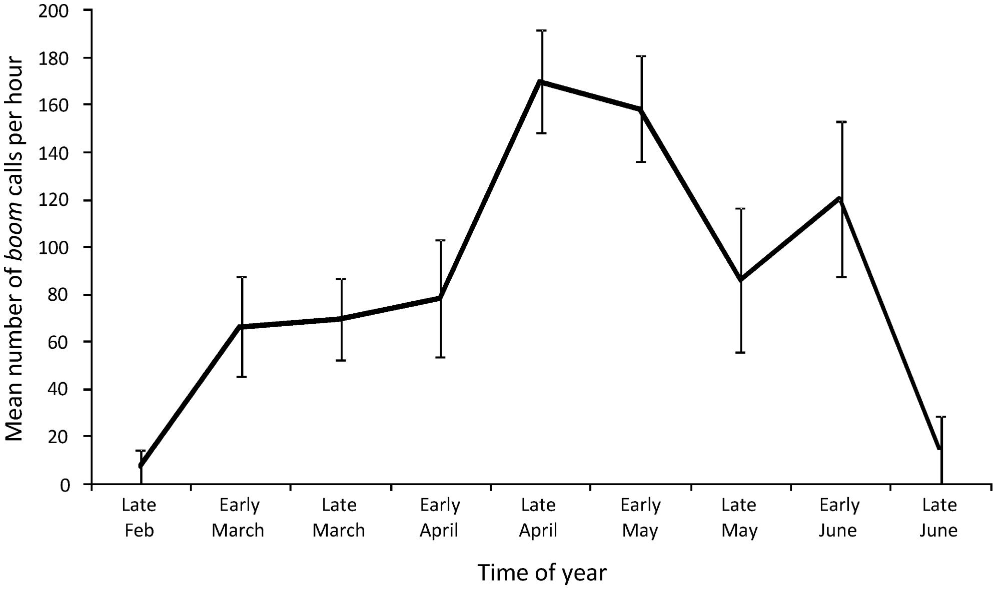

Fig. 3. Seasonal variation in the *boom*-call output of Great Curassows in Costa Rica during the period between 05:00 and 06:00. Whiskers show standard error around the mean for the first and second half of each month.

for several minutes thereafter. No curassows were detected during the subsequent *yip*-call trial.

DISCUSSION

We found that the vocal repertoire of Great Curassows includes five call types, including a *yip* call, *bark* call, descending whistle, *snarl* call, and *boom* call. The *yip* call, *bark* call, descending whistle, and *snarl* call appear to be associated with alarm. *Yip* and *bark* calls are sex-specific alarm calls and may be variants of the same call type. Although our results suggest that male *yip* calls are consistently higher in frequency than female *bark* calls, we occasionally heard calls at intermediate frequencies in the field. Delacour and Amadon (1973) suggested that both males and females produce descending whistles, but that males may produce them more often than females. However, we only observed males giving this call. We detected *snarl* calls only once; a female was accompanied by a young curassow and charged at the human observer before vocalizing. The female then appeared to try and lead the observer away from its young. Russell (1964) also noted that a female Great Curassow produced *snarl* calls and attempted to lead him away from its young. Jones and Gardner (2003) stated that male Great Curassows also produce loud *whooshing* sounds by flapping their wings during courtship displays, but we did not hear this sound and only witnessed silent courtship displays.

Great Curassows uttered *boom* calls more frequently than any other call. This call has previously been described as an "extremely low-pitched *hmmmm* that is barely audible within the human auditory range" (Jones and Gardner 2003), as "such a deep bass *uuuhm* that the sonic waves are almost felt" (Garrigues and Dean 2008), and as "a low, almost subliminal booming" (Howell and Webb 1995). Our analyses indicate that *boom* calls are almost 9-s in duration and consist of four phrases produced with a stereotyped structure. Each phrase has a unique frequency of maximum amplitude and varies in duration and amplitude from the other phrases. All species of curassows are known to produce a version of the *boom* call (Delacour and Amadon 1973, Buchholz 1995), except for the endangered Wattled Curassow (*Crax globulosa*; Delacour and Amadon 1973). The *boom* call appears to have a complex multi-note structure across all curassow species that produce it (Delacour and Amadon 1973); we visualized all recordings of curassow *booms* in the Macaulay Library of Natural Sounds' online collection and consistently found complex multi-note structure.

The near-infrasonic *boom* calls of Great Curassows, with frequencies of maximum amplitude between 100 and 150 Hz, should be effective for long-distance communication because low-frequency sounds attenuate less than high-frequency sounds (Garstang 2004). Adaptations that enhance signal transmission should be useful for species like Great Curassows that live in dense Neotropical habitats where trees and vegetation affect sound transmission (Barker 2008). The *boom* calls of Great Curassows are associated with a unique calling posture and a specialized morphological feature, an enlarged trachea (Delacour and Amadon 1973). The crouched posture and head-throwing behavior we observed has also been reported in other Cracids, such as Horned Guans (*Oreophasis derbianus*; González-García 1995). Delacour and Amadon (1973) suggested that this behavior facilitates inflation of the enlarged trachea.

We found that Great Curassows gave *boom* calls between 01:30 and 17:00. Great Curassows in our study exhibited a peak in calling behavior at dawn, similar to the dawn peak in singing activity of many songbirds (Catchpole and Slater 2008). In addition, Great Curassows in our study called from late February to late June, with peak output of *boom* calls in late April and early May. Similarly, although based on a small sample size, Baur (2008) reported peak vocal output by Great Curassows in northern Guatemala from March to May. We found no Great Curassow nests in our study area, but observations of adult courting behavior (detected from March through May multiple times annually) and of newly fledged birds (detected twice, in two different years, in late June) suggest that the breeding season begins in late April or early May. This matches other accounts that describe nesting as occurring from either February to May (Rios and Muñoz 2006) or March to May in Costa Rica (Stiles and Skutch 1989). The seasonal pattern of *boom*-calling behavior we observed supports the idea that these calls are important in the breeding behavior of Great Curassows. Cox et al. (1997) found similar patterns of vocal activity for Horned Curassows (*Pauxi unicornis*; i.e., more vocal in the morning than the afternoon and more vocal during the breeding season). Garcia and Brooks (1997) referred to the *boom* call as the courtship call of Great Curassows, whereas Brush (2009) referred to it as a territorial call. Additional study will be needed to further clarify the possible function(s) of *boom* calls.

We found interindividual variation in *boom* call structure, suggesting that these calls may provide cues to individual identity. However, this tentative conclusion can only be confirmed through repeated recording of individually marked birds. Delacour and Amadon (1973) indicated that a captive Great Curassows produced at least two different *boom* calls, but we found no changes in *boom* calls that would support that observation. If *boom* calls are individually distinctive, as our analysis suggests, they may be useful for monitoring individuals within populations.

Great Curassows responded weakly to playback of *boom* and *yip* calls, reacting only to *boom* calls during two of 15 trials. Several explanations for this weak response are possible. First, on five occasions, we observed adult birds in groups including up to four males and four females, suggesting that these birds may not be territorial and, consequently, that *boom* calls may not elicit a strong territorial response. Second, we found that *boom* calls were produced during bouts that sometimes lasted many hours, with an average bout length of 35 min; our 10-min playback may have failed to mimic a realistic *boom*-calling session. Third, Great Curassows may not have been within receiving range of our playback signal during some trials. Fourth, birds may have approached silently in the thick vegetation or may have detected us and left the area unnoticed. Fifth, because *yip* calls serve as alarm calls, birds may have retreated from the area upon hearing this stimulus.

Using passive acoustic techniques, dense tropical habitats can be monitored with minimal disturbance. Great Curassows are a good candidate for acoustic surveys because they are more easily heard than seen (Jiménez et al. 2003). Despite earlier claims that using aural cues is an inappropriate way to measure curassow abundance (Strahl and Silva 1997), recent work suggests that aural cues can be an effective tool for surveys and that acoustic monitoring can provide accurate estimates of abundance (Jiménez et al. 2003). Our data suggest that *boom* calls may be a useful way to monitor abundance of male curassows because they are a frequently used acoustic signal that can be detected at distances up to 250 m.

Additional studies are needed to determine if the four alarm calls of Great Curassows described in our study are context-specific. These calls may be given in response to specific threats or may indicate varying levels of threat. The possible sex-specific nature of these calls also merits further investigation. In addition, studies of a marked population are needed to confirm the individual distinctiveness of *boom* calls. Understanding the vocal behavior of Great Curassows increases our knowledge of this little-studied tropical species by providing insight into their communication activities, and may allow us to more effectively monitor and protect their declining populations.

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