THE DESCENDING WHISTLE DISPLAY AND FEMALE VISITATION RATES IN THE YELLOW-KNOBBED CURASSOW, *CRAX DAUBENTONI*, IN VENEZUELA

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Resumen. Se conoce muy poco acerca del comportamiento reproductivo de las especies de Crácidos. En este trabajo reporto observaciones del efecto de las condiciones sociales sobre el «silbido», la «estampida» y el «aleteo», tres componentes del despliegue llamado «silbido descendente», en el Paují de Copete, *Crax daubentoni* y discuto sus posibles funciones. Los ♂ exhibieron este despliegue por un período de tiempo más largo en presencia de otros ♂ pero no alteraron la frecuencia del silbido, la estampida y el aleteo. Adicionalmente, los ♂ fueron atraídos directamente, o respondieron en respuesta, a grabaciones del silbido obtenidas de un individuo mantenido en cautiverio. Los ♂ redujeron la intensidad del aleteo en presencia de ♀ pero la tasa de visitas de las ♀ no estuvo relacionada con este componente del despliegue. La tasa de visitas de las ♀ estuvo correlacionada negativamente con la frecuencia del silbido de los ♂. Pareciera que en esta especie las ♀ no escogen a los ♂ basadas en la energía que estos últimos invierten en sus despliegues. De hecho, el comportamiento de despliegue exhibido por los ♂ es similar a aquel asociado a la comunicación entre individuos del mismo sexo en otras especies de aves. Se discute brevemente la importancia de estos resultados para la conservación de esta especie amenazada.

Abstract. Little is known of the reproductive behavior of species in the family Cracidae. I examined the effects of social conditions on display attributes as a means of determining the function of the whistle, boom and wingflap components of the ♂ Yellow-knobbed Curassow's (*Crax daubentoni*) prominent «descending whistle» display. ♂ displayed longer in the presence of other ♂ but did not alter the frequency of specific components of their display. Also ♂ were attracted directly to, or whistled in response to, a playback of a captive ♂ whistling. ♂ reduced the intensity of wingflapping in the presence of ♀, but fe♂ visitation rates were unrelated to this component of the display. Fe♂ visitation rates were negatively correlated with ♂ whistle frequency. ♂ display behavior in this species is similar to that associated with intrasexual signalling in other bird species and appears not to involve differential energetic assessment of ♂ by ♀. The possible importance of these results to the conservation of this threatened species is briefly discussed. *Accepted 22 March 1995.*

Key words: Yellow-knobbed Curassow, Crax daubentoni, Galliformes, acoustic display, sexual selection, conservation.

INTRODUCTION

In birds acoustic displays are commonly thought to be sexually selected (Catchpole 1982). However, the relative roles of intrasexual and intersexual selection in display evolution have been difficult to elucidate since these components of sexual selection may operate in concert or in conflict to varying degrees and are often difficult to tease apart (Bradbury & Davies 1987). Identical behavioral action patterns may be used in both courtship and intrasexual aggressive encounters (Tinbergen 1939, Borgia 1987, McKinney *et al.* 1990). This problem is perhaps most acute in the study of acoustic displays in which the receiving individual is not observable to the researcher. The «bomb-dropping» whistle of the ♂ Yellow-knobbed Curassow (*Crax daubentoni*), described by Schäfer (1954) as a descending "Yiiiiiiiiii!", can be heard at great distances from the singing ♂ and has been ascribed, with little supportive evidence, to a «territorial» role (Schäfer 1954, Delacour & Amadon 1973, Todd & Bauml 1979). No adaptive explanation has been offered for the grunt-like «boom» and vigorous wingflapping components of the «descending whistle» display. Unfortunately no attempt has been made to demonstrate whether the function of these behavior patterns is primarily intrasexual as believed (Delacour and Amadon 1973) or if ♀ use this display as a basis

for mate choice. The paucity of information on the behavior of the Cracidae is in sharp contrast to our knowledge of most other Galliformes (Beebe 1990; Johnsgard 1986, 1988) and frustrates comparative studies of this otherwise well known Order. I will briefly describe the «descending whistle» display of the threatened Yellow-knobbed Curassow and, by examining its contextual correlates, identify the possible selective pressures maintaining it.

METHODS

Theoretical approach. I modified Catchpole's (1982) three-tiered approach to resolving the possible dual functions of avian acoustical displays for my study of the Yellow-knobbed Curassow. His steps are as follows. (1) Determine the correlations between different singing behaviors and mating or spacing systems among closely related species. Our lack of knowledge of the behavior of curassows precludes this step. Instead the dispersion and behavior of displaying ♂ Yellow-knobbed Curassows was compared with sub-oscine equivalents of passerine systems with known song functions compiled by Catchpole (1982). Although cracids are not closely related to passerines, there are no a priori reasons to expect the selective forces shaping singing behavior in these two groups to be markedly different. (2) If a song is suspected to have a sexual function, the next step is to examine the intraspecific contextual correlations of the song. By observing the social situations in which the song is given, one can deduce to some degree its function. Intersexually selected action patterns can be identified in polygynous species (where ♂ may provide little more than «good genes») by observing which behaviors are emphasized in the presence of ♀ and which affect fe♂ visitation rates (Wiley 1974, McDonald 1989). (3) A more direct test of song function is to observe the effects of song playback on ♂ and fe♂ behavior. For example, Krebs (1977) showed the territorial function of Great Tit (Parus major) song by demonstrating that wandering ♂ avoided vacant territories in woods where loudspeakers played realistic renditions of a resident ♂. Catchpole's (1982) approach provides a valuable framework for the study of display function. I used this framework to investigate the roles of

♂-♂ competition and fe♂ choice in the evolution of the Yellow-knobbed Curassow's "descending whistle" display.

Study species. The Yellow-knobbed Curassow is a large (2—3 kg), sexually dimorphic, ground-walking galliform found primarily in the gallery forests of the Venezuelan and Colombian Llanos. At the beginning of the rainy season (mid-April) ♂ re-establish traditional display areas at the edge of the forest where they routinely «sing» from tall trees. It was this behavior that was quantified during my study. ♀ visit ♂ singing areas singly or in groups and the resident ♂ jumps to the ground and displays to them. This direct courtship is difficult to observe due to the wariness of the birds and has been described only once (Strahl et al., *in press*). Although cracids are generally assumed to be monogamous (Delacour & Amadon 1973), polygyny has recently been documented in the Horned Guan (*Oreophasis*, Gonzalez 1984) and Strahl *et al.* (in press) and Buchholz (1989) provide detailed discussions of the evidence for polygyny in this and other curassow species. In short ♂ Yellow-knobbed curassows may display to more than one fe♂ and may be accompanied by multiple ♀ with oviductal eggs (Schäfer 1954) suggesting they are polygynous.

Study site. The study site was a cattle ranch, Fundo Pecuario Masaguaral, located at 8° 34' N, 67° 35' W in the central Venezuelan state of Guarico. Wildlife on the ranch have been protected from hunting since 1944. The vegetation on the ranch, described by Troth (1979), consists of small sandhills, seasonally flooded savannah, palm and *Ficus* scrub, and gallery forests which line the two water courses that pass through the eastern part of the ranch; the Caño Caracol and Río Guarico. Curassows were primarily found in the gallery forest on the ranch, but also occurred in the scrub areas during the wet season or near windmill water pumps in the dry season. My study region was from just west of the highway that bisects the ranch to the Caño Caracol, with concentrated observations at the western edge of the gallery forest (Fig. 1). The main study was conducted from 12 March to 27 June 1988. Weather data were from the ranch's monitoring station, approximately 7 km from the center of the study site.
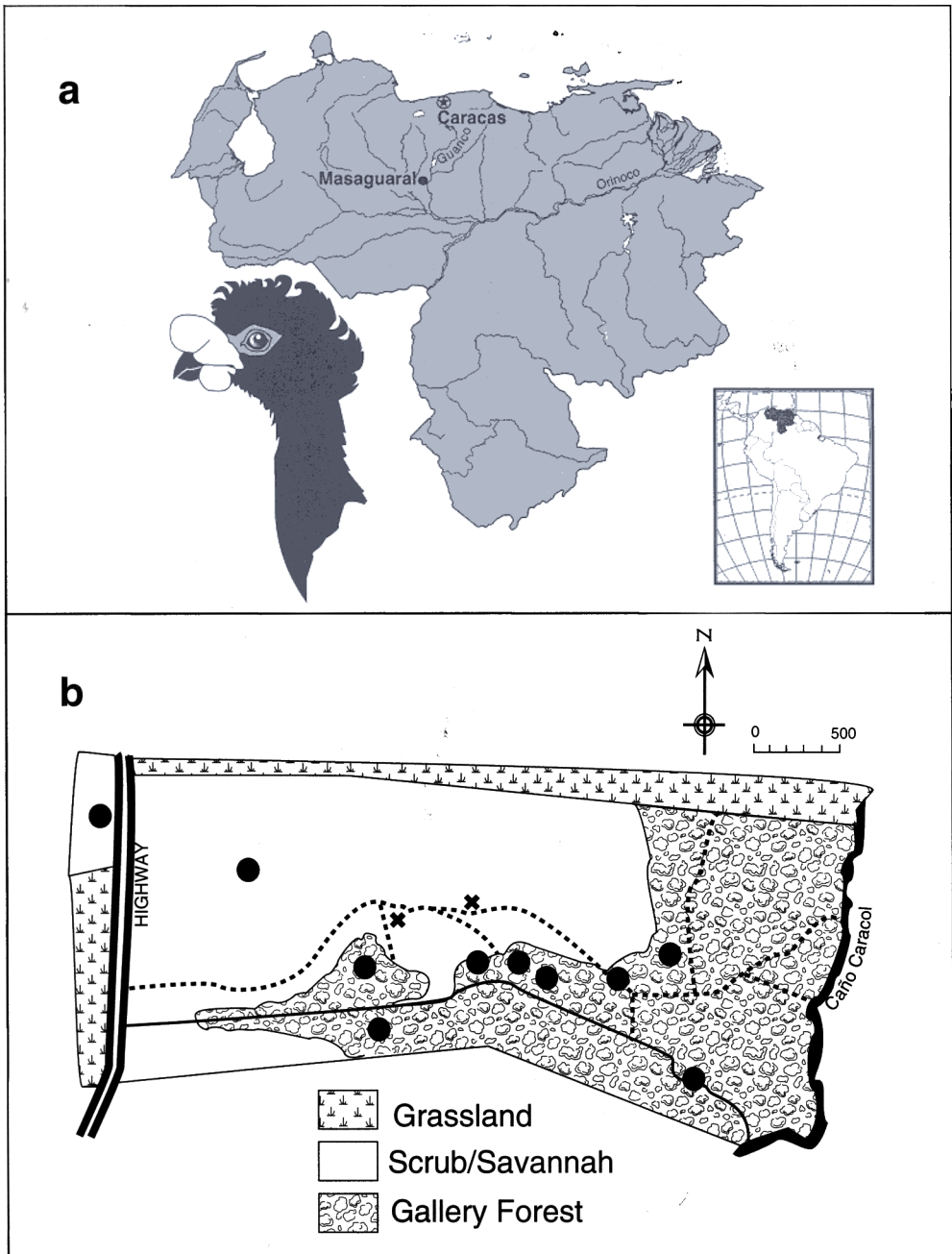
FIG. 1 a) Location of the study site, labelled Masaguaral, in the central Venezuelan state of Guarico. b) Detail of the study site on the eastern side of Fundo Pecuario Masaguaral. Black dots represent the approximate center of the display areas of individual ♂. The two X's represent artificial water sources. Distribution of vegetation types is approximate. Some areas may be unavailable to curassows due to seasonal inundation. Modiefid from Eisenberg (1979).

Observational methods. During the dry season, the study area was surveyed daily by three observers until the entire area had been covered (usually two to three days). These continuous surveys allowed me to determine when ♂ began entering the singing areas identified during a pilot study conducted from 6—27 June 1987. A variety of attempts to trap and individually mark ♂ curassows failed. Instead the ♂ were identified by their individual knob and wattle morphology (Buchholz 1991) and by simultaneous observation of different ♂ in their respective singing areas. Regular observations were conducted between 05:00 (dawn)—11:00 and 16:00—19:00 (dusk) hours. The numbers and sex of curassows encountered were recorded along transects in order to follow their movements. An observation blind was placed near the center of each of five singing areas in order to facilitate observations. Fe ♀ visits to each ♂'s singing area were observed from the hidden blinds and during surveys on foot. Only ♀ accompanied by the resident ♂ were considered "visitors". Fe ♀ visitation rates were corrected for observation time in each calling area. Fe ♀ visitation rates are frequently used in lieu of actual copulations in elusive or cryptic species (Davison 1981, Andersson 1982, von Schantz *et al.* 1989). Temporal biases in observations were avoided by alternating morning and afternoon observation periods in each singing area. When a ♂ was heard singing, the observer got as close as possible to his location and recorded singing data for 15 min. The individual whistle lengths in seconds, the frequency of occurrence of individual whistles per minute, the inter-whistle interval (the time between the end of one whistle and the start of the next whistle), the boom frequency (number of booms per minute) and the wingflap frequency (number of wingflap bouts per minute), as well as the total number of individual flaps given per wingflap bout, were recorded. The data for each of these variables were averaged to get a value representative of the «descending whistle» display bout. The total duration of the display bout was recorded only when the start and end times were known. Display bouts always ended with the ♂ flying or walking out of sight or out of hearing distance of the observer. When possible the displaying ♂'s height from the ground, the height of the

tree and the height of the surrounding canopy were recorded. The presence of ♀ or other ♂ in the immediate area or vocalizing nearby was also noted. Data collected on the song variables of lone ♂ and ♂ with ♂ or fe♂ visitors provide some indication of the context in which these song components were used.

A single 20-minute playback of a cassette recording of the whistle call of a captive ♂ *Crax daubentoni* was conducted in the center of the singing areas of five ♂. These playbacks provide evidence of the direct affect of ♂ curassow song on conspecifics. Comparison of the booming frequencies of eight species of curassow are based on sonograms in Delacour & Amadon (1973) and recordings of captive individuals made by S. D. Strahl.

RESULTS

General results. ♂ started singing in early April before the seasonal rains began. Although 245 singing bouts were observed during the study period, display data were recorded only from the 94 singing bouts that occurred between 25 April and 19 June 1988, when fe♂ visitations were most frequent. Ten singing ♂ were identified on the study site. Although curassows were found throughout the forested area of the study site, ♂ singing areas were not evenly dispersed. Seven of the ♂ were concentrated around the western most edge of the gallery forest on the ranch, two others were found in the western savannah regions of the study site and one ♂ called along a road in the eastern most forest area (Fig. 1). They were not sampled equally due to the extreme wariness of some ♂ and differences in visibility between the singing areas (Table 1).

Almost all (98 %) of the observed "descending whistle" displays occurred while the ♂ perched in a tree, with the remaining 2 % singing on the ground. Eight of the ten ♂ whose height while displaying was determined, positioned themselves in an emergent tree so that they were above the surrounding canopy (Fig. 2). ♂ called most often in the morning between 06:00—10:00 hours. Although ♂ displayed earlier on clear, hot days (Spearman Rank Correlation, r_s = —0.24, n = 72, $P < 0.05$) and later on rainy days (Spearman Rank Correlation, r_s = 0.31, n = 74, $P < 0.01$), there was no individual effect of each

TABLE 1. Sample size, mean value and standard error of display variables and mean ♀ visitation rates for the ten ♂ Yellow-knobbed Curassows singing on the study site.

Male No.	BD			WHF			WHL			IWI			BF			WFF			NF			FVR
	n	mean	± SE	n	mean	± SE	n	mean	± SE	n	mean	± SE	n	mean	± SE	n	mean	± SE	n	mean	± SE	
1	(04)	48.3	12.6	(04)	03.1	0.26	(04)	3.6	0.08	(01)	17.7	—	(01)	0	—	(04)	0.04	0.04	(0)	—	—	0
2	(02)	26.0	09.0	(01)	04.0	—	(02)	3.6	0.40	(01)	15.2	—	(01)	0	—	(02)	0.05	0.05	(1)	4	—	0.14
3	(08)	42.8	13.7	(06)	03.4	0.30	(08)	3.7	0.10	(05)	13.3	0.40	(03)	1.2	1.2	(08)	0.06	0.03	(4)	6.3	0.9	0
4	(05)	43.6	06.4	(05)	03.6	0.20	(05)	4.0	0.10	(01)	10.8	—	(03)	0.7	0.7	(06)	0.03	0.02	(2)	8.5	1.5	0.07
5	(07)	55.7	11.2	(06)	04.1	0.40	(06)	3.0	0.10	(04)	10.4	0.90	(03)	0	0	(06)	0.05	0.02	(4)	5.0	0.7	0
6	(02)	67.5	32.5	(02)	03.2	0.02	(02)	4.0	0.10	(01)	15.2	—	(01)	2.8	—	(02)	0.14	0.09	(2)	7.0	0.6	0.05
7	(17)	32.5	04.5	(15)	03.1	0.10	(16)	3.8	0.10	(06)	13.3	1.60	(04)	0.4	0.4	(14)	0.08	0.03	(7)	7.3	0.4	0.04
8	(08)	26.4	06.7	(07)	03.2	0.50	(08)	3.7	0.30	(02)	13.0	1.30	(05)	0	0	(08)	0.05	0.03	(3)	8.5	1.3	0.17
9	(18)	86.3	38.3	(13)	03.3	0.20	(18)	3.7	0.10	(09)	14.6	1.00	(04)	0.8	0.8	(18)	0.05	0.02	(7)	6.9	0.5	0.12
10	(21)	43.7	05.6	(14)	03.4	0.07	(18)	3.7	0.90	(11)	16.4	1.10	(03)	0	0	(19)	0.03	0.01	(5)	6.8	0.8	0.03

BD, bout duration; WHF, whistle frequency; WHL, whistle length; IWI, inter-whistle interval; BF, boom frequency; WFF, wingflap frequency; NF, Number of flaps per wingflap event; FVR, female visitation rate.

of the four climatic variables measured (maximum and minimum temperature, barometric pressure, rainfall) on any of the singing variables measured when lone ♂, those accompanied by other singing ♂, or those with ♀ present were examined as separate groups (Spearman Rank Correlation, all $P > 0.05$).

Display action patterns. Detailed descriptions of the action patterns used in the "descending whistle" display are given by Buchholz (1989) and some aspects are similar to those given by other curassow species (Delacour & Amadon 1973). Whistle song (WS): The posture of the ♂ during singing is his normal alert standing or perched position. The whistle begins with a high frequency (3500 Hz) as the bird opens his mouth exposing the yellow oral lining. The mouth closes as the descending whistle ends at a frequency of approximately 1750 Hz. The whistle lasts for about 4 seconds. Wingflap (WF): From the normal standing position, the bird extends its neck upwards and forwards. Just as it reaches its most extended position, the bird lifts its wings over its back so that the outer surfaces of the wings strike one another 4—10 times (mean = 6.7, n = 31) in one to 2 seconds, producing a "wapp!, wapp!, wapp!-wapp!-wapp!" sound. The first two "waps" are spaced while the latter ones occur in rapid succession. Boom (B): Five of the ten ♂ began to "boom" at the beginning of June and continued throughout that month. During this part of the display, the ♂ stands perched on a branch or fallen tree and hunches down. The wings are dropped from their resting position over the sides and, simultaneously, the neck retracts posteriorly so that it appears shortened and the back of the head just barely touches the bird's back. The head moves mandible-first, in a downward arc, stopping when the mandible points at the feet. The head rapidly returns to the retracted position, the neck swells slightly and the bird emits a barely audible "Gmp!gmp!" sound. Shortly thereafter, when the ♂ returns to the hunched position the bird releases a deep "uuumh…uhh" sound. This species does not appear to gulp air as does the Black Curassow (Beebe 1909). Relative to other curassows, booming in the Yellow-knobbed Curassow is markedly diminutive in volume and is barely audible in the wild (personal observation). Therefore it is

not surprising that booming behavior had not been described for this species when Delacour and Amadon (1973) wrote their monograph on the Cracidae. Subsequently, however, Todd and Bauml (1979) described booming in a captive ♂ at the Houston Zoo. My description confirms that this behavior occurs under natural conditions as well.

A comparative approach. Most aspects of the ♂ Yellow-knobbed Curassow display suggests that it serves an intrasexual function (Table 2). The descending whistle song is stereotyped and used in countersinging by two or three ♂, characteristics which are common to song used in intrasexual selection by other birds (Catchpole 1982, Loffredo & Borgia 1986). When countersinging, the individuals alternated singing so that one bird began a whistle just as another ended. Countersinging between ♂ occurred most often when singing areas were separated by a road or other open areas. It is probable that these open areas acted as singing area boundaries. It was not possible to determine the exact distance between the ♂ without disturbing them, but the closest
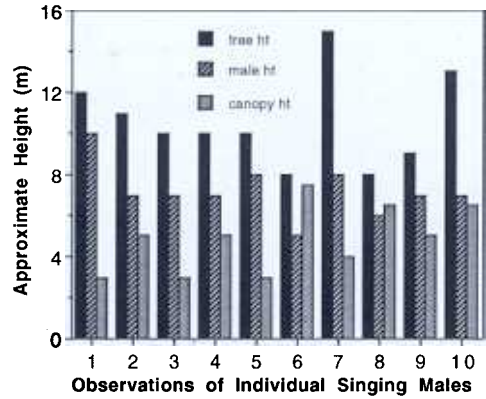

FIG. 2. The perched height of 10 whistling ♂ relative to the height of the singing tree and the average height of the surrounding canopy.

countersingers seen were in different trees, less than 10 m apart. Without exception one of the countersingers continued to call much longer than the others. Although the comparative evidence suggests an intrasexual function of the descending whistle display, the low frequency of countersinging (25 % of the 245 episodes encountered; Fig. 3) suggests that intrasexual competition is not intense.

Contextual effects. Of the 7 singing parameters recorded (bout duration, whistle length, frequency of whistling, inter-whistle interval, frequency of booming, wingflap frequency and flaps per wingflap), only bout duration was significantly

TABLE 2. A checklist for interpreting the function of acoustic displays in the Yellow-knobbed Curassow based on Catchpole's (1983) checklist of passerine singing behavior with known intersexual and intrasexual function. Asterisks denote display types observed in the study species.

Selective pressure	Intersexual	Intrasexual
Proximate function	Attract females	Repel males
Diagnostic characters		
Display structure	Many display components[a]*	few display components
Contextual correlations	display before oviposition only	continues displaying after oviposition*
	Does not respond to playback post mating	does respond to playback post-mating*
Direct effects on ♂	do not countersing	countersing*
Direct effects on ♀	high intensity displayers get more mates	high intensity displayers do not get more mates*

[a] The number of action patterns involed in display relative to the mean number of types of reproductive display sounds used by another family of galliformes, the Phasianidae (N = 36, mean = 1.5; Loffredo & Borgia 1986).
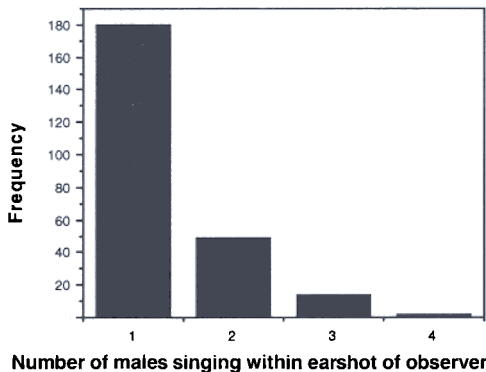

FIG. 3. The number of singing bouts in which an observer heard ♂ whistling alone or at the same time as one to three other ♂ (n = 245).

affected by the presence of other ♂ (M-Rank Distribution-free Multivariate Test, Chi² = 5.8, n = 85 observations of 9 ♂, P <0.02; SAS Institute Inc. 1986; Table 3). In general direct ♂-♂ aggression seems to be peculiarly rare in this species. During the field study ♂ were occasionally seen traveling in pairs (n = 7) but only one aggressive interaction was witnessed. Two ♂ were approaching a watering hole. One ♂ ran in front of the other and gave a display similar to the «tail up» described by Beebe (1909) for a courting *Crax alector*. The interaction was entirely silent and did not utilize the wingflap or boom behaviors.

A comparison of the respective ♂'s display parameters showed that only whistle length, inter-whistle interval and frequency of booming differed significantly among the ten ♂ sampled (Kruskal-Wallis ANOVA, H = 17.2; H = 17.7; H = 20.5, P <0.05). Although ♂ flapped fewer times during wingflap events in the presence of ♀ (M-Rank Distribution-free Multivariate Test, Chi² = 5.92, n = 29 observations of 9 ♂, P = 0.02; Table 3), fe♂ visitation rates to the different singing ♂'s areas were not correlated with this display attribute. Only the mean whistle frequency adequately explained variation in fe♂ visitation. Oddly ♀ were seen most often with the ♂ that whistled the least (Spearman Rank Correlation, n = 10, r_s = —0.69, P <0.05)! Contrary to what might be expected, ♂ that whistled less frequently did not have significantly longer whistles (Spearman Rank Correlation, n = 10, r_s = —0.34, P >0.05). Thus ♀ did not appear to be assessing the energetic cost of the ♂ whistling display.

Some ♂ began to boom in the beginning of June but this did not affect the rate of fe♂ visitations (Spearman Rank Correlation, n = 10, r_s = —0.47, P >0.05) and booming ♂ were no more likely to be visited by ♀ than were non-boomers (Mann-Whitney U-test, U = 4, U^1 = 20, n_1 = 5, n_2 = 5, P >0.05). Of thirteen captive ♂ observed during a two-week period near Mexico City, Mexico in August 1987, only two were booming, although all were actively whistling.

Direct effects. Playback of a 20-minute sequence of "whistling" by a captive ♂ in each of five calling areas resulted in the close approach of the resident ♂ (n=3) or his countersinging nearby (n=2). In one case two ♂ began countersinging from either side of the speaker. ♂ response to playback in late June (when ♀ are thought to be incubating; Schäfer 1954) indicates that the whistle song probably has an intrasexual function (Catchpole 1982; Table 2).

DISCUSSION

My observations concur with previous assertions that the descending whistle display in the Yellow-knobbed Curassow is largely intrasexual in function. ♂ changed the frequency of only one of the display behaviors in the presence of ♀. When a fe♂ was nearby, ♂ significantly reduced the number of wingflaps, a behavior associated with intrasexual aggression by some authors (see below). Although ♂ that wingflap less often are preferred mates in another galliform, the Red Junglefowl (*Gallus gallus*, Zuk et al. 1992), fe♂ visitation rates in the Yellow-knobbed Curassow were not negatively cor-

TABLE 3. Mean rank of male display parameters when singing alone, singing with another maler nearby and singing with a female nearby as generated by the M-Rank distribution-free multivariate hypothesis test (SAS Institute Inc. 1986).

| Display variables | Alone | | Males Nearby | | Alone | | Females Nearby | |
	n	mean rank	n	mean rank	n	mean rank	n	mean rank
	64			0.1166*	74	0.0031	12	—0.0189
	52			—0.0416	58	0.0021	10	—0.0123
	62			—0.0469	70	0.0083	12	—0.0485
	27			0.0904	31	—0.0090	5	0.0556
	16			0.0344	21	—0.0095	3	0.0667
	60			—0.0614	71	—0.0071	11	0.0459
	22			0.0452	26	0.0369	3	—0.3194*

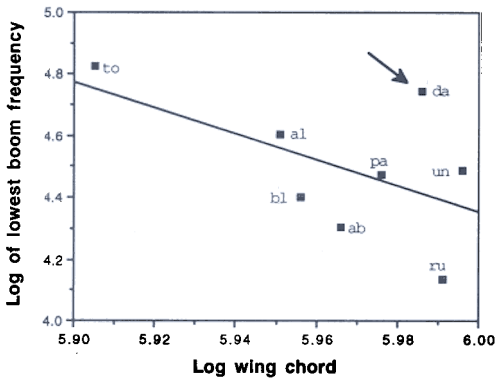* statistically significant at P = 0.015; Chi² test, d. f. =

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FIG. 4. Regression of lowest frequency in the boom call with ♂ size for eight species of curassows. Frequency and wing chord data from Delacour & Amadon (1973) and S.D. Strahl (unpublished data). ab = *Crax alberti*, al = *C. alector*, bl = *C. blumenbachii*, da = *C. daubentoni*, pa = *Pauxi pauxi*, ru = *C. rubra*, to = *Mitu tomentosa*, un = *P. unicornis*; classification follows Blake (1977).

related with wingflapping. However they were negatively correlated with ♂ whistling frequency, another behavior previously associated with aggression in curassows.

There are many anecdotes in the literature that suggest that whistling, booming and wingflapping are aggressive behaviors. For example Schwartz (*in* Delacour & Amadon 1973) found that Yellow-knobbed Curassow ♂ wingflapped in response to whistle playbacks. Sick (1968) found that Red-billed Curassow (*C. blumenbachii*) ♂ faced one another on the ground and wingflapped during aggressive encounters and Beebe (1909) asserted that the courting ♂ Black Curassow (*C. alector*) he observed, used wingflapping in response to disturbance by other ♂ booming in the distance. Given these anecdotes and the observation that ♂ wingflap less in the presence of ♀, it is unusual that the Yellow-knobbed ♂ observed in this study did not wingflap more often in the presence of other ♂ than when alone. These somewhat contradictory results suggest that intrasexual selection in this population is not particularly intense. Nevertheless the observation that ♂ displayed for longer when other ♂ were displaying nearby and that ♀ appeared to avoid ♂ that whistled often, support an intrasexual or aggressive role for these display components. This conclusion

concurs with that of the comparative results (Table 2).

The absence of any ♂-♂ fighting is also consistent with a low level of intrasexual competition. The lack of direct ♂ combat may be the result of low densities (1.1 singing ♂/km²) or because curassows are long-lived and the dominance hierarchies of the local population are well established and new battles are rare.

The function of booming and the explanation for the absence of booming in some ♂ remains unknown. Booming frequency was not affected by the presence of ♂ or ♀, nor was it correlated with fe♂ visitation rates. In open habitats such as the savannah and gallery forests of the Llanos high frequency sounds such as whistling may be more effective conveyors of information over distance than low frequency booming (Morton 1975, Wiley & Richards 1978). The relatively high tonal frequency of the boom call in the Yellow-knobbed Curassow in comparison with the booms of other curassows of similar size supports this hypothesis (Fig. 4). Unfortunately the only other curassow that clearly whistles as a part of its display, the Wattled Curassow (*C. globulosa*, Delacour & Amadon 1973), lives in dense tropical forest, an environment that would not select for high frequency calls, casting doubt on this hypothesis. Further investigation of the vocalizations and tracheal growth and modification in the Cracidae in relation to habitat and mate choice are necessary.

The critical conservation status of many cracids, two-thirds of which are threatened or endangered (Strahl, *in press*), demands that I address the management implications of my results (Risser 1993). Elusive habits, dense habitat and low population densities have dissuaded researchers from studying the behavior and ecology of the Cracidae. However even limited observations such as mine can be important to the conservation management of these animals. First, it appears that traditional display sites are important to calling ♂. ♂ routinely called from the same individual trees in both 1987 and 1988. Installation of an electric powerline in early 1988 removed the display tree of one ♂ but left a nearby ♂'s tree untouched. Apparently as a consequence, the ♂ who lost his display tree disappeared from the study site, while the other ♂ continued to display in his tree on the edge of

the deforested swath. Therefore I suggest the possibility that preservation of traditional display trees may reduce the disturbance-related dispersal of breeding ♂. Second, field observations of highly skewed fe♂ visitation rates provide further evidence that this species is polygynous. Typically the skewed pattern of ♂ mating success seen in polygynous systems results in a lower effective population size than a similarly-sized population with a monogamous breeding system (Lande & Barrowclough 1987). Because time to extinction is thought to be dependent on effective population size rather than observed population size, mere census counts of this polygynous species are not adequate measures of population viability. Third, although more detailed studies are needed to clarify the function of the descending whistle display in this species, the results of this study suggest that it has a primarily intrasexual role as earlier authors suggested and that whistle playbacks may be used to census displaying ♂, but not ♀. Widespread censusing is necessary to track the conservation status of the Yellow-knobbed Curassow because low population densities, low effective population size and over-hunting (Silva & Strahl 1991), coupled with deforestation for rice farming and cattle ranching in its Llanos stronghold (personal observation), bodes poorly for the future of this formerly common cracid.

ACKNOWLEDGMENTS

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