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Evolution of *Crax* Sociobiology and Phylogeny using Behavioral and Ecological Characters

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Resumen

Se obtuvieron datos sobre el comportamiento de alguans especies del género y *Pauxi pauxi* en cautiverio la cual se complementó con datos disponibles en la literatura. Esto tuvo la finalidad de alcanzar dos objetivos: 1) utilizar el comportamiento y carácteres ecológicos para examinar la evolución de sociobiología en *Crax*, y 2) examinar carácteres del cortejo en species de Crácidos que utilizan el retumbado como forma de llamado, para elucidar afinidades taxonómicas en el género *Crax*. Se hizo uso de dendrogramas creados mediante el uso de simple cotejo de coeficientes (simple matching coefficient; Sokal y Michener 1958); estos coeficientes fueron sujetos a un análisis UPGMA. Resultados del análisis de la evolución de la sociobiología encajaron con predicciones *a-priori* con *C. daubentoni* siendo la especie más "avanzado" en términos de su sociobiología. Se interpretan resultados en luz de factores tales como la variación en el llamado, la estratégia de cría, y asociación con el habitat. Se ofrece una breve discusión acerca de la diferencia en comportamiento en *C. globulosa* comparado a otros *Crax*, el cual es atribuido a la falta de encuentros en el campo entre *C. globulosa* y otros miembors de género Crax. Resultados del análisis filogenético muestran que *Pauxi* es el grupo mas apartado, lo cual concuerda con predicciones hechas *a-priori*. Se muestra un modelo interesante entre distribución geográfica y la parsimonia en le cortejo entre las especies que comparten el retumbado como forma de cortejo, siendo la más parsimoniosa (*C. alector/C. daubentoni*) en la parte oriental del escudo de Guiana y especies cada vez más distantes (*C.alberti/C. rubra*) hácia el oeste. En contraste la especie más distante en el análisis (*C. fasciolata*) es separada de los otras species por el Río Amazonas. Se da énfasis a la naturaleza preliminar de estos resultados hasta que comparaciónes más ámplias entre la morphología y análisises cladisticos y moleculares sean disponibles.

Resumo

Obtivemos dados sobre o comportamento de algumas espécies de *Crax* e de *Pauxi pauxi* em cativeiro, os quais foram complementados com dados disponíveis na literatura, com a finalidade de 1) utilizar o comportamento e características ecológicas para examinar a evolução da sociobiologia de *Crax*, e 2) examinar características do comportamento de corte de espécies de Cracídeos com vocalizações semelhantes a *Crax* a fim de elucidar suas afinidades taxonômicas. Fizemos uso de dendrogramas criados segundo a combinação simples de coeficientes (simple matching coefficiente, Sokal e Michener 1958); estes coeficientes foram analisados através de uma UPGMA. Os resultados da análise da evolução sociobiológica concordaram com as previsões a priori de que *C. daubentoni* seria a espécie mais avançada. Interpretamos os resultados à luz de fatores como a variação no chamado, a estratégia reprodutiva e associações com habitats. Oferecemos uma breve discussão a respeito da diferença de comportamento em *C. globulosa* em relação a outros *Crax*, à qual é atribuída à falta de encontros, na natureza, entre esta espécie e outros *Crax*. Os resultados da análise filogenética mostram que *Pauxi* é o grupo mais distante, o que concorda com as previsões a priori. Apresentamos um modelo que relaciona a distribuição geográfica e as combinações mais parsimoniosas para as espécies com vocalizações do tipo “boomoing”, sendo que as mais próximas (*C. alector/C. daubentoni*) ocorrem na parte oriental do escudo das Guianas,

e espécies cada vez mais distantes (*C. alberti/C. rubra*) a oeste do mesmo. Em contraste, a espécie mais divergente na análise (*C. fasciolata*) é separada das outras pelo rio Amazonas. Damos ênfase ao resultado preliminar destes resultados até que comparações mais amplas entre a morfologia e análises cladísticas e moleculares sejam disponíveis.

Introduction

Congeners in the genus *Crax* include *alector, alberti, blumenbachii, daubentoni, fasciolata, globulosa,* and *rubra*. These species show a distribution which strongly correlates with the forest refugium theory of Haffer (1974), with closely related species replacing each other geographically. Species are often separated from their nearest relative by a geographical barrier and little or no secondary contact or hybridization is known in nature (O’Neill this vol.). Moreover, males exhibiting the most similar cere ornamentation are allopatric which confounds taxonomic relationships among congeners even more. For example, the *daubentoni/globulosa/blumenbachii* group occur primarily in Venezuela, western Amazonia, and the central Atlantic rainforest, respectively - regions whose borders do not even abut geographically.

Over half a century ago it was recognized that the fundamental importance in the representation of homology is continuity in phylogeny that must hold for behavior as well as structure (de Beer 1940). Despite such, most taxonomists and systematists have predominantly based their classifications upon morphological or genetic data. The study of Vaurie (1968) for example is well known. Studies utilizing behavioral characters to elucidate avian phylogenies have been practiced for at least two decades (e.g., Archibald 1976). Utilizing this method to answer systematic questions has recently become popular again, with studies utilizing behavioral characters to elucidate phylogenetic relationships of birds at specific (e.g., Gaucher et al. 1996), familial (e.g., Hughes 1996), and ordinal (e.g., Kennedy 1996) levels.

The paucity of information on behavior of the Cracidae is in sharp contrast to our knowledge of most galliformes. However, there are some exceptions. Buccholz (1995) for example, found that the whistle display in *Crax daubentoni* functions mainly as an intrasexual signal. The objectives of the study presented herein are twofold. First we utilize behavioral and ecological characters to examine evolution of sociobiology in the group. We predict *a-priori* that *C. daubentoni* will be the most distantly similar to the other species considering the differences of this species compared to others (e.g., calling behavior, habitat, reproductive strategy, etc.). Secondly we examine courtship characters of booming species that are constrained by phylogeny to elucidate taxonomic affinities in the genus *Crax*. We also include *Pauxi pauxi* in the analyses, and predict *a-priori* that this species will be the outgroup.

Methods

Behavioral data were collected using one-zero sampling (Altman 1973) at two sites: the Houston Zoological Gardens and R. Powers' private facility in Alvin, Texas. Sampling at the Zoo took place from 07:00 - 10:00 on June 15, 16, 22, 29, 30, July 6, 7, 13, 14 and August 25, 1996; sampling at Powers' took place from 08:00 - 11:00 on July 27, 28, August 3, 4, 11, and 17.

All species of *Crax* (*alector, alberti, daubentoni, fasciolata, globulosa,* and *rubra*) were studied except for C. *blumenbachii* because this species was not kept in either collection. Additionally two different subspecies of *C. alector*, the yellow cered E. form (*C. a. alector*) and the orange cered W. form (*C. a. erythrognatha*), were studied at Powers' collection. Nevertheless, as no differences between the two forms were detected data on both forms were lumped. Data were also collected on *Pauxi pauxi,* which we considered *a-priori* as an outgroup. Additionally, it was only possible to collect limited data for *C. rubra* because the number of study subjects was limited to 1 male. Table 1 provides a breakdown of the number of each species studied at each facility. These empirically collected data were supplemented with data from the literature, especially for ecological information and species for which we were unable to obtain quantitative data.

Two analyses were performed using 42 behavioral and ecological characters. The first analysis was aimed at determining evolution of sociobiology in the group. For this analysis we considered all species of *Crax*, as well as *Pauxi,* utilizing broader sociobiological and ecological characters. These characters included type of call (n=4 characters), displays (n=6), breeding strategy (n=5) and ecological aspects (n=7) (Table 2).

The second analysis assessed booming courtship characters to examine phylogenetic relationship among booming species (*C. alberti, C. alector, C. daubentoni, C. fasciolata, C. rubra,* and *P. pauxi*). *C. blumenbachii* was not included in the phylogenetic analysis because detailed information was not available from the literature. Characters used included both auditory (n=12 characters) and visual components (n=8) (Table 3).

Analyses were done with dendrograms created using simple matching coefficients (Sokal and Michener 1958). Each analysis of coefficients produced a triangular matrix, the data from which were subjected to the unweighted pair-group mathematical average (UPGMA) analysis.

Results and Discussion

Evolution of Sociobiology

Table 2 shows tabularized data and Figure 1 illustrates relationships among species. As predicted, the most sociobiologically different species (i.e., apparently "advanced") is *C. daubentoni*, as indicated by its being the least similar to all other species. Other distantly related species include *Pauxi* and *C. globulosa*, among others.

C. daubentoni is the only species besides *C. globulosa* that whistles, and is the only species which calls using both booming and whistling. The more open nature of *C. daubentoni* habitat (e.g., Llanos) may provide part of the explanation for its behavioral ecology being different from the others, although *C. fasciolata* is an open forest specialist in many areas as well (F. Olmos pers. comm.). Strahl et al. (this vol.) found that seasonally abundant resources will influence the way that *C. daubentoni* alters its breeding strategy. When resources are abundant males are able to spend less time defending territories and more time investing in mating with multiple females (e.g., Emlen and Oring 1977).

The differences associated with *Pauxi* were expected since this species is placed in a different genus. It is the only species to occupy montane cloud forest and has a relatively unique type of alarm call compared to *Crax*. Moreover *Pauxi* is the only species where males are actively territorial towards the opposite sex throughout the year, except for during brief mating episodes. Consequently, with the exception of *C. daubentoni*, *Pauxi* is the only species in this study exhibiting female nesting without help from the male.

The two major factors which distinguish *C. globulosa* from the other species are the aforementioned descending whistle call instead of a boom, and the fact that this species is almost entirely arboreal. Indeed, the status of *C. globulosa* is considered highly precarious throughout its range, whether in Perú (e.g., Ortiz and O'Neill this vol., Brooks 1994), Bolivia (e.g., Cox this vol), or elsewhere. It is rarely encountered, and when summing the areas where it has been recorded the distribution is disjunct and spotty (e.g., Greenfield this vol.). However, *C. globulosa* may be more difficult to detect than other species because its call is less easily detected, it is restricted to the higher strata of the forest, and it often flies away silently in retreat (Ortiz and O'Neill this vol., Brooks 1994). Although rarely encountered, we pose the question of whether this may be an artifact of relative inconspicuousness when compared to the other species. This would be an interesting topic for future research.

Phylogeny of Booming Species

The characters in this study were carefully selected. Caution was made to select shared, assumingly derived characters with subtle differences and idiosyncracies. These data are tabularized in Table 3. Figure 2 depicts variation in booming sequence and Figure 3 illustrates the dendrogram.

As predicted, *Pauxi* is indeed the outgroup. However, this difference is not attributed to auditory components as much as visual components (Table 3, Fig. 2). *Pauxi* holds its wing, head and tail in a slightly different position than *Crax* when booming.

It is interesting to note that the pattern of geographic distribution fits well with parsimony of species sharing booming courtship (Fig. 4). That is, the more closely grouped species in Figure 3 are also nearest to one-another geographically (Figure 4). Beginning with the most derived *Crax* species pair and proceeding with more distant branching we see that *C. alector/C. daubentoni, C. alberti, C. rubra* (Fig. 3) are distributed across the Guianan Shield from east to west: from the Guianas and Brazil north of the Amazon (*C. alector*) to Venezuela (*C. daubentoni*), Colombia (*C. alberti*), and the transition between Middle and South America (*C. rubra*). The fact that *C. fasciolota* is the most distantly related member of the genus suggests that *Crax* evolution is strongly influenced by the major rivers; *C. fasciolata* is the only species in the analysis occurring south of the Amazon. However, these results remain preliminary until comparison with morphological and molecular cladistic analyses is possible.

Olmos (in litt.) offers a hypothesis explaining phylogeography of species restricted south of the Amazon (i.e., *C. blumenbachii* and *C. fasciolata*). *C. blumenbachii* is restricted to the more Amazonian-like part of the Atlantic forest, with taller trees and isolated populations of many Amazonian species (e.g., *Lipaugus vociferans*). It prefers more continuous forest but will also utililize forest edge. *C. blumenbachii* is perhaps more forest-dependent and is isolated from its Amazonian counterparts by more open Cerrado habitat that is occupied by *C. fasciolata*. While restricted to the north and south by large rivers, the plasticity of *C. fasciolata* may have permitted occupation of the expanse of open habitats south of the Amazon during past glacial periods. Again, further analyses will permit testing this hypothesis.

Vaurie (1968) considers the phylogeny of *Crax* difficult to assess since all members of the genus evolved from a common ancestor. He attempts constructing the phylogeny based upon female plumage variation. However, Vaurie (1968) also provides data for measurements (wing, tail, tarsus, and exposed culmen) among *Crax* species. When the 4 measurements are summed for each species, the results suggests that *C. fasciolata* is also the most distantly related *Crax* when compared to other species if morphology alone is considered. Regrettably, it is not possible to compare these results to molecular sequences as such studies are unavailable. Determining the phylogeny of *Crax* (and indeed, all cracids) using other methods is an important goal for future research.

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Table 1 - Numbers of study subjects of each species included in this study

Institution	***albrt.***	***alect. alect.***	***alect. eryth.***	***daub.***	***fasc.***	***glob.***	***rubra***	***Pauxi***
Houston Zoological Gardens	2.2	-	-	1.1	1.1	1.1	-	2.2
Roy Powers (private facility)	-	2.2	1.2	4.4	4.4	1.1	1.0	2.0
TOTAL	2.2	2.2	1.2	5.5	5.5	2.2	1.0	4.2

Key: Males to left of dot . Females to right of dot

Table 2 - Behavioral and ecological characters

Character	***albrt***	***alector***	***blum.***	***daub.***	***fasc.***	***glob.***	***rubra***	***Pauxi***
Type of Call								
boom (courtship call)	x	x	x	x	x	-	x	x
descending whistle (courtship)	-	-	-	x	-	x	-	-
alarm whistle (alarm call)	x	x	-	x	x	x	x	-
alarm call (other)	-	-	-	-	-	-	-	x
Displays								
Male's Wing-flap display								
wingflap between singing bouts	-	x[1]	-	x	x[2]	-	-	x
flaps not nec. part of song	x	x	x[2]	x	x	x	x	x
Male's "head-back" display								
Stationary[A]	-	x	-	x	-	-	x[1]	-
Running[B]	-	-	-	-	-	x	-	x
Displays with F participating								
Mutual bowing display[C]	-	x	-	x	-	-	-	-
M feeding F/allofeeding	x	x	-	x	x	-	x[3]	-
Breeding Strategy								
Pair fidelity								
Polygamous or Monogamous	-	x[1]	-	x[4]	-	-	x[5]	-
Monogamous pairs	x	-	x[2]	-	x	x	-	x
F in M territ. for breeding	-	-	-	-	-	-	-	x
M contribution to nest building								
both sexes help build nest	x[1]	x[1]	x[1]	-	x[1]	x[1]	x[6]	-
only female builds nest	-	-	-	x[7]	-	-	-	x[1]
Ecological Aspects								
General habitat association[8]								
inhabits lowland forest	x	x	x	x	x	x	x	-
inhabits montane forest	-	-	-	-	-	-	-	x
General habitat use								
primarily terrestrial	x[1]	x[9]	-	-	x[10]	-	x[5]	-
primarily scansorial	-	-	x[2]	x[11]	-	-	-	x[12]
primarily arboreal	-	-	-	-	-	x[13]	-	-
Calling substrate								
scansorial	x	x[11, 14]	-	-	x[1]	-	x[5]	x[11]
perch	-	-	x	x[1]	-	x[14]	-	-

Key: M = Male; F = Female; [A] = Male is typically stationary, head is thrown far back, and tail is pointed upward; [B] = Male is running, head is slightly tilted back with neck straight up, and tail is typically in normal position; [C] = M and F bowing with lowerd wings, and tail straight up.

References: [1]Delacour and Amadon 1973; [2]Sick 1968; [3]Heron 1836; [4]Strahl, Silva, and Buccholz this vol.; [5]Sermeño this vol.; [6]Sutton and Pettingill 1942; [7]Buccholz 1991; [8]O'Neill this vol; [9]Defler and Defler this vol.; [10]Contreras and Acevedo this vol.; [11]Hilty and Brown 1986; [12]Strahl, Rojas, and Herrera this vol.; [13]Koepcke and Koepcke 1963; [14]Todd and Carriker 1923.

Table 3 - Associated characters of booming courtship

Character	***alberti***	***alector***	***daub.***	***fasc.***	***rubra***	***Pauxi***
Auditory Components						
Number of notes/boom						
7 notes/boom	-	x	-	x	-	-
6 notes/boom	-	-	x	-	-	-
5 notes/boom	-	-	-	-	x[1]	x
4 notes/boom	x	-	-	-	-	-
No. of notes/1st sequence of boom						
1 note in first part of boom	-	-	-	-	-	-
2 notes in first part of boom	x	x	-	x	-	-
3 notes in first part of boom	-	-	x	-	-	x
4 notes in first part of boom	-	-	-	-	x[1]	-
No. of notes/2nd sequence of boom						
1 note in last part of boom	-	-	-	-	x[1]	-
2 notes in last part of boom	x	-	-	-	-	x
3 notes in last part of boom	-	-	x	-	-	-
5 notes in last part of boom	-	x	-	x	-	-
Visual Components						
Wing position during boom						
wings in normal position	-	-	-	-	-	x
extended slightly below body	x	x	x	x	x[1]	-
Head position during boom						
head down, parallel with body	x	x	x	x	x[1]	-
normal position, slightly retracted	-	-	-	-	-	x
Tail position during boom						
may be slightly below (20^0) body parallel x	-	-	x	-	-	
tail slanted downward at 45^0 angle	-	x	x	-	x[1]	-
may point down, perpendicular to ground	-	-	-	-	-	x
Other components of boom display						
manipulating object in bill	x[1]	x	x	-	-	-

Reference: [1]Delacour and Amadon 1973.

Figure 1 - Dendrogram depicting relationships among *Crax* using sociobiological and ecological characters

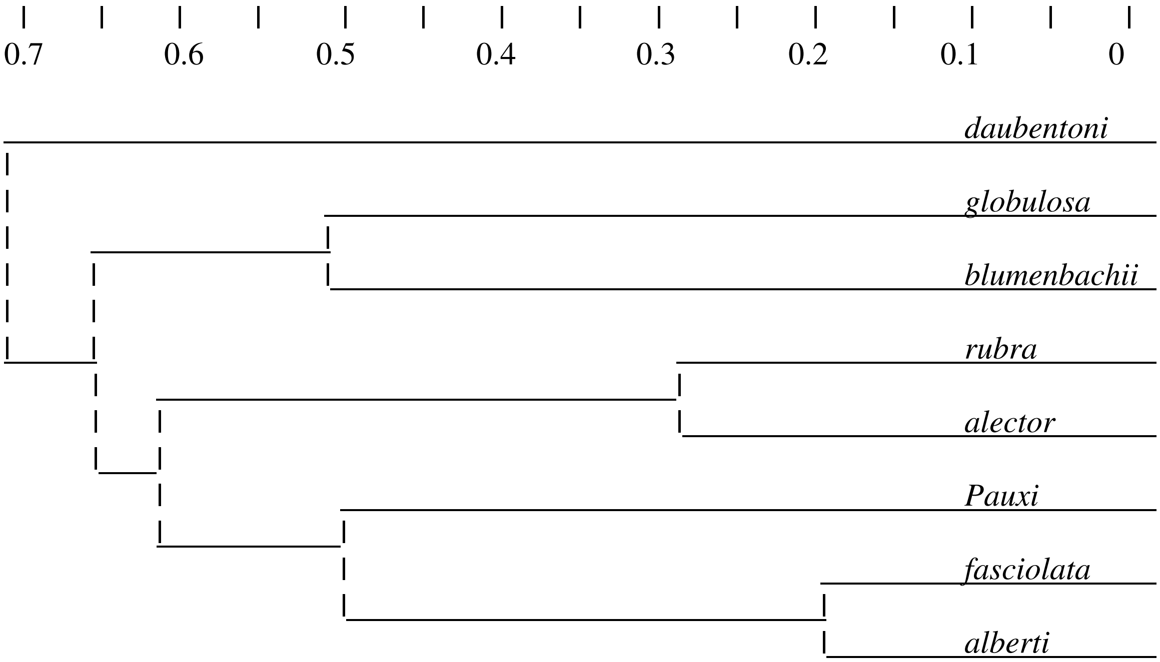

Figure 2 - Booming sequences of different species

<table>
<tr><td>alberti</td><td>. . | . --</td></tr>
<tr><td>alector</td><td>- - | - - . - .</td></tr>
<tr><td>fasciolata</td><td>-- - | . . - . -</td></tr>
<tr><td>Pauxi</td><td>. . - | . -</td></tr>
<tr><td>daubentoni</td><td>- . . | - . .</td></tr>
<tr><td>rubra</td><td>. - . . | -</td></tr>
</table>

Code: . = short boom; - = long boom; -- = extended boom; | = pause

Figure 3 - Dendrogram depicting relationships among *Crax* using characters of booming courtship

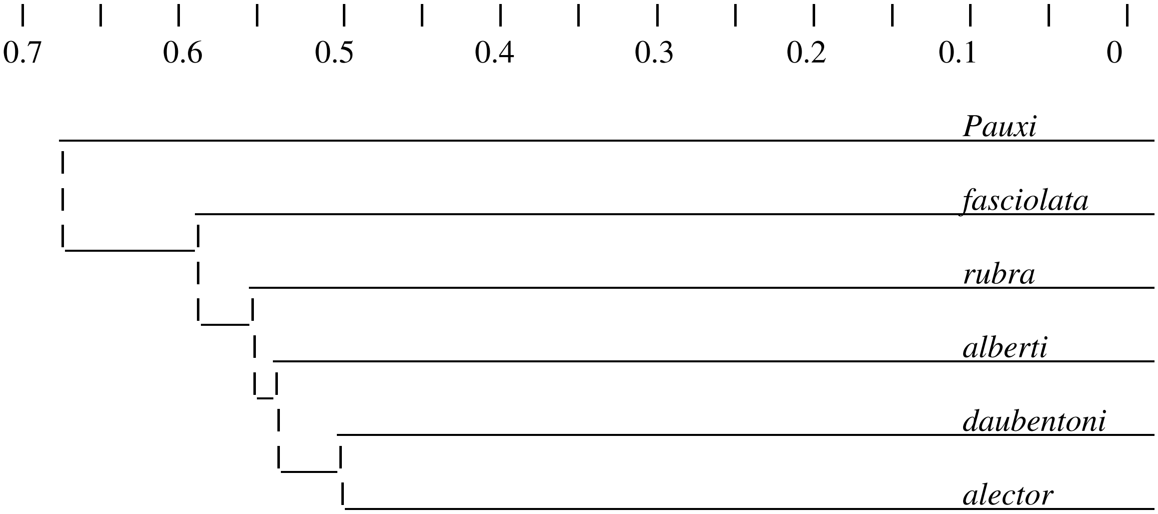

Figure 4 - Map depicting distributions of *Crax alector* (Ce)*, C. daubentoni* (Cd)*, C. alberti* (Cb)*, C. rubra* (Cr), and *C. faxcioloata* (Cf) (modified from Delacour and Amadon 1973)