COMPARATIVE LIFE HISTORY OF COTINGAS IN THE NORTHERN PERUVIAN AMAZON

Daniel M. Brooks, Lucio Pando-Vasquez, and Angel Ocmin-Petit

1Department of Wildlife and Fishery Science, Texas A&M University, College Station, Texas 77843, USA.
2Explorama, Box 446, Iquitos, Peru.
3Deceased.

Abstract. We investigate sociobiology of sympatric cotingas by comparing variation of common characters. The species studied (smallest to largest) are: Colaptes placidus, Porphyrolophus rupicola, Cotungia mayia, C. frigida, Upadgus mcukferans, Phoenicirctus nigrofollis, Quinclula magnipura, Gymnodoenis furtivus and Cephalopterus ornatus. The relationship between size and sexual dimorphism was correlated, with mass and tail length being significant, and all other characters (total length, wing chord, sexual dichromatism and ornamentation) being non-significant. For mass and tail length, smaller species are characterized by females being larger than males, whereas females are smaller in the larger species. Although not significant with all species along the size gradient, sexual dichromatism is more extreme in certain smaller species (i.e., Porphyrolophus and Cotungia), and sexual ornamentation is present primarily in larger species. Dietary specialization increases with size, and most species exhibit low food resource defense, intra- and interspecifically. Smaller species use higher parts of habitat structural attributes, whereas larger species use lower parts. Most of the smaller species are solitary, whereas larger species tend to travel in small flocks. Regarding courtship, smaller species are characterized by solitary male systems (including polygamy), with lekking in the medium species and/or monogamous courtship in the larger species. We offer three hypotheses (modified from Alcock's model) as they relate to cotinga courtship strategy: 1) Solitary, dichromatic males of smaller species are attracted above the canopy because it highlights their iridescence and lures in females (cost — increased predation risk above the canopy, benefit = lower energy expenditure). 2) Actively courting males of medium species are attracted below the canopy to more aggregated fruit clumps; since bright coloring cannot be detected as well below the canopy, the males compensate through active courtship such as lekking and/or vocalizing to lure in females (benefit = decreased predation risk below the canopy, cost = increased energy expenditure during courtship). 3) Males of larger species are lured to their courting sites by females that are attracted to the habitat containing the preferred resource; males typically court a single female using subtle ornamentation, as well as calling in some species.

Accepted 24 June 1999.

INTRODUCTION

The family Cotingidae contains 25 genera and approximately 66 species (Stotz et al. 1996). This family is characterized by extensive morphological and chromatic variation at the generic level. For example this family contains the most variable size range of all Passerines, with the largest species weighing 80 times that of the smallest (Snow 1982). Although the primary factors (i.e., habitat separation and size assortment) driving cotinga community...
METHODS

Herein we examine life history correlates of 9 species of sympatric cotingas in the northern Peruvian Amazon comparing variation among common characters. The species studied include Black-necked Red Cotinga (Ocyptila rubicunda), Black Cheeked Cotinga (Ocyptila nigriceps), Bare-necked Fruitcrow (Gymnopithys depressus), Black-billed Cotinga (Heliocichla nigricapilla), Black-browed Nightingale (Icteria nigra), Brown Capped Cotinga (Cyanerpes caeruleus), Snowy-collared Cotinga (Cerulopterus personatus), Plum-throated Cotinga (Ocyptila plumifrons), and the Splendid Cotinga (Cerulopterus splendidus).

We collected data during 11 weeks from November 1993 to October 1998 at the end of high water (March-May) and low water (October-November) seasons to account for seasonal variation, that did not appear to vary significantly (Brooks 1998). Sampling methods were similar to those used previously by others. Habitat associations were logged for each site.

Sampling was done during 11 weeks from November 1993 to October 1998 at the end of high water (March-May) and low water (October-November) seasons to account for seasonal variation, that did not appear to vary significantly (Brooks 1998). Sampling methods were similar to those used previously by others. Habitat associations were logged for each site.

Habitats have been overviewed elsewhere (Terborgh 1967). Additionally, canopy walkway at ACKKR (Amerindian Community of Karamajuyu, Karamajuyu, Terborgh 1990, 1996). Herein we examine life history correlates of 9 species of sympatric cotingas in the northern Peruvian Amazon comparing variation among common characters. The species studied include Black-necked Red Cotinga (Ocyptila rubicunda), Black Cheeked Cotinga (Ocyptila nigriceps), Bare-necked Fruitcrow (Gymnopithys depressus), Black-billed Cotinga (Heliocichla nigricapilla), Black-browed Nightingale (Icteria nigra), Brown Capped Cotinga (Cyanerpes caeruleus), Snowy-collared Cotinga (Cerulopterus personatus), Plum-throated Cotinga (Ocyptila plumifrons), and the Splendid Cotinga (Cerulopterus splendidus).

We collected data during 11 weeks from November 1993 to October 1998 at the end of high water (March-May) and low water (October-November) seasons to account for seasonal variation, that did not appear to vary significantly (Brooks 1998). Sampling methods were similar to those used previously by others. Habitat associations were logged for each site.

Habitats have been overviewed elsewhere (Terborgh 1967). Additionally, canopy walkway at ACKKR (Amerindian Community of Karamajuyu, Karamajuyu, Terborgh 1990, 1996). Herein we examine life history correlates of 9 species of sympatric cotingas in the northern Peruvian Amazon comparing variation among common characters. The species studied include Black-necked Red Cotinga (Ocyptila rubicunda), Black Cheeked Cotinga (Ocyptila nigriceps), Bare-necked Fruitcrow (Gymnopithys depressus), Black-billed Cotinga (Heliocichla nigricapilla), Black-browed Nightingale (Icteria nigra), Brown Capped Cotinga (Cyanerpes caeruleus), Snowy-collared Cotinga (Cerulopterus personatus), Plum-throated Cotinga (Ocyptila plumifrons), and the Splendid Cotinga (Cerulopterus splendidus).

We collected data during 11 weeks from November 1993 to October 1998 at the end of high water (March-May) and low water (October-November) seasons to account for seasonal variation, that did not appear to vary significantly (Brooks 1998). Sampling methods were similar to those used previously by others. Habitat associations were logged for each site.

Habitats have been overviewed elsewhere (Terborgh 1967). Additionally, canopy walkway at ACKKR (Amerindian Community of Karamajuyu, Karamajuyu, Terborgh 1990, 1996). Herein we examine life history correlates of 9 species of sympatric cotingas in the northern Peruvian Amazon comparing variation among common characters. The species studied include Black-necked Red Cotinga (Ocyptila rubicunda), Black Cheeked Cotinga (Ocyptila nigriceps), Bare-necked Fruitcrow (Gymnopithys depressus), Black-billed Cotinga (Heliocichla nigricapilla), Black-browed Nightingale (Icteria nigra), Brown Capped Cotinga (Cyanerpes caeruleus), Snowy-collared Cotinga (Cerulopterus personatus), Plum-throated Cotinga (Ocyptila plumifrons), and the Splendid Cotinga (Cerulopterus splendidus).
An effort was made to measure at least throughout the study. Courtship strategy (r = 0.431, ns, N = 9), sexual dichromatism (r = -0.554, ns, N = 9), and ornamentation (r = 0.730, ns, N = 9) were examined in the same tree at the same time. The second study focused on the sexes competing for the same food resources.

Feeding strategy for the cooperative breeder, sexual dimorphism, and ornamentation at the same tree were examined in the same tree at the same time. The second study focused on the sexes competing for the same food resources.

Habitat association. The general trend is for seasonal specialization, with the largest species exhibiting no sexual dimorphism whatsoever. The case of is equally interesting because all measured sexual dimorphism ratios break the continuous trend towards increasingly larger males in larger species. In contrast, the medium to larger species use their voice to lure females, and largest species exhibit ornamentation.

TABLE 1. Both of the largest species exhibit ornamentation. C. cayana is a forest canopy specialist, and C. maynana is an island specialist. Since most of the smaller species are forest canopy specialists, with the most diminutive species being an island specialist.

RESULTS

The most extreme measures of sexual dichromatism characterize species at the minimum mandibular width (Selander 1966). The two species exhibiting no sexual dichromatism whatsoever are the two species where group living evolved to enhance food finding and largest two species exhibiting sexual dichromatism characterizes species at the minimum mandibular width (Selander 1966). The two species exhibiting no sexual dichromatism whatsoever are the two species where group living evolved to enhance food finding.
<table>
<thead>
<tr>
<th>Parameters</th>
<th>Li</th>
<th>Pp</th>
<th>Cm</th>
<th>Ce</th>
<th>Lx</th>
<th>Pn</th>
<th>Qp</th>
<th>Gf</th>
<th>Co</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean mass (g)</td>
<td>18</td>
<td>49</td>
<td>70</td>
<td>76</td>
<td>77</td>
<td>95</td>
<td>111</td>
<td>284</td>
<td>571</td>
</tr>
<tr>
<td>Sexual dimorphism</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male/Female mass</td>
<td>0.80</td>
<td>0.91</td>
<td>0.93</td>
<td>1.00</td>
<td>0.99</td>
<td>0.97</td>
<td>1.06</td>
<td>1.49</td>
<td>1.65</td>
</tr>
<tr>
<td>M/F total length</td>
<td>0.91</td>
<td>0.97</td>
<td>0.96</td>
<td>1.08</td>
<td>0.99</td>
<td>0.92</td>
<td>0.93</td>
<td>1.02</td>
<td>1.14</td>
</tr>
<tr>
<td>M/F tail length</td>
<td>0.87</td>
<td>0.91</td>
<td>0.91</td>
<td>1.01</td>
<td>1.00</td>
<td>0.89</td>
<td>0.93</td>
<td>1.03</td>
<td>1.08</td>
</tr>
<tr>
<td>M/F wing chord</td>
<td>1.03</td>
<td>1.03</td>
<td>1.02</td>
<td>0.94</td>
<td>1.06</td>
<td>0.93</td>
<td>1.05</td>
<td>1.09</td>
<td>1.12</td>
</tr>
<tr>
<td>Sexual dimorphism</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Sexual ornamentation</td>
<td>1''</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Feeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>c''</td>
<td>v</td>
<td>c/v</td>
<td>c</td>
<td>m</td>
<td>u</td>
<td>u</td>
<td>v</td>
<td>i</td>
</tr>
<tr>
<td>Solitary</td>
<td>Mean flock size</td>
<td>1.0</td>
<td>1.0</td>
<td>1.2</td>
<td>1.5</td>
<td>2.9</td>
<td>1.0</td>
<td>2.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Relative abundance</td>
<td>1</td>
<td>2</td>
<td>11</td>
<td>29</td>
<td>44</td>
<td>29</td>
<td>31</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td>Courtship strategy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sexual dichromatism and sexual ornamentation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of males/display group</td>
<td>&gt; 1'</td>
<td>1'</td>
<td>1</td>
<td>1</td>
<td>Several''</td>
<td>Several''</td>
<td>1/fem.</td>
<td>1'/fem''</td>
<td>For all species, see values above</td>
</tr>
<tr>
<td>Solitary male or lek''</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual or vocal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Competiton at feeding trees''</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>More than 1 sex present yes</td>
<td>yes</td>
<td>b</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other cotingas present''</td>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Species: L. isidella = Li, P. purpiloquama = Pp, C. meijuna = Cm, C. cyana = Ce, L. tuiferans = Lx, P. nigricollis = Pn, Q. parvata = Qp, G. fusciceps = Gf, C. ornatus = Co.

Data not available.

1Sexual dichromatism: 0 = none, 1 = slight, 2 = moderate, 3 = extreme.

2Sexual ornamentation: 0 = none, 1 = slight, 2 = moderate.

3Feeding strategy: g = gorgers, s = seasonally resource specialist, r = riverine specialist.

Habitat association: m = mid-upper strata, u = upper strata, c = canopy, v = varzca/water edge, i = island varzca.

4A male may displace another male from a preferred calling site.

5Leks are often loosely associated.

6Quantified by whether other individuals were ever observed at tree or not. Lack of data should be interpreted as species possibly shared resource patches with other individuals, but it went undetected.

coloring cannot be detected as well under the

length and wing chord) show a significant
cineral species if fruit clumps

are "thinner" above than below the canopy.

Courtship strategy.

Smaller, supra-canopy dwell-

ship. 3) Males of larger species are lured to

may be closer related to manakins

in larger species (see VX'ebster

Pboenicimts


C. cayana


females of the larger species (see Downer-

2) Medium sixed species

may benefit through

enhanced defense of resources such as court-

resources defense in these species.

The brightness of males of the

common underlying pattern

here is that males utilize different adaptations

to lure females to their courting site.

Data for seven of

the nine species indicate that more than one

females can he divided into three general pat-

resource defense in these species.

The number of males displaying to

between sexes (Fig. 3). Nonetheless, several

observations suggest relatively low food

natural and is encountered with far less

and are present at the site as part of an inte-

another meaning to "trekking" and/ or vocalizations,

breeding at a younger age would favor smaller

females of the larger species (see Downer-

ancestors interactions despite being courted by

there is one, there are many). For example, of 11 for-

non-dichromatic species also com-

with slight or moderate sexual ornamen-

there was one, there are many). For example, on one occasion we observed three male

mobbing a female

Gymnoemts.

flew off

shortly after being mobbed and was probably

simply moving through atypical habitat.

DISCUSSION

The benefits of females generally being

for mating rights. For example two female

C.

may be closer related to manakins

and/ or monogamous courtship in the

or are present at the site as part of an inte-

mately moving through atypical habitat.

The brighter coloration of males of the

benefit of females generally being

enhanced defense of resources such as court-

male systems including polygamy in

The common underlying pattern

here is that males utilize different adaptations

to lure females to their courting site.

Data for seven of

the nine species indicate that more than one

females can he divided into three general pat-

resource defense in these species.

The number of males displaying to

between sexes (Fig. 3). Nonetheless, several

observations suggest relatively low food

natural and is encountered with far less

and are present at the site as part of an inte-

another meaning to "trekking" and/ or vocalizations,

breeding at a younger age would favor smaller

females of the larger species (see Downer-

ancestors interactions despite being courted by

there is one, there are many). For example, of 11 for-

non-dichromatic species also com-

with slight or moderate sexual ornamen-

there was one, there are many). For example, on one occasion we observed three male

mobbing a female

Gymnoemts.

flew off

shortly after being mobbed and was probably

simply moving through atypical habitat.

DISCUSSION

The benefits of females generally being

for mating rights. For example two female

C.

may be closer related to manakins

and/ or monogamous courtship in the

or are present at the site as part of an inte-

another meaning to "trekking" and/ or vocalizations,

breeding at a younger age would favor smaller

females of the larger species (see Downer-

ancestors interactions despite being courted by

there is one, there are many). For example, of 11 for-

non-dichromatic species also com-

with slight or moderate sexual ornamen-

there was one, there are many). For example, on one occasion we observed three male

mobbing a female

Gymnoemts.

flew off

shortly after being mobbed and was probably

simply moving through atypical habitat.
Model for smaller-sized species

- Smaller species

Larger species

Model for medium-sized species

- Preferred foods along the river

Model for larger-sized species

Preferred foods: riverine fruits

Despite lack of competition for food resources, there is a difference in the energy expenditure of males and females of most species. Males and females of some species only utilize the same food resources, rather than compete as a clumped resource that varies seasonally in spatial distribution. It is not profitable for primary frugivores to defend a resource that is defended is strengthened even more by looking at the lack of social mimicry between two congeners: C. maynana and C. cayana. The fact that food resources are not predictable with regard to the same resource patch on more than one occasion makes it less likely for competition for food resources to occur within the territory (see Brown 1964, Snow 1985). Although C. maynana and C. cayana are more distantly related species, they are chromatically similar to one another than to other more closely related species. Perhaps this merely suggests that the main benefit of a clumped, temporally predictable resource is decreased foraging time (i.e., take/search time) that permits a male to mate with more than one female. The primary frugivores to defend a resource that is unpredictable spatially is not likely to occur with any predictability within one occasion. The lack of territorially between species in terms of habitat preference. This is probably a consequence of their preference for riverine fruits (Sick 1993). Thus it is plausible that it is possible for social mimicry to be achieved, if two species show strong sexual dichromatism but different size dimorphism (Snow 1982), contrary to the findings observed herein.
South America. Volume 2: The suboscine pas-

behavior may explain the increased male sex-

ual competition and the evolution of

ual dimorphism in such larger species (see

tations on bird distribution and feeding assem-


Sick, H. 1951. An egg of the umbrellabird. Wilson

Sick, H. 1954. Ziir Biologic des amazomschen


REFERENCES

ACKNOWLEDGMENTS
BROOKS ET AL.

Von Hagen, W. 1937. On the capture of the 207 umbrellabird (Cephalopterus penduliger Sclater).

Webster, M. S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds.