ORNITOLOGIA NEOTROPICAL 10: 193–206, 1999
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COMPARATIVE LIFE HISTORY OF COTINGAS IN THE NORTHERN PERUVIAN AMAZON

Daniel M. Brooks[1,4], Lucio Pando-Vasquez[2] & Angel Ocmin-Petit[2,3]

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

Abstract. We investigate sociobiology of sympatric cotingas by comparing variation of common characters. The species studied (smallest to largest) are: *Iodopleura isabellae*, *Porphyrolaema porphyrolaema*, *Cotinga maynana*, *C. cayana*, *Lipaugus vociferans*, *Phoenicircus nigricollis*, *Querula purpurata*, *Gymnodoerus foetidus* 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., *Porphyrolaema* and *Cotinga*), 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 under 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.*

Key words: Cotingas, comparative sociobiology, Amazonian birds, resource distribution.

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

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[4] *Current address:* Cracid Specialist Group Headquarters, PO Box 132038, Houston, Texas 77006, USA.
E-mail: Ecotropix@aol.com

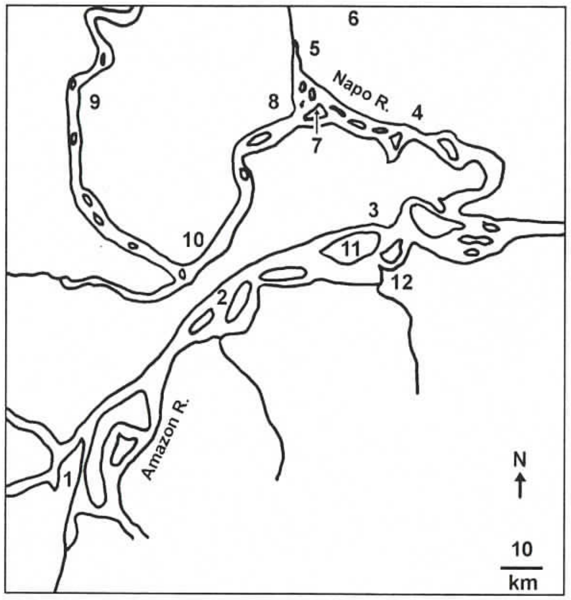

FIG. 1. A map of the study region. 1 = Iquitos (major city), 2 = Amazon River bank site, 3 = Yana Mono Tributary/Yana Mono Lodge, 4 = Napo River bank site, 5 = Sucusari Tributary/Camp, 6 = ACEER, 7 = Yarina Island/Rosario Island, 8 = Chimiguy Lake, 9 = Lorenzo Lake, 10 = Urco Tributary, 11 = Casares Lake, 12 = Manati Tributary.

structure in the northern Peruvian Amazon have been identified (Brooks 1998), relatively little is known about the amount of variation in sociobiology, particularly for cotingas living in the same region.

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 *Phoenicircus nigricollis*, White-browed Purple-tuft *Iodopleura isabellae*, Screaming Piha *Lipaugus vociferans*, Plum-throated Cotinga *Cotinga maynana*, Spangled Cotinga *C. cayana*, Purple-throated Cotinga *Porphyrolaema porphyrolaema*, Bare-necked Fruitcrow *Gymnoderus foetidus*, Purple-throated Fruitcrow *Querula purpurata*, and Amazonian Umbrellabird *Cephalopterus ornatus*. Although former classification (e.g., Snow 1973a) included tityras and becards in this family, we follow current classification (e.g., Stotz *et al.* 1996).

METHODS

Data collection can be divided into data collected from the field and data collected from the museum. Mensural data were obtained

from museum specimens and other dimorphism characters (sexual dichromatism and ornamentation) were obtained from both field and museum data. Other data including habitat association, sociality and courtship were obtained from the field. Field data on feeding (limited observations) and species with limited sample size (i.e., *Phoenicircus*, *Iodopleura* and *Porphyrolaema*) were supplemented with museum specimen tag data or obtained from available literature (e.g., Wallace 1849, Von Hagen 1937, Nicéforo 1947, Sick 1951, 1954, 1979, 1993; Ellis 1952, Pinto 1953, Snow 1961, 1971, 1982, 1985; Diamond & Terborgh 1967, Haverschmidt 1968, Béraut 1970, Howe 1982, Hilty & Brown 1986, Terborgh 1986, Terborgh *et al.* 1990, Trail & Donahue 1991, Davis 1993, Ridgely & Tudor 1994, Thiollay 1994, Brooks 1998).

Field collected data. Field data were collected in the Napo River intersect region (2°45'S; 72°55'W, see Fig. 1) of the Peruvian Amazon. Habitats have been overviewed elsewhere (e.g., Brooks 1997, 1998), but will be described here briefly. The habitats sampled are primarily situated along water, within forest, or a transition/edge situation between these habitats. Regions along the immediate edges of water (e.g., marshes, lakes, streams and rivers) are often dominated by sawgrass or cane, followed by thick undergrowth further inland from the water. Island edge vegetation is similar, unless the island is young, in which case it will be monocultured with rapidly colonizing plant species that are primary successional island specialists (e.g., *Cecropia* sp., *Gynerium* sp., and *Heliconia* sp.). Aquatic edge vegetation is separated from interior rainforest by dense forest with thick undergrowth, with canopy height often not exceeding 10–15 m. The exception includes floodplain, which is characterized by continuous short stems and grasses (e.g., *Tridescantia* sp.) and tall, leafy trees with trunks spaced 5–20 m apart. Primary, interior rainforest is high in plant diversity, is characterized by a dark understory due to few penetrable light gaps, and contains tall trees that form part of the canopy, buttresses, or canopy emergents (e.g., *Cedrela* sp., *Ceiba pentandra*, *Ficus insipida* and *Inga* sp.), often exceeding 35 m. Other tall trees in the region include palms (e.g., *Euterpes prectoria*, *Mauritia flexuosa*, *Scheelea* sp., *Socratea* sp.), often occupying a gradient of habitats, from river edge to interior forest.

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 all visually or auditorily recorded encounters of Cotingids at each site visited per trip. Data were collected by walking slowly along transects with frequent stops (Pearson 1975) and boating along waterways (Diamond & Terborgh 1967). Additionally supra-canopy observations were facilitated by using the canopy walkway at ACEER (Amazonian Center for Environmental Education and Research). Species were identified using Hilty & Brown (1986) and Parker *et al.* (n.d.).

Museum collected data. Mensural data were collected at the Museum of Natural Science, Louisiana State University on 3 October 1996. Mass (indicative of size) was recorded (in g) from the tags when available; standard measurements taken in cm using a metal ruler included total length, wing chord and tail length (indicative of size and maneuverability in habitat). Measurements taken in cm with standard dial calipers include maximum mandibular height (indicative of masticator musculature – bite force) and maximum mandibular width (indicative of gape-size of food taken) (Snow 1973b).

An effort was made to measure at least four specimens of each sex per species. In cases where specimens were represented by less than four individuals of a given sex from Dpto. Loreto, additional specimens measured included those that were closest to the sampling region.

Analytical methods. Morphological life history parameters included size and sexual dimorphism. Mass was used to measure size, ranking the species from smallest to largest in range. Sexual dimorphism was measured by obtaining male/female (M/F) ratios for mass, total length, tail length, and wing chord. Values < 1 indicated females were larger than males; values >1 indicated males were larger than females. Sexual dimorphism was also measured by examining degree of sexual dichromatism and ornamentation. Sexual dichromatism was defined as extreme coloration differences where the female is more drab and was ranked as: 0 (none, for no differences between male and female), 1 (slight, for subtle differences, with both sexes relatively drab), 2 (moderate, for subtle differences with both sexes relatively colorful) and 3 (extreme, for male relatively colorful and female drab). Sexual ornamentation was defined as modified external morphology adapted for displaying and was ranked as: 0 (none, for no differences), 1 (slight, for slight differences between male and female) and 2 (moderate, for both sexes sharing similar ornamentation, but male having stronger ornamentation). Pearson product-moment correlations were used to assess the relationship between size [ranked from smallest (1) to largest (9)] and each sexual dimorphism character, using the computer program SPSS (1996).

Other life history parameters include feeding strategy, habitat association, sociality [mean flock size and relative abundance (expressed by numbers of encounters/species throughout the study)], courtship strategy (type of courtship and number of males/display group) and competition at feeding trees.

Information on feeding strategy was largely supplemented with the literature, and species were identified as gorgers (species that sit in low bushes or mistletoe and gorge), seasonal resource specialists (species that seasonally concentrates on insects or fruit) and riverine specialists (species preferring fruits growing along river, such as palm fruits). Species habitat associations were identified based upon strata of tropical forest occupied (i.e., mid-upper, upper or canopy) or type of aquatic habitat occupied (i.e., varzea/water edge transition or island varzea).

Competition at feeding trees was examined at two levels. The first involved different scales of taxonomic orientation: whether conspecifics of the same or different sexes, other cotingas, or other avian species were present in the same tree at the same time. The second examined intraspecific competition between sexes more closely by plotting M/F ratios of maximum mandibular height against maximum mandibular width (Selander 1966). The closer the value is to 1, the more likely the chance of the sexes competing for the same food resources.

RESULTS

Size. The plotted trend in size from smallest to largest is as follows (with letter codes used in tabularized data following each species parenthetically): *I. isabellae* (Ii), *P. porphyrolaema* (Pp), *C. maynana* (Cm), *C. cayana* (Cc), *L. vociferans* (Lv), *P. nigricollis* (Pn), *Q. purpurata* (Qp), *G. foetidus* (Gf) and *C. ornatus* (Co).

Sexual dimorphism. Sexual dimorphism closely matches the range of sizes. Significant correlations occur between size and M/F mass ($r = 0.976$, $P < 0.001$, $N = 9$) and M/F tail length ($r = 0.728$, $P < 0.05$, $N = 9$), but not for M/F total length ($r = 0.502$, ns, $N = 9$), M/F wing chord ($r = 0.431$, ns, $N = 9$), sexual dichromatism ($r = -0.554$, ns, $N = 9$) or ornamentation ($r = 0.730$, ns, $N = 9$).

For mass and tail length there is a trend of females being relatively larger in the smaller species towards the reverse (i.e., males being larger) in the larger species (Table 1). The strongest exception to this rule is wing chord, which is relatively longer in females in all species except for *C. cayana* and *Phoenicircus*. It is interesting to note that *C. cayana* is the only smaller-sized species that shows reverse trends in dimorphism; total and tail lengths in *C. cayana* are relatively longer in males than in females and wing chord is shorter in males. The case of *Phoenicircus* is equally interesting because all measured sexual dimorphism ratios break the continuous trend towards increasingly larger males in larger species.

The most extreme measures of sexual dichromatism characterizes species at the smaller end of the spectrum (i.e., *Cotinga* and *Porphyrolaema*), with the most diminutive species (*Iodopleura*) and some of the larger species showing slight or moderate sexual dichromatism (Table 1). The two species exhibiting no sexual dichromatism whatsoever (*Lipaugus* and *Cephalopterus*) are the two species where males use their voice to lure females.

Cotingids show relatively little sexual ornamentation, with only the smallest (*Iodopleura*) and largest two species exhibiting slight to moderate ornamentation (Table 1). Both of the largest species exhibit ornamentation in the head and throat region; *Gymnoderus* males have fleshy facial folds whereas *Cephalopterus* males have larger crests and an external air sac projecting from the throat.

Feeding strategy. All species are primary frugivores, consuming small invertebrates such as insects to a lesser extent. Although all literature reports *Phoenicircus* to be a strict frugivore, at least one specimen (LSUMNS-110267) had arachnid remains in its stomach.

The most general trend for feeding strategy was that smaller species tend to be gorgers, medium and larger sized species shift their diet seasonally depending upon whether fruits or animal prey are more abundant, and the largest two species enjoy fruits such as palm fruits that grow along the river (Table 1). In sum there appears to be a general trend towards increased dietary specialization with larger size.

Habitat association. The general trend is for smaller species to be associated with higher parts of the forest and larger species to use lower parts of the forest (Table 1). Smaller species are forest canopy specialists and/or are often observed perched along the upper part of a tree within thick riverine vegetation. In contrast, the medium to larger species utilize the middle and/or upper strata of interior forest. The two largest species are water edge specialists, with the largest (*Cephalopterus*) being an island specialist.

Sociality. Most of the smaller species are solitary whereas larger species tend to travel in small flocks (Table 1). It is possible that group living evolved to enhance food finding in larger, sub-canopy dwelling species versus smaller, supra-canopy dwelling species. Since all species are frugivorous and fruit is spatially non-predictable, it should be beneficial to have multiple individuals search for a fruit patch that provides plenty of food for all group members. Group living may benefit riverine species such as *Gymnodoerus* in finding preferred resources such as palm fruits. This may also explain subtle differences in breeding strategy for the cooperative breeder, *Querula* (Snow 1971). In contrast solitary, supra-canopy dwelling individuals can perhaps locate fruit easier because they can see farther distances unobstructed by forest growth. It should be more profitable for

TABLE 1. Life history parameters of nine sympatric cotingas.

Parameters	Species[a]								
	Ii	Pp	Cm	Cc	Lv	Pn	Qp	Gf	Co
Mean mass (g)	18	49	70	76	77	95	111	284	571
Sexual dimorphism									
Male/Female mass	0.80	0.91	0.93	[b]	0.99	0.97	1.06	1.49	1.65
M/F total length	0.91	0.97	0.96	1.08	0.99	0.92	0.93	1.02	1.14
M/F tail length	0.87	0.91	0.91	1.01	1.00	0.89	0.93	1.03	1.08
M/F wing chord	1.03	1.03	1.02	0.94	1.06	0.93	1.05	1.09	1.12
Sexual dimorphism[c]	1	3	3	3	0	2	1	1	0
Sexual ornamentation[d]	1[m]	0	0	0	0	0	0	1	2
Feeding[e]	g	[b]	g	g	s	[b]	s	r	r/s
Habitat[f]	c[m]	v	c/v	c	m	u	u	v	i
Soliality									
Mean flock size	1.0	1.0	1.2	1.5	2.9	1.0	2.4	1.5	2.1
Relative abundance	1	2	11	29	44	2	29	31	35
Courtship strategy									
Sexual dichomatism and sexual ornamentation	For all species, see values above								
Number of males/display group	> 1[m]	1[m]	1	1	Several[m]	Several[m]	1/fem.	[b]	1/fem[g]
Solitary male or lek[h]	[b]	[b]	sol.	b	lek	lek[m]	lek/sol.	lek/sol.	sol.
Visual or vocal	[b]	[b]	visual	[b]	vocal	visual	visual	visual	vocal
Competition at feeding trees[i]									
More than 1 sex present yes	yes	[b]	yes	yes	[b]	yes	[b]	[b]	[b]
Other cotingas present[j]	[b]	[b]	c	m,q,g[k]	[b]	[b]	c	m[k]	[b]

TABLE 1. Continuation.

Parameters	Species[a]								
	Ii	Pp	Cm	Cc	Lv	Pn	Qp	Gf	Co
Other species present[l]	[b]	[b]	s,p	m[k],t,f	[b]	[b]	yes	k,m[k]	c
Food competion between sexes									
M/F maximum gape	0.98	0.99	1.03	0.99	0.93	0.97	1.07	0.95	1.10
M/F mandible height	0.95	1.01	0.73	1.00	1.00	0.77	0.84	1.10	1.47

[a] Species: *I. isabellae* = Ii, *P. porphyrolaema* = Pp, *C. maynana* = Cm, *C. cayana* = Cc, *L. vociferans* = Lv, *P. nigricollis* = Pn, *Q. purpurata* = Qp, *G. foetidus* = Gf, *C. ornatus* = Co.

[b] Data not available.

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

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

[e] Feeding strategy: g = gorger, s = seasonally resource specialist, r = riverine specialist.

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

[g] A male may displace another male from a preferred calling site.

[h] Leks are often loosely associated.

[i] Quantified 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.

[j] c = *C. cayana*, m = *C. maynana*, q = *Q. purpurata*, g = *G. foetidus*.

[k] Incident involving a female *C. cayana* and *L. hypopyrrha* simultaneously mobbing a female *Gymnoderus* in primary rainforest canopy, atypical habitat for *Gymnoderus*. The *Gymnoderus* flew off shortly after being mobbed and was probably simply moving through the atypical habitat.

[l] k = Plumbeous Kites (*Ictinia plumbea*); s = Short-tailed Parrot (*Graydidascalus brachyurus*); p = Cobalt-winged Parakeet (*Brotogeris cyanoptera*); m = Cinereous Mourner (*Laniocerca hypopyrrha*); f = Crowned-slaty (*Empidonomus aurantioatrocristatus*) and Dusky-chested Flycatchers (*Tyrannopsis luteiventris*); c = Giant Cowbird (*Scaphidura oryzivora*); t = Blue-gray Tanager (*Thraupis episcopus*).

[m] Data supplemented or obtained with one or more of the following: Wallace 1849, Von Hagen 1937, Nicéforo 1947, Sick 1951, 1954, 1979, 1993; Ellis 1952, Pinto 1953, Snow 1961, 1971, 1982, 1985; Diamond & Terborgh 1967, Haverschmidt 1968, Béraut 1970, Howe 1982, Hilty & Brown 1986, Terborgh 1986, Terborgh *et al.* 1990, Trail & Donahue 1991, Davis 1993, Ridgely & Tudor 1994, Thiollay 1994, Brooks 1998.

smaller species to forage alone if fruit clumps are "thinner" above than below the canopy.

There is an interesting relationship between sexual dichromatism and group size. The species with extreme or moderate sexual dichromatism tend to be solitary (Table 1). The brighter coloration of males of the smaller, solitary species serves to attract females. However this does not mean that females of these solitary species are territorial for mating rights. For example two female *C. maynana* sharing the same tree showed no agonistic interactions despite being courted by the same male. Females of the more social species are lured to a display site by male activity such as lekking and/or vocalizations, or are present at the site as part of an integrated social unit (e.g., *Querula*).

Despite species packing rules (i.e., an area of the same size will contain more smaller species and fewer larger species; see Cotgreave 1993) the trend of relative abundance from smallest to largest species is somewhat reversed (Table 1). This can perhaps be explained by variation in species biology. For example, *Porphyrolaema*, a smaller species, is naturally rare and is encountered with far less frequency in the field than most of the other species with the possible exceptions of *Iodopleura* and *Phoenicircus*. Therefore the low abundance (2 individuals) can be explained by naturally low numbers of this species in nature. In contrast *Lipaugus* is a loosely-associated lekking species. A solitary individual was only encountered on one occasion; on all other occasions they were in groups. Thus the higher abundance of *Lipaugus* is perhaps due to social courtship constraints (i.e., where there is one, there are many). For example, on one occasion we observed a group of *Lipaugus* in a loosely associated lek, when suddenly they formed a very tight lek, calling more rapidly and louder. It is possible that a female entered the arena at that time, though we were unable to verify this since the sexes are not dimorphic.

Courtship strategy. Smaller, supra-canopy dwelling species tend to be more colorful (Table 1). The males of primarily larger species (that show the least amount or no sexual dichromatism) attract females through vocalizations and/or subtle ornamentation (Table 1). Such vocalizations are often more intensified in birds dwelling in interior forest (Morton 1975) as seen in the case of *Lipaugus* for example. The common underlying pattern here is that males utilize different adaptations to lure females to their courting site.

The number of males displaying to females can be divided into three general patterns (Table 1). 1) Smaller species tend to have only one male courting at a time, even if polygamy is involved. In one aforementioned case a single male *C. maynana* displayed to two females about 25 m away in an adjacent tree. 2) Medium sized species (*Lipaugus* and *Phoenicircus*) have communal display sites where several males will display at once. These display arenas often span areas of 2500 – 40,000 m^2. Finally, 3) the larger species (e.g., *Querula* and *Cephalopterus*) are quite variable depending upon the situation, but a single male tends to court one female. In sum we see a trend from solitary male systems including polygamy in the smallest species, to lekking in the medium species and/or monogamous courtship in the larger species (Table 1).

Figure 2 depicts three courtship models (modified from Alcock's model 1984), each describing hypotheses built upon life history patterns described herein: 1) Solitary, dichromatic males of smaller species are attracted above the canopy because it highlights their iridescence and lures in females. The cost is increased predation risk above the canopy but the benefit is lower energy expenditure. 2) Actively courting males of medium species are attracted below the canopy where fruit clumps may be more aggregated. Since bright coloring cannot be detected as well under the canopy the males compensate through active courtship such as lekking and/or vocalizing to lure in females. The benefit is decreased predation risk below the canopy but the cost is 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. The male typically courts a single female using subtle ornamentation, as well as calling in some species.

Competition at feeding trees. Data for seven of the nine species indicate that more than one sex, species of cotinga or species of bird may be present at the same feeding tree (Table 1). However, with the possible exception of *Cephalopterus*, there appears to be a relatively high amount of feeding morphology overlap between sexes (Fig. 3). Nonetheless, several observations suggest relatively low food resource defense in these species.

For example, the same sexes of a given species may share feeding sites for at least some species. We observed three male *Cotinga maynana* foraging together on one occasion. On other occasions we observed groups of two male *Cotinga cayana* foraging together with or without females present.

Moreover, during more than 10 weeks of field time we only observed a single direct agonistic interaction at a feeding tree. This was an incident involving a female *Cotinga cayana* and *Laniocerca hypopyrrha* simultaneously mobbing a female *Gymnodoerus* in primary rainforest canopy, which is atypical habitat for *Gymnodoerus*. The *Gymnodoerus* flew off shortly after being mobbed and was probably simply moving through atypical habitat.

DISCUSSION

Sexual dimorphism. Size dimorphism characters of mass and tail length (rather than total length and wing chord) show a significant pattern of females being larger than males in smaller species towards males being larger than females in larger species (see Webster 1992). *C. cayana* and *Phoenicircus* are the two species that show exception to this rule. *Phoenicircus* may be closer related to manakins (Pipridae) than other cotingas, perhaps serving as the phylogenetic link between the two groups (Trail & Donahue 1991).

The benefit of females generally being larger in smaller species may be linked to parental investment (see Payne 1984). For example, larger egg and offspring size would have a reduced chance of predation and therefore favor mothers of smaller species being larger (see Lack 1968, Andersson 1994). Alternatively, smaller females in fluctuating environments may be able to breed at an earlier age than larger females, therefore breeding at a younger age would favor smaller females of the larger species (see Downerhower 1976). Finally, males of larger species (e.g., *Cephalopterus*) may benefit through enhanced defense of resources such as courting sites (see Andersson 1994).

The pattern of size dimorphism (mass and tail length) increasing with larger males is concordant with Snow's hypothesis (1982). Although not significantly correlated with size, smaller species such as *Porphyrolaema* and *Cotinga* show increased sexual dichromatism whereas *Iodopleura* and the largest species show slight or moderate ornamentation. Thus what certain species lack in sexual dichromatism they may partly compensate for with slight or moderate sexual ornamentation. Non-dichromatic species also compensate through intense vocalizations produced by the males to lure in the females.

It is important to note that different results might be obtained at other study sites, even with slightly different communities (M. Théry pers. comm.). For example, of 11 forest-dwelling cotingas in French Guiana, at

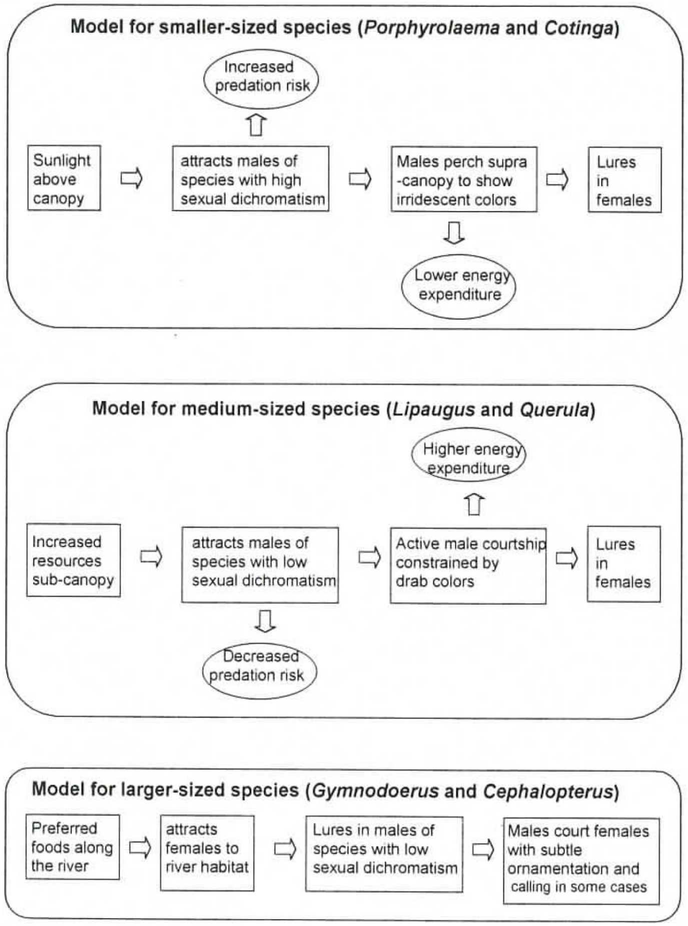

FIG. 2. Variability in life history strategies among different groups.

lease three larger species (*Haematoderus militaris, Procnias alba* and *Rupicola rupicola*) show strong sexual dichromatism but little size dimorphism (Snow 1982), contrary to the findings observed herein.

What lures females to their habitat? Larger species tend to be increasingly selective in their diet, enjoying items such as palm fruits. The two largest species were both water edge specialists in terms of habitat preference. This is probably a consequence of their preference for riverine fruits (Sick 1993). Thus it is plausible, at least for these larger species, that distribution within a landscape is dictated by their preferred foods (Fig. 4). In contrast females of the smaller, solitary species appear to be lured to the brighter coloration of males (Fig. 4). Whereas females of the more social species are lured to display sites by male activity (e.g., lekking, vocalizations, etc.) (Fig. 2).

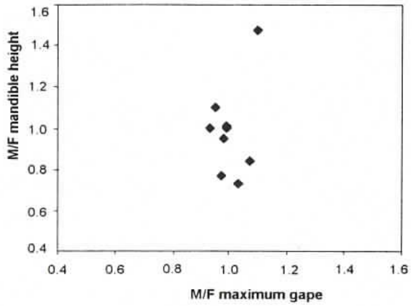

FIG. 3. Food overlap between sexes.

Lack of competition for food resources. There appears to be relatively little competition for similar food resources. Moreover fruit grows as a clumped resource that varies seasonally in spatial distribution. It is not profitable for primary frugivores to defend a resource that may not occur with any predictability within that territory (see Brown 1964, Snow 1985).

The fact that food resources are not defended is strengthened even more by looking at the lack of social mimicry between two congeners: *C. cayana* and *C. maynana.* The benefits of social mimicry include: 1) escaping attack from larger models, and 2) deriving higher status at a resource site – smaller species may be deterred from occupying the same site where the seemingly larger model (that is really the mimic) is present (Diamond 1982). For social mimicry to be achieved, two more distantly related species must be more chromatically similar to one another than they are to other more closely related species. Although *C. maynana* and *C. cayana* look similar from a distance, specimens in the hand reveal a different picture. Of those species in the *Cotinga* clade that *C. maynana* is closest related to (e.g., *C. amabilis, C. ridgwayi* and *C. nattereri*), *C. maynana* resembles *C. cayana* the least because it has a yellow iris and predominantly blue wings rather than dark iris and wings like *C. cayana* and the other species.

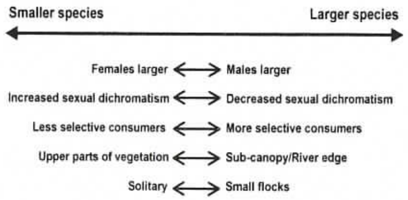

FIG. 4. General life history trends in nine species of cotingas.

Despite lack of competition for food resources, there is a relatively low amount of feeding morphology overlap between sexes (Fig. 3). Perhaps this merely suggests that males and females of most species only utilize the same food resources, rather than compete for them (see Clutton-Brock & Harvey 1977). We observed different sexes of *Cotinga* associated at the same resource patch on more than one occasion.

Male reproductive strategy. Fruit as the main food resource appears to play an important role in the lives of most species. Fruit is always present temporally but often unpredictable spatially. A lack of territoriality is beneficial in areas where food resources are spatially unpredictable because the fruit may not blossom within the defended area. 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, and allows the female to raise the offspring alone (Snow 1985). The lack of territoriality between males combined with the potential to mate with more than one female results in intense sexual competition and the evolution of extreme courtship displays (Snow 1985). This pattern is especially apparent in the smaller species that show higher sexual dichromatism (see Bradbury & Vehrencamp 1998).

Bradbury & Vehrencamp (1998) have overviewed the pattern of more brightly colored species living above the canopy to opportune sunlight in order to advertise their iridescent coloration to females. Moreover, it is more difficult for smaller species to advertise auditorily (see Bradbury & Vehrencamp 1998), which may explain the bright iridescent coloration in species such as *Cotinga*. Alcock (1984) predicts that species advertising with visual cues spend a low amount of energy doing so. The trade-off is that such bright colors may also advertise the males presence to predators (Endler 1991). In contrast, the pattern of more drab species living below the canopy perhaps favors decreased predation (Bradbury & Vehrencamp 1998). However some of these species with decreased sexual dichromatism (e.g., *Lipaugus*) advertise to females using auditory cues that Alcock (1984) predicts are energetically high, as confirmed in multiple subsequent studies (e.g., Eberhardt 1994). Nonetheless, auditory signals are less constrained by environmental factors (e.g., filtering by sub-canopy vegetation) than visual signals (Bradbury & Vehrencamp 1998). It appears that the courting site of a male(s) is established to attract a female(s) in the smaller and medium-sized species (Fig. 2). In this case the females pattern of spatial distribution may be a consequence of male distribution rather than presence of food resources.

There is a trend from solitary male systems including polyandry in the smallest species, to lekking in the medium species and/or monogamous courtship in the larger species. Indeed, as mentioned previously male *Cephalopterus* have been observed displacing other males from a favored courting site. This behavior may explain the increased male sexual dimorphism in such larger species (see Andersson 1994).

ACKNOWLEDGMENTS

We thank Marc Théry, David Snow and Ken Risenhoover for helpful comments on this ms. We are indebted to CONEPAC and INRENA for allowing us to work in the region. Logistical support was provided by Explorations, Inc. and Peter Jenson of Explorama.

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