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DIETS OF CRACIDS: HOW MUCH DO WE KNOW?

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Resumen. – Dietas de crácidos: ¿qué tánto sabemos? – Los Cracidae son una familia Neotropical de 50 especies de aves galliformes, muchas de las cuales están amenazadas. A través de una revisión de literatura, evaluamos el conocimiento actual de los hábitos alimentarios de los crácidos y establecimos algunos patrones generales. La dieta ha sido relativamente bien documentada para 17 especies, mientras que para otras 19 especies hay información anecdótica, y para 14, no hay información disponible. La fruta es la categoría de alimento más importante para los crácidos y se han documentado 672 especies de frutas de todos los tipos en sus dietas (tales como drupas, bayas y arilos). Las familias de plantas más importantes en la dieta de la mayoría de los crácidos son también las más comunes y diversas en los bosques Neotropicales. El follaje, las flores y el material animal (vertebrados e invertebrados) también son comunes en la dieta. El consumo de follaje en particular es común en la mayoría de las especies, pero la folivoría no ha sido adecuadamente estudiada en estas aves. Las especies de la subfamilia Penelopinae generalmente pasan las semillas intactas a través del tracto digestivo y son potenciales diseminadoras de semillas. Las especies de Cracinae, en cambio, tienen mollejas fuertes y se alimentan de las semillas grandes; sólo las semillas pequeñas pasan por el tracto intactas. En general los crácidos parecen tener dietas amplias y generalistas, aunque se han documentado dietas restringidas en respuesta a condiciones locales. Pocos estudios han evaluado las variaciones estacionales y entre hábitats en la disponibilidad de recursos y las respuestas de los crácidos a tales variaciones. El estudio de los patrones de uso y disponibilidad de recursos es esencial para entender los patrones de uso de hábitat, las necesidades de espacio y la dinámica poblacional de los crácidos.

Abstract. – The Cracidae are a Neotropical family of 50 species of galliform birds, many of which are threatened. Through a literature review, we evaluated current knowledge of cracid food habits and established general dietary patterns. Diet has been relatively well documented for 17 species, anecdotal information is available for 19 species, and no information is available for 14 species. Fruit is the most important food category for cracids, and 672 species in all fruit types (e.g., drupes, berries, arillate fruits) are reported. For most species, the most important plant families in their diets are also the most common and diverse families in Neotropical forests. Foliage, flowers and animal foods (invertebrate and vertebrate) are also common items in cracid diets. Consumption of foliage, in particular, is widespread but folivory has not been adequately studied in these birds. Penelopinae usually pass seeds intact through the digestive tract and are potential seed dispersers. Cracinae, in contrast, have strong gizzards and usually feed on large seeds, with only small seeds passing intact. In general, cracids seem to have broad and generalist diets, although restricted diets in response to local conditions have been reported. Few studies have evaluated seasonal and habitat variations in resource availability and cracid responses to such variation. An understanding of patterns of resource use and availability is essential for understanding habitat use, space needs and population dynamics of Cracids. *Accepted 14 October 2006*.

Key words: Cracidae, Cracinae, diet, frugivory, folivory, Penelopinae, seed dispersal.

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INTRODUCTION

The Cracidae (chachalacas, guans and curassows) are a family of 50 species of large-bodied, galliform birds with a Neotropical distribution. Most species inhabit dense tropical and subtropical forest; only a few species of chachalacas are found in open woodlands (del Hoyo 1994, Delacour & Amadon 2004). Almost all species in this family are under some degree of threat because of habitat loss and hunting (Strahl & Grajal 1991, Collar *et al.* 1992, del Hoyo 1994, Stattersfield & Capper 2000, Brooks & Strahl 2000, BirdLife International 2004). This situation has led to the development of conservation action plans for some species (e.g., Brooks & Strahl 1998, Kattan & Valderrama 2006).

One limitation for developing conservation plans for these species is the lack of detailed knowledge of their biology, particularly in basic aspects such as patterns of habitat and space use. Some species are sedentary, but others apparently perform seasonal movements (habitat shifts or regional migrations) (Chaves-Campos 2004). This knowledge is critical for designing conservation areas that can sustain viable populations.

An important factor determining movement patterns is resource use. Cracids are omnivores, feeding on fruit, foliage and insects (Delacour & Amadon 2004), but curassows have also been reported feeding on vertebrates and seeds (Érard *et al.* 1991, Yumoto 1999, Santamaría & Franco 2000, Jiménez *et al.* 2001). However, the diet of few species has been studied in detail, and it is unclear to what extent they have specialized or generalized diets. Here we present a review of studies on cracid diets. In addition to reviewing current knowledge on the food habits of this family, information provided here could be useful for guiding future studies and developing models for understanding cracid ecology.

We conducted a literature search to compile information on cracid diets. From each study we extracted information on geographic location, methods, and food items reported in the diet. Because of the heterogeneity in methods and the nature of data, we quantified diets in terms of the number of taxonomic units (number of items) reported for each cracid species. For plants (fruits, leaves and flowers), items represent species, but for insects items represent orders or families, and vertebrates include items such as "frog" or "rat".

We organized this review as a series of topics or questions. After presenting the two cracid subfamilies, we review information on the qualitative and quantitative composition of cracid diets. Next, we discuss food quality and digestive adaptations, and review our knowledge of seasonal and geographic variation in cracid diets. Then we discuss the question whether cracids are selective or have generalist diets. We finish by discussing the role of cracids as seed dispersers.

THE CRACIDAE

The family Cracidae is divided into two subfamilies, the Penelopinae and the Cracinae (del Hoyo 1994, Pereira *et al.* 2002). Penelopinae (36 species of guans and chachalacas, 42–91 cm in total length, and 385–2430 g in body mass) have arboreal habits. Cracinae (14 species of curassows) are larger (50–95 cm in total length and 1250–4800 g in body mass) and mostly terrestrial, although they may roost and nest in trees (del Hoyo 1994).

Recently, the genera *Ortalis* and *Oreophasis* were transferred to the subfamily Cracinae (Pereira *et al.* 2002). These birds, however, are ecologically more similar to the Penelopinae, and we followed del Hoyo (1994) and Delacour & Amadon (2004) in retaining them in this subfamily. Both genera are old, having diverged about 31.1 and 30.9 million years

TABLE 1. Species of cracids with information about diet, type of study in which information was obtained, country where studied, and conservation priority according to IUCN/Cracid Specialist Group.

Species	Conservation priority[1]	Type of study[2]	Country	References[3]
Ortalis				
O. vetula		Sp, Co	Unites States	7, 19, 27
O. garrula				
O. cinereiceps		Co		7
O. poliocephala		Sp	Mexico	12
O. wagleri				
O. leucogastra				
O. ruficauda	INCP	Sp	Venezuela	2, 7
O. erythroptera	VHCP	Co	Ecuador	15
O. canicollis		Sp, Co	Argentina	5, 7
O. guttata		Co		7
O. superciliaris	ICP			
O. motmot				
Penelope				
P. purpurascens	INCP	Co, Tc	Colombia, Costa Rica	26, 28
P. perspicax	ICP	Tc, Co	Colombia	22, 23, 30, 35
P. albipennis	ICP	Co	Peru	7, 36
P. ortoni	HCP			
P. marail		Sp	Guyana, Surinam	14, 37
P. jacquacu		Sp, Co	Colombia, Venezuela	3, 40
P. ochrogaster	HCP	Co	Brazil	24
P. pileata	HCP			
P. dabbenei	HCP			
P. jacucaca	HCP			
P. superciliaris		Tc, Co	Brazil	7, 21
P. obscura	INCP	Tc, Co	Argentina	6, 18, 20
P. argyrotis	INCP	Co		7
P. barbata	APC			
P. montagnii	INCP	Co	Colombia	23
Pipile				
P. pipile	INCP	Co	Trinidad	7, 16
P. cumanensis		Sp, Co	Venezuela	7, 40
P. cujubi	INCP			
P. jacutinga	VHCP	Tc, Co	Brazil	9, 25
Aburria				
Aburria aburri	HCP	Co	Colombia	32
Chamaepetes				
C. goudotii	INCP	Co	Colombia	7, 23, 29
C. unicolor	VHCP	Co	Costa Rica	7, 38
Penelopina				
P. nigra	HCP	Co	Mexico	7, 11
Oreophasis				
O. derbianus	ICP	Co, Tc	Mexico	7, 10

TABLE 1. Continued.

Species	Conservation priority[1]	Type of study[2]	Country	References[3]
Nothocrax				
N. urumutum		Co	Colombia	3
Mitu				
M. mitu	ICP	Co		7
M. tuberosa	INCP	Co	Peru	7, 13
M. salvini	INCP	Tc	Colombia	7, 33, 39
M. tomentosa		Sp	Venezuela	40
Pauxi				
P. pauxi	ICP	Co	Venezuela	4, 7
P. unicornis	VHCP	Co	Bolivia	7, 31
Crax				
C. rubra	HCP	Tc	Salvador	7, 34
C. alberti	ICP			
C. alector		Tc, Sp, Co	Colombia, Guyana, Surinam, Venezuela	1, 3, 8, 14, 17, 40
C. daubentoni	HCP			
C. fasciolata	HCP	Co		7
C. globulosa	HCP			
C. blumenbachii	ICP	Co		7

[1]ICP: Immediate conservation priority, VHCP: very high conservation priority, HCP: high conservation priority, INCP: intermediate conservation priority.

[2]Co: Casual observations in short-term studies, Sp: data obtained from specimens, Tc: methodical studies with temporal continuity.

[3]1 (Álvarez-Cordero 1997), 2 (Arriaga & Bermúdez 1997), 3 (Benett & Defler 1997), 4 (Calchi & Pérez 1997), 5 (Caziani & Protomastro 1994), 6 (Chalukian 1997), 7 (Del Hoyo 1994), 8 (Érard *et al.* 1991), 9 (Galetti *et al.* 1997), 10 (González-García 1994), 11 (González-García *et al.* 2001), 12 (Gurrola 1981), 13 (Gutiérrez 1997), 14 (Held & Werkhoven 1997), 15 (Isherwood & Willis 1999), 16 (James & Hislop 1997), 17 (Jiménez *et al.* 2001), 18 (Malzof *et al.* 2006), 19 (Marion 1976), 20 (Merler *et al.* 2001), 21 (Mikich 2002), 22 (Muñoz 2003), 23 (Nadachoswki 1994), 24 (Olmos 1998), 25 (Paccagnella *et al.* 1994), 26 (Pacheco 1994), 27 (Pence & Scott 1978), 28 (Pérez & Pinedo 2002), 29 (Renjifo 1997), 30 (Renjifo 2002), 31 (Renjifo & Renjifo 1997), 32 (Ríos *et al.* 2005), 33 Santamaría & Franco 2000), 34 (Sermeño 1997), 35 (Silva 1997), 36 (Tejada & Díaz 1997), 37 (Théry *et al.* 1992), 38 (Wheelwright *et al.* 1984), 39 (Yumoto 1999), 40 (Zent 1997).

TABLE 2. Items recorded in the diets of cracids. The table indicates the total number of items (plant species, order or class of invertebrates and vertebrates[1]) and its percent in the diet of each species.

Species	# Items	%Fruits	%Leaves	%Flowers	%Invertebrates	%Vertebrates	%Others
Penelopinae							
O. erythroptera	1	100					
O. vetula	48	63.8	19.1	6.4	4.3 (Ga)		6.4
O. cinereiceps	12	75	16,7		8,3		
O. poliocephala	21	66.7	14.3	9.5	9.5		
O. ruficauda	32	78.1			21.9 (Co, Le, Hy, Ho)		
O. canicollis	8	87.5		12.5			
O. guttata	1	100					
P. jacquacu	23	100					
P. ochrogaster	2		50	50			
P. montagnii	4	75		25			
P. perspicax	128	78.9	8.6	9.4	3.1 (Ho, Di, Co, Ho)		
P. marail	37	72.9		24.4			2.7
P. argyrotis	1	100					
P. superciliaris	54	94.4		5.6			
P. albipennis	30	66.6	16.7	16.7			
P. obscura	48	77.1	16.7	6.3			
P. purpurascens	52	76		21	3		
A. aburri	8	87.5	12.5				
P. cumanensis	22	100					
P. jacutinga	46	100					
P. pipile	15	86.6	6.7		6.7		
C. unicolor	34	97.1	2.9				
C. goudotii	11	72.7	9.1	9.1			9.1
P. nigra	20	95				5 (Mo)	
Cracinae							
O. derbianus	42	83.3	14.3		2.4		

TABLE 2. Continued.

Species	# Items	%Fruits	%Leaves	%Flowers	%Invertebrates	%vertebrates	%Others
N. urumutum	1	100					
M. salvini	86	84.9	4,6		1.2	2.3	7.0
M. tomentosa	12	100					
M. tuberosa	27	52	8		12 (Le, Or, Co)	12 (Fro, Gym)	16
M. mitu	2	100					
P. pauxi	2	50					50
P. unicornis	4	25			50 (Di, Col)	25	
C. alector	306	70.6	1.9	2.9	5.8 (Od, Or, Ph, Ma, Is, Ho, He, Di, Co, Le, Hy, Ur, Ar, Am, Op, De)	1.6 (Fro, Li, Mo, Se, Ar)	17.2
C. rubra	20	70	20		5.0	5.0	
C. fasciolata	1			100			
C. blumenbachii	13	76.9	7.7		15.4		

[1]Am: Amblypygi, Ar: Araneae, Co: Coleoptera, De: Decapoda, Di: Diptera, Ga: Gastropoda, He: Hemiptera, Ho: Homoptera, Hy: Hymenoptera, Is: Isoptera, Le: Lepidoptera, Ma: Mantodea, Od: Odonata, Or: Orthoptera, Ph: Phasmida, Ur: Uropygi, Op: Opiliones, Ar: Armadillo, Gym: Gymnophiona, Li: Lizard, Fro: Frog, Mo: Mouse, Se: Snake.

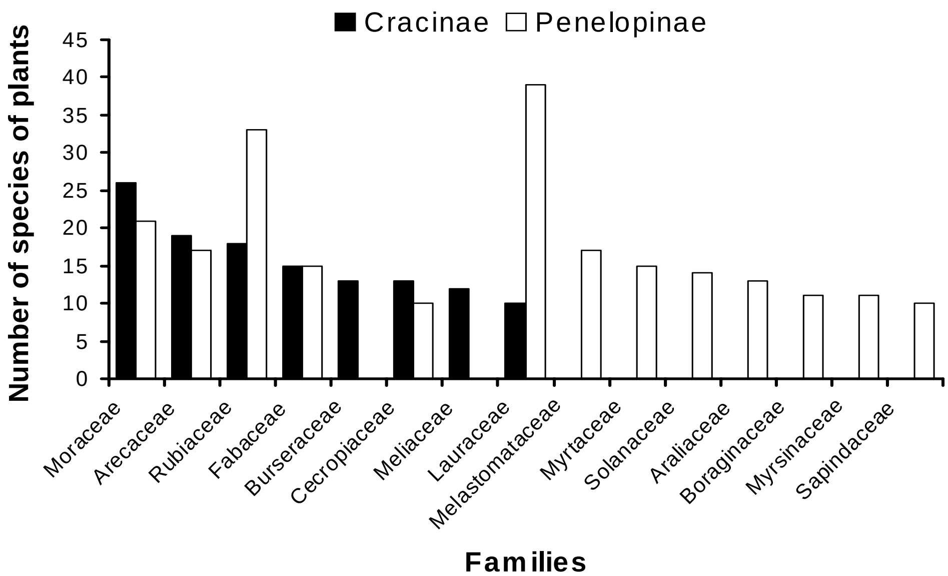

FIG. 1. Number of plant species most consumed per family by the two subfamilies of cracids.

ago, respectively (Pereira *et al.* 2002). Likewise, the current Penelopinae genera are the oldest in the family, having diverged on average 18–19 million year ago, whereas Cracinae are more recent, appearing 6–12 millions year ago (Pereira *et al.* 2002).

WHAT DO CRACIDS EAT?

Information on food habits of cracids has been published for 36 of the 50 species. Most of the information consists of lists of items eaten by cracids and comes from anecdotal studies (19 species) or from examination of stomach contents (8 species). Only 9 species have been studied methodically and with some temporal continuity: *Penelope perspicax* was studied for over 2 years (Muñoz 2003, Kattan *et al.* in press, Muñoz *et al.* in prep.), *P. obscura* for 4 months (Merler *et al.* 2001) and 1 year (Malzof *et al.* in press), *P. superciliaris* for 8 years (Mikich 2002), *P. purpurascens* for 1 year (Pacheco 1994), *Pipile jacutinga* for 2 years (Galetti *et al.* 1997), *Oreophasis derbianus* for 8 months (González-García 1994), *Mitu salvini* for 14 months (Santamaría & Franco 2000), *Crax alector* for 10 months (Jiménez *et al.* 2001) and *C. rubra* for 16 months (Sermeño 1997). Information is lacking for the other 14 species, 10 of which are under some threat category (Table 1).

The mean number of food items reported in the diet is 32 for 36 species of cracids (Table 2). The mean number of items for Penelopinae is 27.2, varying between 1 (*Ortalis erythroptera* and *Penelope argyrotis*) and 128 (*P. perspicax*). For Cracinae, the mean is 43 and the range is 1 (*Nothocrax urumutum* and *C. fasciolata*) to 306 (*C. alector*). Fruit is an important component in the diet of all species, ranging from 50 to 100% of recorded items (ignoring species with less than 20 records; Table 2). A total of 672 species of fruits have been reported in cracid diets. All fruit types are represented. Drupes are the most common fruit type (41% of species), followed by berries

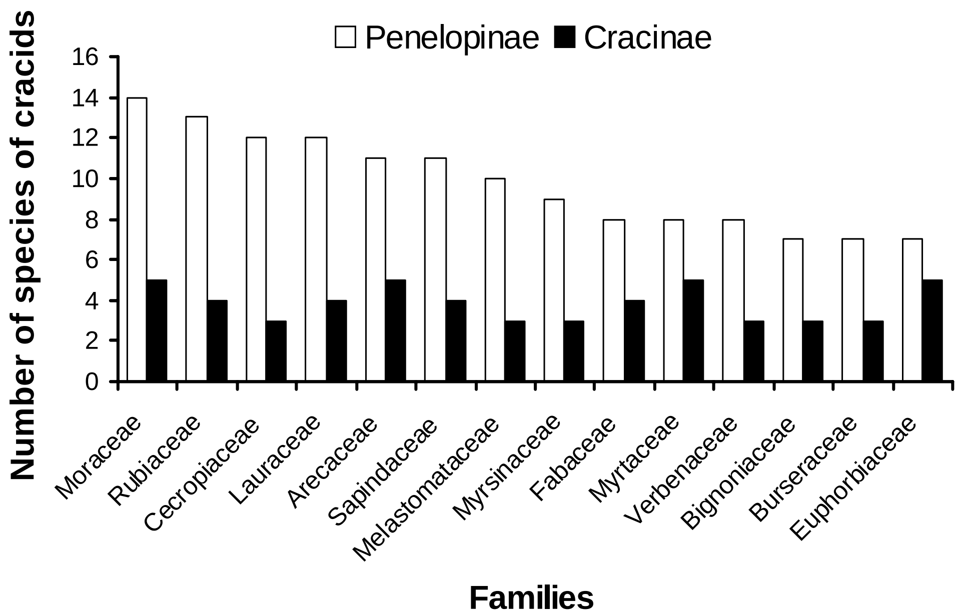

FIG. 2. Number of species of cracids reported eating different plant families.

(19%), capsules (11%), arillated seeds (4%), legumes (4%), syconia (*Ficus* spp.; 4%) and multiple fruits (3%). Other fruit categories (e.g., nut, sorosis, samara) add to 14%.

The six most important plant families in cracid diets are Moraceae, Arecaceae, Rubiaceae, Fabaceae, Cecropiaceae and Lauraceae (Fig. 1), but a total of 113 families are reported. Diets of Penelopinae are broader, including more plant families than Cracinae (Fig. 1) and conversely, more species of Penelopinae are reported feeding on each plant family (Fig. 2).

Foliage and flowers usually represent less than 20% of items, but may be over 30% (*Penelope albipennis*). In the two best studied species, *P. perspicax* and *C. alector*, these two food categories represent 18% and 4.8%, respectively. In general, foliage and flowers seem to represent a more important food source for Penelopinae than for Cracinae. In contrast, seeds are more important in the diet of Cracinae (Érard *et al.* 1991, Jiménez *et al.* 2001; see seed dispersal below).

Feeding on invertebrates has been reported for 14 species and may represent over 20% of items. Feeding on vertebrates (frogs, rats) has only been reported for 5 species of Cracinae and for *Penelopina nigra*. Most studies suggest that cracids feed on animals opportunistically and occasionally, but it may be more important than previously thought (e.g., *P. perspicax*; Rios *et al.* 2006).

Few studies present quantitative data on cracid diets. Fruit may represent over 90% of the bulk of the diet of *Penelope marail* in French Guiana (Érard & Théry 1994). A study based on stomach contents of *C. alector* in French Guiana (69 birds hunted between 1977 and 1981) showed that fruit represented 84% of dry matter and that insects, leaves and flowers represented less than 1% each (Érard *et al.* 1991). Another study in eastern Colombia followed three individuals of *C. alector* for

7 months, determining the number of items eaten per day (Jiménez *et al.* 2001). Overall, fruit represented almost 50% of items ingested per day, leaves about 15%, and invertebrates a little over 10% for the three curassows; these animals also fed on seeds and seedlings (Jiménez *et al.* 2001).

The diet of *O. vetula* has been determined in Texas on the basis of 42 stomach contents (Marion 1976). Invertebrates were a small proportion of the diet (3.0% of diet by volume) and included hemipterans (less than 0.1%), insect larvae (1.4%) and gastropods (1.6%). This species ate large quantities of seeds (three species). The most consumed seed species accounted for 10.1% of the diet by volume, and the others 0.2% and 0.1%. Leaves represented 6.5% (five species), but one species represented most of this consumption (3.8%). Stamens and fruit were the parts with the highest volume (19.2% and 57.3%, respectively) in the diet of this chachalaca. On the other hand, another study on the same species suggested that it is herbivorous and frugivorous because arthropods were not found in 19 chachalacas collected in one month (Pence & Scott 1978).

FOOD QUALITY AND DIGESTIVE ADAPTATIONS

The variety of food types eaten by cracids suggests that these birds are behaviorally plastic and have digestive tracts adapted to a generalist diet. Cracinae have well developed gizzards capable of crushing seeds, which is helped by ingesting grit (Moermond & Denslow 1985, Érard *et al.* 1991), while Penelopinae do not have this capacity. Otherwise, no special morphological or physiological digestive adaptations have been reported for cracids.

Cracids eat a very wide variety of fruit types, ranging from large drupes (Lauraceae and Arecaceae) to small berries (Melastomataceae and Solanaceae). Eating such a diversity of fruits provides energy in the form of carbohydrates, lipids and proteins (e.g., Muñoz 2003). Drupes and arillate fruits tend to be rich in lipids, and berries tend to be rich in carbohydrates (Moermond & Denslow 1985), but great variation exists even within genera. For example, among fruits eaten by the Cauca Guan, Muñoz (2003) found that *Miconia acuminifera* (Melastomataceae) had a much higher lipid content than *Aniba muca* (Lauraceae).

Feeding on foliage is reported for most species, but its importance in cracid diets has not been rigorously quantified. Comparing foods as different as fruits, foliage and insects in terms of their contribution to the energy and nutrient budget is difficult. Studies on foraging ecology usually quantify foods in terms of feeding bouts or food volume, but these do not reflect the energetic contribution of the different items. On the other hand, some foodstuffs may provide essential nutrients, even if consumed in small quantities.

Foliage is a low-quality food compared to fruits or insects. In the absence of special adaptations such as gut fermentation, as occurs in the Hoatzin (*Opisthocomus hoatzin*) (Grajal *et al.* 1989), folivorous birds such as geese (Anseriformes) compensate by processing large quantities of foliage and passing it rapidly through the digestive tract (Buchsbaum *et al.* 1986). With the exception of *P. perspicax*, which seasonally feeds on large quantities of foliage when fruit is scarce (Muñoz 2003), cracids reportedly eat leaves in small quantities and mixed with other foodstuffs. Preliminary data indicate that with a highly folivorous diet, guans loose weight (Muñoz unpubl.). It is unlikely, therefore, that guans derive an important proportion of their energy budget from foliage. Plant foods are more nutritionally diverse than animal foods (Klasing 1998), so cracids may be obtaining important nutrients from foliage. Folivory in cracids is an open research line, with important ecological and physiological implications.

Animal foods (insects and vertebrates), on the other hand, although making up a small proportion of cracid diets in terms of volume or feeding bouts (Marion 1976, Jiménez *et al.* 2001), may provide an important portion of their energy and nutrient budget. Lepidopteran larvae, for example, provide 49.4–58.1% protein and 10–20.7% lipids on a dry weight basis (Landry *et al.* 1986) and are important sources of calcium and phosphorus (Robel *et al.* 1995).

Assessing diet quality requires not only determining nutrient content of foodstuffs, but also the capacity of animals to digest the food and assimilate nutrients. In addition, changes in diet may induce morphological and physiological changes in bird digestive tracts (e.g., Martínez del Río *et al.* 1995), so studies on diet quality must take into account these considerations. These aspects have not been investigated in cracids.

VARIATIONS IN CRACID FOOD HABITS

Little information is available on temporal and spatial variation in cracid diets. In subtropical and temperate zones, food availability changes drastically between summer and winter. Thus, in Texas the diet of *O. vetula* was dominated by berries and seeds during spring and fall, and leaves and buds during winter and summer. Lowland forests in the Neotropics may also show marked seasonality in fruit availability (Frankie *et al.* 1974, Van Schaik *et al.* 1993), even causing animal mortality (Foster 1982). In contrast, fruit availability in montane forest varies seasonally, but apparently there is no season of absolute scarcity (Giraldo 1990, Ataroff 2001, Cavelier *et al.* 2001, Muñoz 2003).

Fruit-eating animals may show varied responses to periods of fruit scarcity, including habitat and diet shifts, resorting to low-quality foods, or performing local to regional (elevational) migrations (Fleming *et al.* 1987, Van Schaik *et al.* 1993, Sun *et al.* 1997, Sun & Moermond 1997, Stiles 1988, Jiménez *et al.* 2001). For instance, in Costa Rica, some individuals of *P. purpurascens* remained in the same place throughout the year, but part of the population migrated altitudinally in response to fruit abundance (Chaves-Campos 2004). A population of Cauca Guans in the central Andes of Colombia showed a diet shift, resorting to folivory in response to a decrease in fruit availability (Kattan *et al.* in press, Muñoz *et al.* in prep.). *M. salvini* also performed habitat shifts in response to changing resource availability in lowland forest (Parra *et al.* 2001).

In contrast, studies on *C. alector* in French Guiana (Érard *et al.* 1991) and eastern Colombia (Jiménez *et al.* 2001) have shown little variation in diet composition among seasons, except for an increase in the consumption of seeds and seedlings during the rainy season in the Colombian study.

SELECTIVE FEEDERS?

Some authors have suggested that cracids are selective frugivores. For example, Théry *et al.* (1992) found that *P. marail* in French Guiana fed mostly on drupes, and preferred four out of 23 fruit species recorded in the diet. In southern Brazil, *P. superciliaris* was found to feed heavily on one species of palm (*Euterpe edulis*) for a period of several months (Mikich 2002).

Other studies, however, have found that cracids are opportunistic generalists. For example, *P. perspicax* was observed eating 89 species of fruit (80.2% of items) in 1 year, and species were eaten in proportion to their availability (Muñoz *et al.* in prep.). This species also fed on foliage (9.9%), flowers (9.9%), and insects (fragments found in 111 fecal samples of 391 samples collected) during a 1-

year study (Muñoz *et al.* in prep.). This species was also observed following army ants and feeding on flushed insects (24 observations in eight months; Rios *et al.* 2006), and eating filamentous algae on boulders in the river (W. Cardona, pers. com.).

Another line of evidence suggesting that cracids are generalists is that the most common plant families in cracid diets (Fig. 1) correspond to the most common and diverse plant families in Neotropical forests. Most Penelopinae inhabit montane forest, and the most common plant families in their diets (Lauraceae, Rubiaceae, Moraceae, Melastomataceae and Arecaceae) are also the most diverse in mid- and high-elevation (1500–2900 m) Andean forest (Gentry 2001). Cracinae, in contrast, are mostly lowland forest species. The most common families in Cracinae diets (Moraceae, Arecaceae, Rubiaceae, Leguminosae and Meliaceae) are also the most common among 90 plant families in Neotropical lowland forest (Gentry 2001).

The available data, thus, suggest that cracids have broad diets, feeding on a variety of plant and animal foods (and other minor food categories) that are probably obtained opportunistically. Extrapolating from general patterns at the family level to particular species should be made with caution, however, as even congeneric species may diverge in their food habits. Species may exhibit restricted diets in response to local conditions (Mikich 2002). Diets may also change seasonally, and short-term studies do not reflect the amplitude of conditions to which cracids are exposed (see seasonal variation above).

CRACIDS AS SEED DISPERSERS

The role of fruit-eating animals as seed dispersers partially depends on the fate of seeds passing through the digestive tract. Penelopinae usually pass seeds intact through their digestive tracts and may act as seed dispersers (Galetti *et al.* 1997, Merler *et al.* 2001, Mikich 2002, Muñoz 2003). For example, seeds maintain their germination capacities after passing through the digestive tract of *P. marail* and *P. perspicax*, and birds disperse them away from parent trees, depositing them at the edges of treefall gaps and other situations conducive to forest regeneration (Érard & Théry 1994, Théry *et al.* 1992, M. Muñoz, unpubl.).

Some Penelopinae, however, may digest seeds. Stomachs of *O. vetula* contained seeds of *Ulmus crassifolia*, *Acacia farnesiana* and *Serjania brachycarpa* (Marion 1976). These species produce dry fruits, so chachalacas likely digested the seeds. Another Penelopinae species, *P. albipennis*, fed on *Bombax* sp. seeds, which also produces dry fruits.

For Cracinae, in contrast, seed consumption is a routine part of their diets, but they may act as dispersers of small seeds (Yumoto 1999, Santamaría & Franco 2000, Jiménez *et al.* 2001). For example, *M. salvini* feeds on big seeds and is a disperser of small seeds (< 5.5 mm length), as only small seeds are excreted intact. Érard *et al.* (1991) showed that *C. alector* crushes seeds in its gizzard, which contains large amounts of grit.

The potential of cracids as seed dispersers is important from a conservation perspective (the role they play in the ecosystem; Strahl & Grajal 1991). The effectiveness of a frugivore as a seed disperser depends on two parameters, the number of seeds dispersed and the quality of dispersion (Schupp 1993). Each parameter, in turn, has several components, including number of visits to the plant, number of seeds removed per visit, seed manipulation and movement patterns of frugivores. Cracids, particularly Penelopinae, have the capacity to move enormous numbers of seeds and to deposit them in varied situations, but the exact role that they play as dispersers in comparison with other frugivores remains to be determined. Currently, there is only one study evaluating dispersion by *M. salvini* (Yumoto 1999). This species is a seed predator, but it is the most important disperser of *Geophila rupens*. Out of 11 species of plants consumed by this curassow, two species of plant (*G. rupens* and *Ficus sphenophylla*) were dispersed.

CONCLUSIONS

This review revealed that few rigorous quantitative studies on cracid diets are available. The bulk of cracid diets is made up by fruits, but they opportunistically feed on a variety of plant and animal foods. However, it is unknown to what extent the different components of the diet are providing energy or essential nutrients. More importantly from a conservation perspective, little is known about seasonal and geographic variation in resource use. In particular, the role of foliage as a complementary or seasonal resource in cracid diets needs to be elucidated.

Patterns of resource use may have important consequences for population dynamics and habitat requirements. Under certain circumstances, cracid diets may be specialized or restricted, but it is unknown whether this is a local or seasonal response to food availability. A varied diet may be important for the general health and vigour of the animals. Isolated populations may survive on a few food sources (e.g., Merler *et al.* 2001), but are not necessarily healthy. Understanding all these features of cracid biology is essential for developing conservation plans that take into account habitat and resource needs of threatened populations.

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