

# Trophic Structure and Food–Niche Relationships of Nearctic and Neotropical Raptors: an Inferential Approach

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## Abstract

We defined two trophic axes (body weights and diets) to determine and contrast the frequency distributions of these variables in five Neotropical and two Nearctic raptor assemblages, paying special attention to where in those trophic axes migrants and residents were located. Our results do not support explanations based on size-mediated niche segregation or on dietary specialization as a means to secure exclusive resources. Tracking of superabundant prey seems a plausible working hypothesis to orient further research.

## Introduction

Nonpasserine birds have been largely neglected by students of migration of Nearctic birds into the Neotropics (Rappole *et al.* 1983). This neglect is even more evident among migrating raptors, despite the fact that these birds seem ideal model organisms on several counts:

- (a) They are large, diurnal, conspicuous birds that often form sizeable flocks, making possible detailed study of their migration routes (Smith 1985).
- (b) They are often interspecifically territorial, and their agonistic interactions are usually fully visible to interested observers (Jaksić 1985). They thus may help elucidate the potential role of interference interactions among Neotropical assemblages that receive migrants from Nearctica (Keast and Morton 1980).
- (c) Being at the top of food chains, they readily accumulate high doses of chlorinated pesticides still widely used in most of Neotropica (Ellis 1985). They are valuable bioindicators: monitoring of pesticide levels in migrating raptors should provide early warning of the potential danger of such poisoning for other birds.

- (d) Because foods eaten by raptors can often be identified to comparatively detailed levels of taxonomic resolution (Greene and Jaksić 1983), these birds make interesting subjects for the study of food-niche relationships between Nearctic migrants and Neotropical residents.

Here we will address only the latter aspect of the biology of migratory raptors. By presenting an exploratory and inferential analysis of the few data available, we hope to interest other ornithologists in pursuing more rigorous studies of such interesting birds.

### Objectives

Our aims are: (a) to define two trophic axes—diets and body weights of raptors—and determine the frequency distributions of these variables in different localities of South and North America; (b) to contrast these frequency distributions both within and between Neotropical and Nearctic areas; and (c) to scrutinize where migrants and residents are located in the two trophic axes. Our general question is, how do migrant raptors fit trophically into both Nearctic and Neotropical assemblages?

### Methods

Our criteria of selection of Neotropical raptor assemblages were, in order of priority: (a) localities for which the food habits and body weights of the whole set of raptors had been reported in primary literature sources; we detected three such localities: Surinam, central Chile, and Tierra del Fuego; and (b) physiologically similar localities for which the whole set of raptors had been documented in primary literature sources, whose raptors' body weights and food habits could be reasonably extrapolated from a nearby locality in the previous category; we included two such localities: the Colombian Orinoco Basin, and Argentina's Córdoba Province.

In Nearctica, we chose localities with an additional criterion: those with raptor assemblages that included populations of species known to be Nearctic migrants. We obtained adequate data from only two Nearctic locations: neighboring Michigan and Wisconsin, and Florida. The code numbers for all raptor species considered in our analysis are listed in Appendix 1. Selected literature sources used in the compilation of local species lists, weights, and diets are documented in Appendix 2.

When no distributional, weight, or diet data were available in primary sources, we relied on Brown and Amadon (1968) and on information contained on field tags of specimens preserved in the Centro Regional de Investigaciones Científicas y Tecnológicas (CRICYT), Mendoza; the Museo Nacional de Historia Natural (MNHN), Santiago; the Museum of Vertebrate Zoology (MVZ), Berkeley, Calif.; and the U.S. National Museum of Natural History (USNMNH), Washington, D.C.

The two trophic axes were categorized as follows:

- (a) For the profile of body weights: in decimal logarithmic intervals of 0.2 log units between 1.8 and  $>4.0$ . Species were placed on this axis after computing

mean body weights for males and females separately, transforming them into logarithms, and averaging male and female figures.

- (b) For the profile of diets: using the highest possible level of taxonomic resolution, we compiled the diet of each raptor species in each locality. We defined raptor diets as follows: large mammals and birds (M/Bd); small mammals (Smam); small birds (Sbrd); lizards (Lzrd); snakes (Snke); anurans (Anur); fishes (Fish); molluscs (Moll); crustaceans (Crus); insects and arachnids (In/A); omnivorous diet with frequent aquatic prey (O/aq); omnivorous diet of mainly terrestrial prey (O/te); omnivorous diet with frequent fruit items (O/fr); carrion (Carr).

## Results

In Neotropica, there was a marked north-south decrease in the number of raptor species (from 50 to 14) in the sequence Orinoco Basin, Surinam, Córdoba, central Chile, and Tierra del Fuego (Table 1). The Nearctic migrants that arrived in each of these five localities never exceeded three species; however, owing to the north-south decrease in resident species richness, they contributed a small 6-7% in the Orinoco Basin and Surinam and a substantial 12-13% in Córdoba and central Chile. No Nearctic migrant reached Tierra del Fuego.

In the two Nearctic localities examined, the species richness was the same (16 species) and comparable to that in southern Neotropica, but "potential migrants" contributed a higher proportion of the raptor avifauna (31% in Michigan and Wisconsin, 19% in Florida) (Table 1). The lower figure in Florida is due to the fact that both *Buteo swainsoni* and *Pandion haliaetus* winter there.

The frequency distributions of body weights in all seven localities appeared bell-shaped owing to the logarithmic transformation applied to the data (Table 2). Nearctic migrants fell within weight categories between 2.0 and 3.4. The smallest migrant recorded was *Accipiter striatus*, the largest, *P. haliaetus*. "Potential migrants" from the northern United States fell within weight categories between 2.2 and 3.2, i.e., between the sizes of *Falco columbarius* and *P. haliaetus*. Those from Florida fell within a single category, 2.6-2.8, which included *Elanoides forficatus*, *Ictinea misisippiensis*, and *Buteo platypterus*.

In terms of diet, most Nearctic migrants in Neotropica appeared to be specialized (Table 3). They were bird eaters (*Accipiter striatus*, *Falco columbarius*, *F. peregrinus*), fish eaters (*Pandion haliaetus*), or arthropod eaters (*Elanoides forficatus*, *Ictinea misisippiensis*, and *B. swainsoni*). Only *B. platypterus* appeared to behave as a generalist that ate all sorts of terrestrial prey in Surinam, despite the fact that in the northern United States it was a mammal eater. Also, *B. swainsoni* ate primarily mammals in Michigan and Wisconsin, expanded its diet in Florida to include arthropods, and ate only the latter prey in Córdoba.

## Discussion

Nearctic migrants are capable of invading both species-rich (Orinoco Basin, Surinam) and species-poor (Córdoba, central Chile) raptor assemblages in the

Table 1. Nearctic migrant raptors.

Nearctic migrant raptors	Ori	Sur	Cor	CCh	TDF	M-W	Fla
07 <i>Pandion haliaetus</i>	-	N	N	N	-	[N]	R
10 <i>Elanoides forficatus</i>	R	R	-	-	-	-	[N]
18 <i>Ictinia mississippiensis</i>	-	-	N	-	-	-	[N]
25 <i>Accipiter striatus</i>	N*	-	R	-	-	R	-
46 <i>Buteo platypterus</i>	N	-	-	-	-	[N]	[N]
47 <i>Buteo swainsoni</i>	-	-	N	-	-	[N]	R
76 <i>Falco columbarius</i>	N	-	-	-	-	[N]	-
81 <i>Falco peregrinus</i>	-	N <sup>a</sup>	R <sup>b</sup>	N <sup>c</sup>	R <sup>b</sup>	[N] <sup>a</sup>	-
Total no. of species	50	40	25	16	14	16	16
No. of Nearctic migrants	3	2	3	2	0	5	3
% Nearctic migrants	6	5	12	13	0	31	19

Note: Localities are: Ori = Orinoco Basin; Sur = Surinam; Cor = Córdoba; CCh = central Chile; TDF = Tierra del Fuego; M-W = Michigan and Wisconsin; Fla = Florida. R = Nearctic or Neotropical resident; - = absent; N = Nearctic migrant; N\* = both Nearctic migrants and Neotropical residents coexist; [N] = "potential Nearctic migrant."

<sup>a</sup>*F. p. anatum*.

<sup>b</sup>*F. p. cassini*.

<sup>c</sup>Both *F. p. tundrius* and *F. p. cassini*.

Neotropics. Apparently, trophically complex tropical assemblages are no less susceptible to invasion than simpler temperate raptor assemblages. That Tierra del Fuego, with a species richness comparable to that of central Chile, does not receive Nearctic migrants may speak to the influence of increasing distance with decreasing land area from the Nearctic source of species.

Nearctic migrants fall into weight categories seemingly unrelated to weight distributions of resident raptors: no migrant fits neatly into size gaps nor into size categories with low species representation of Neotropical residents. Actually, it is often the case that migrants have sizes similar to those of residents. These observations speak against the role of body size *per se* as an attribute that aids in niche segregation (a common assumption in ecomorphological studies). Also, if body size is correlated with aggressive dominance, these observations downplay the potential role of interference competition between migrants and residents.

If any pattern exists, it appears that Nearctic migrants tend to be relatively specialized in diet. However, most Nearctic diet specialists seem to leave their breeding ranges only to encounter Neotropical residents similarly specialized. Both *Accipiter striatus* and *Falco columbarius* have to deal with seven bird-eating resident raptors in Orinoco Basin, five of which are larger than themselves. On the contrary, *F. peregrinus* is larger than its only potential bird-eating













competitor in Surinam and larger than two sympatric bird eaters in central Chile. Both *Buteo swainsoni* and *Ictinea mississippiensis*, which in Córdoba apparently monopolize the arthropod-eater diet category, actually have to cope with eight sympatric resident raptors (listed as terrestrial omnivores) that eat arthropods too. The only species that fits neatly into an otherwise empty diet category is *P. haliaetus*, which in Surinam, Córdoba, and central Chile is the only fish eater. Consequently, reduced competition for food cannot easily be invoked as an explanation for the migratory mode of Nearctic raptors. It is interesting, however, that in Argentina *B. swainsoni* follows locust swarms (Liebermann 1935), and that *F. peregrinus* preys heavily on the young of resident birds (McNutt 1981), thus pointing to the importance of temporary superabundant prey resources in wintering grounds. Perhaps migrants track these resources, breeding in Nearctica and wintering in Neotropica according to predictably alternate peaks in prey supply.

Conspicuously missing in this paper is the consideration of habitat segregation: perhaps Nearctic migrants indeed fit into habitat categories that are not occupied by Neotropical residents. However, our field experience in the temperate—and structurally simple—ecosystems of central Chile, Córdoba, and Tierra del Fuego does not lend support to this alternative. We do not know what the situation may be in the tropical Neotropics (e.g., Orinoco Basin, Surinam).

As a final comment, we should like to stress the importance of conducting detailed studies of wintering Nearctic migrant raptors in the temperate Neotropics rather than in the more complex tropical areas. For example, the structurally simple pampas of Argentina do not seem to provide much potential for habitat partitioning, thus allowing easy observation of other ecological interactions among sympatric raptors.

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**Appendix 1.** Code numbers for raptor species in the seven localities analyzed (after Brown and Amadon 1968 in both taxonomy and sequence).

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CATHARTIDAE: 01 *Cathartes aura*, 02 *C. burrovianus*, 03 *Coragyps atratus*, 04 *Sarcorhamphus papa*, 06 *Vultur gryphus*. PANDIONIDAE: 07 *Pandion haliaetus*. ACCIPITRIDAE: 08 *Leptodon cayanensis*, 09 *Chondrohierax uncinatus*, 10 *Elanoides forficatus*, 11 *Gampsonyx swainsonii*, 12 *Elanus leucurus*, 13 *Rostrhamus sociabilis*, 14 *R. hamatus*, 15 *Harpagus bidentatus*, 16 *H. diodon*, 17 *Ictinia plumbea*, 18 *I. mississippiensis*, 19 *Haliaetus leucocephalus*, 20 *Geranospiza caerulescens*, 21 *Circus cyaneus*, 22 *C. cinereus*, 23 *C. buffoni*, 24 *Accipiter gentilis*, 25 *A. striatus*, 26 *A. collaris*, 27 *A. superciliosus*, 28 *A. cooperii*, 29 *A. bicolor*, 30 *A. poliogaster*, 31 *Leucopternis schistacea*, 32 *L. melanops*, 33 *L. albicollis*, 34 *Buteogallus anthracinus*, 35 *B. aequinoctialis*, 36 *B. urubitinga*, 37 *Harpyhaliaetus coronatus*, 38 *Heterospizias meridionalis*, 39 *Busarellus nigricollis*, 40 *Geranoaetus melanoleucus*, 41 *Parabuteo unicinctus*, 42 *Buteo nitidus*, 43 *B. magnirostris*, 44 *B. leucorrhous*, 45 *B. lineatus*, 46 *B. platypterus*, 47 *B. swainsoni*, 48 *B. albicaudatus*, 49 *B. polyosoma*, 50 *B. albonotatus*, 51 *B. ventralis*, 52 *B. jamaicensis*, 53 *B. lagopus*, 54 *B. brachyurus*, 55 *Morphnus guianensis*, 56 *Harpia harpyja*, 58 *Spizastur melanoleucus*, 59 *Spizaetus tyrannus*, 60 *S. ornatus*, 61 *Oroaetus isidori*. FALCONIDAE: 62 *Daptrius ater*, 63 *D. americanus*, 64 *Phalcoboenus megalopterus*, 65 *P. albogularis*, 66 *P. australis*, 67 *Polyborus plancus*, 68 *Milvago chimango*, 69 *M. chimachima*, 70 *Herpetotheres cachinnans*, 71 *Micrastur ruficollis*, 72 *M. mirandollei*, 73 *M. semitorquatus*, 74 *Spizapteryx circumcinctus*, 75 *Falco sparverius*, 76 *F. columbarius*, 77 *F. rufigularis*, 78 *F. femoralis*, 79 *F. mexicanus*, 80 *F. deiroleucus*, 81 *F. peregrinus*.

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**Appendix 2.** Sources for raptor lists, weights, and diets. When no information was available from primary sources, we relied on Brown and Amadon (1968).

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ORINOCO BASIN: List, Olivares (1982); weights and diets, Haverschmidt (1948, 1952, 1962), Voous (1969), MNHN, MVZ. SURINAM: List, synthesized from Haverschmidt (1948, 1952, 1962), Voous (1969); weights and diets, Haverschmidt (1948, 1952, 1962), Voous (1969). CORDOBA: List, Nores *et al.* (1983); weights and diets, Greer and Bullock (1966), Contino (1972), Jaksić *et al.* (1981), Jiménez (unpublished data), Schlatter (unpublished data), CRICYT, MNHN, MVZ, USNMNH. CENTRAL CHILE: List, Schlatter (1979); weights and diets, Greer and Bullock (1966), Jaksić *et al.* (1981), Jaksić (unpublished data), Jiménez (unpublished data), Schlatter (unpublished data), CRICYT, MNHN, MVZ, USNMNH. TIERRA DEL FUEGO: List, Humphrey *et al.* (1970); weights and diets, Humphrey *et al.* (1970), McNutt (1981), Jiménez (unpublished data), Schlatter (unpublished data), MVZ. MICHIGAN AND WISCONSIN: List, Errington (1933), Van Tyne (1938), Craighead and Craighead (1956); weights and diets, Errington (1933), Craighead and Craighead (1956), MVZ, USNMNH. FLORIDA: List, synthesized from Brown and Amadon (1968), Rappole *et al.* (1983); weights and diets, Toland (1986), MVZ.

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