DYNAMICS OF GUILD STRUCTURE AMONG AVIAN PREDATORS: COMPETITION OR OPPORTUNISM?

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ABSTRACT. Does guild structure of predatory birds at top trophic levels reflect competition, with or without the addition of migrants? We examined the dynamics of guild composition of predatory birds (raptors) in three seasonal environments: Auco, Chile (no migrants), Donana, Spain (some migrants), and Washtenaw County, Michigan, USA (many migrants). Guild structure remained surprisingly stable from non-breeding to breeding seasons in both Chile and Spain, despite seasonality in prey abundance at both sites, and the arrival of three migrants in Spain. Guild structure in Michigan shifted seasonally, reflecting increased prey diversity in the breeding season. Nevertheless, there was no obvious displacement of residents' diets by migrants, which either joined existing guilds or specialized on seasonally abundant prey. Overall, raptor diets appeared to reflect species-specific preferences intersecting with basic prey availability, resulting in a guild structure not obviously affected by competition.

Keywords: Guilds, competition, opportunism, Falconiformes, Strigiformes, residents, migrants, Chile, Spain, United States.

INTRODUCTION

Assemblages of avian consumers need not always reflect competitive processes. Competition that is intense only during occasional "ecological crunches" in resource levels may be insufficient to impose recognizable pattern (Wiens 1977), although seasonal fluctuations could still induce predictable shifts in niche relationships among consumers (Schoener 1982). The relationship between fluctuating resource levels and niche relationships becomes more complex when communities are composed of both migrant and resident populations. Do niche relationships of resident consumer populations change in connection with seasonal influxes of migrants? Or, are migrants superimposed, in resource-rich seasons, on residents that maintain more or less consistent relationships among themselves? Predatory birds in the orders Falconiformes and Strigiformes (diurnal and nocturnal raptors) constitute ideal model assemblages for examining these questions. Raptors are often assumed to be limited by their prey resources, and their food habits can be examined at very detailed levels of resolution. Furthermore, assemblages exist both with and without migratory members.

Some previous studies on the trophic guild structure of raptors have disputed the role of interspecific competition in shaping these predatory assemblages, proposing that they are simply groupings of species that opportunistically exploit superabundant prey (e.g. Jaksic & Braker 1983). These studies, though, are weakened by relying on static pictures of average conditions of prey levels and on niche descriptors that pool data from different regions over extended time spans.

Here, we examine whether three raptor assemblages that exist in seasonal environments exhibit seasonal shifts in guild structure in the absence (Chile) or presence (Spain, United States) of migrant populations. We evaluate evidence for patterns reflecting competition versus opportunism. Finally, we discuss the role of biogeographical idiosyncrasies in the dynamics of raptor assemblages.

MATERIALS AND METHODS

Chile

Our study site is the Reserva Nacional Las Chinchillas, at Auco (31°30'S; 71°06'W), 300 km north of Santiago. The area is semi-desert, with thorn scrub vegetation (Jimenez & Jaksic 1989). Common species of raptors at the study site are listed in the Appendix.

We sampled regurgitated pellets at known roosts, nests, and perches monthly throughout 1988 and part of 1989. In the laboratory, pellets were dissected and their contents identified to species (vertebrate prey) or family level (invertebrates). Information from pellet collections was pooled into two biological seasons: non-breeding (from 1 March to 31 August) and breeding (from 1 September to 28 February). Mammalian prey densities were somewhat higher during the non-breeding season, but avian and reptilian prey were the reverse (Jaksic, Jimenez & Feinsinger, unpublished data).

Spain and Michigan

In two other sites, food habits of local raptors had previously been sorted by season: Reserva Biologica de Donana, Huelva Province, Spain (Kufner 1986), and Superior Township, Washtenaw County, Michigan, USA (Craighead & Craighead 1956). In Spain, shifts in prey density from breeding to non-breeding season apparently resembled those in Chile. Craighead & Craighead (1956) provided crude estimates for mammalian and avian prey abundance.

Assessment of trophic guild structure

Predator diets from the three study sites were analyzed quantitatively using three metrics: (1) Diet breadth (= diet diversity) was computed as $B = 1/\Sigma(p_i^2)$, where p_i is the relative occurrence of prey category i in a given predator's diet. This index reflects population-wide use of resources regardless of their relative availability (Feinsinger et al. 1981). We computed diet breadth using only broad prey categories (mammals, birds, reptiles, amphibians, fish, terrestrial and aerial invertebrates, aquatic invertebrates) that require different foraging techniques and/or capture methods on the part of raptors. (2) Diet overlap (= diet similarity) of Pianka (1973) was computed as $Ov = \Sigma\, p_i q_i / [\varepsilon(p_i^2)(\varepsilon(q_i^2)]^{-0.5}$, where p_i is the relative occurrence of prey category i in one predator's diet, and q_i is its relative occurrence in another predator's diet. Here we used the highest possible taxonomic resolution of prey in all cases. (3) Trophic clusters. Using entries in the diet similarity matrices for calculating Ov, we applied the unweighted pair-group clustering method with arithmetic averaging (UPGMA, Sneath & Sokal 1973). We arbitrarily set a threshold at 70% diet similarity to assign predators to trophic guilds.

RESULTS

Chile

During the non-breeding season of 1988, the raptors formed three trophic guilds (Figure 1): (a) Omnivorous guild. The Burrowing Owl and the Ferruginous Pygmy Owl consumed primarily mammals and insects. (b) Mammalivorous hawk guild. The Red-backed Hawk and the Black-chested Eagle consumed primarily Darwin's Leaf-eared Mouse *Phyllotis darwini* but ate some reptiles as well. (c) Mammalivorous owl guild. The Great Horned Owl and the Common Barn Owl ate only mammals, primarily Darwin's Leaf-eared Mouse. Two species were isolated in the cluster analysis: The Harris' Hawk, primarily consuming the Degu Fence Rat *Octodon degus* and secondarily Darwin's Leaf-eared Mouse, and the American Kestrel, whose primary prey was birds.

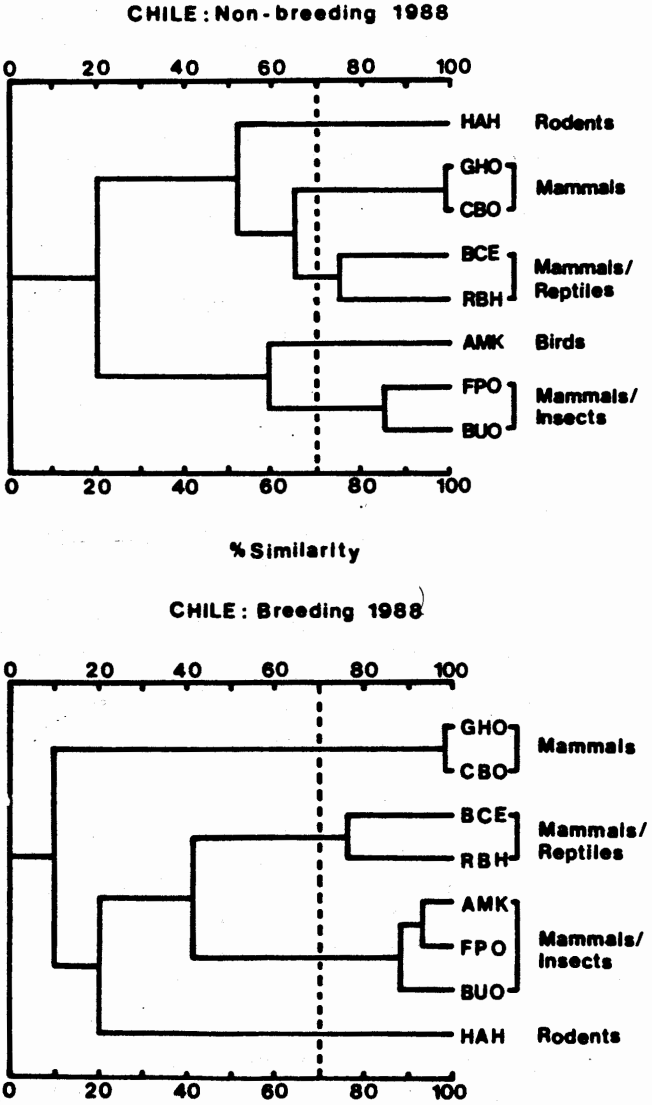

FIGURE 1 – Guild structure of raptors in Auco, Chile, resulting from UPGMA cluster analysis. Dashed vertical line here and in the following figures indicates the arbitrary criterion of guilds at > 70% diet similarity. Data collected by the authors. Abbreviations as in Appendix.

During the breeding season of 1988, the same species occurred at the site and formed the same guild pattern, with only slight modifications: (a) In the omnivorous guild, the Burrowing Owl increased slightly its relative consumption of mammals, whereas the Ferruginous Pygmy Owl became somewhat more insectivorous. The American Kestrel joined this guild by becoming strongly insectivorous. (b) In the mammalivorous hawk guild, the Red-backed Hawk increased its consumption of reptiles and its primary prey became the Degu Fence Rat, while the Black-chested Eagle increased its consumption of birds. (c) In the mammalivorous owl guild, diets of the Great Horned Owl and the Common Barn Owl remained the same. Harris' Hawk, now isolated in the cluster analysis, still ate the Degu Fence Rat but increased its consumption of birds. Thus, of the few seasonal changes in guild structure, most involved raptors that presumably keyed in on abundant alternate prey such as birds and reptiles.

On average, the level of diet similarity at which guilds formed in the cluster analysis did not move up or down between non-breeding and breeding seasons (Mann-Whitney U-test; $P > 0.10$). There was no trend for diet breadths to change between non-breeding and breeding seasons (Wilcoxon signed-ranks test; $P = 0.10$).

Spain

During the non-breeding season, two trophic guilds occurred: (a) Mammalivorous/avivorous guild. The Red Kite and the Imperial Eagle ate mainly mammals and birds. (b) Omnivorous guild. The Little Owl and the Eurasian Tawny Owl ate large numbers of insects, although the Eurasian Tawny Owl also ate some vertebrates. One species, the Common Barn Owl, remained alone in the cluster analysis because of its strictly mammalivorous food habits.

During the breeding season three species, the Black Kite, Old World Kestrel, and Eurasian Buzzard, immigrated into the locality, changing the guild membership observed during the non-breeding season: (a) Mammalivorous/avivorous guild. The Eurasian Buzzard joined the resident Red Kite and Imperial Eagle. All ate primarily mammals and birds, with reptiles as secondary prey. (b) Omnivorous guild. The Black Kite and the Old World Kestrel joined the resident Little Owl and Eurasian Tawny Owl. All ate large numbers of insects (the Little Owl almost exclusively so), together with some vertebrates. The Common Barn Owl remained a mammalivorous specialist. In summary, three species migrated into the area to breed, but the nature of guilds remained essentially unchanged.

As in Chile, on average the level of diet similarity at which guilds formed did not change between non-breeding and breeding seasons (Mann-Whitney U-test; $P > 0.10$), and diet breadths remained the same (Mann-Whitney U-test for all species, $P > 0.10$; Wilcoxon signed-ranks test for year-round residents only, $P = 0.20$). Thus, the scenario in Spain resembles that of Chile, except for the migration of raptor species that bred in the Spanish site but left in the autumn.

Michigan

During the non-breeding season of 1942, all raptors belonged to a single cluster of mammal eaters. Two groups with slightly different specialties occurred: The Great Horned Owl and Eastern Screech Owl, whose primary prey were the white-footed mice *Peromyscus* spp., versus the Red-tailed Hawk, Red-shouldered Hawk, Rough-legged Hawk, Short-eared Owl, Common Long-eared Owl, American Kestrel, and Northern Harrier, whose primary prey was the meadow mouse *Microtus pennsylvanicus*.

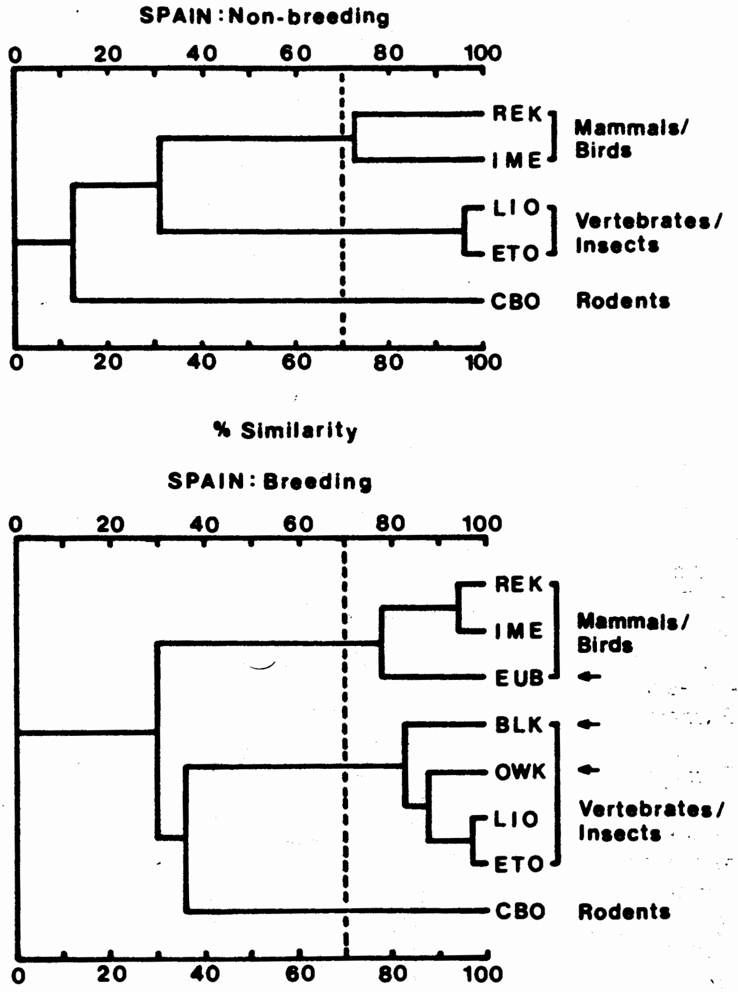

FIGURE 2 – Guild structure of raptors in Donana, Spain. Data from Kufner (1986). Abbreviations as in Appendix.

During the breeding season, a complex exchange of species occurred and the guilds prevailing during the nonbreeding season dissociated. Rough-legged Hawks, Short-eared Owls, and American Kestrels emigrated, while Cooper's Hawks and Common Barn Owls immigrated. The mammalivorous guild shrunk to the Eastern Screech Owl (which started eating insects also) and Common Long-eared Owl, but these were now joined by the Common Barn Owl. Three previous members of this guild, the Great Horned Owl, Red-tailed Hawk, and Northern Harrier, formed a distinct mammalivorous/avivorous guild, greatly increasing their consumption of birds at the expense of mammals. Another ex-mammalivore, the Red-shouldered Hawk, became more omnivorous than the previous three species by eating snakes in addition. The second of the two immigrants, the Cooper's Hawk, ate almost exclusively birds.

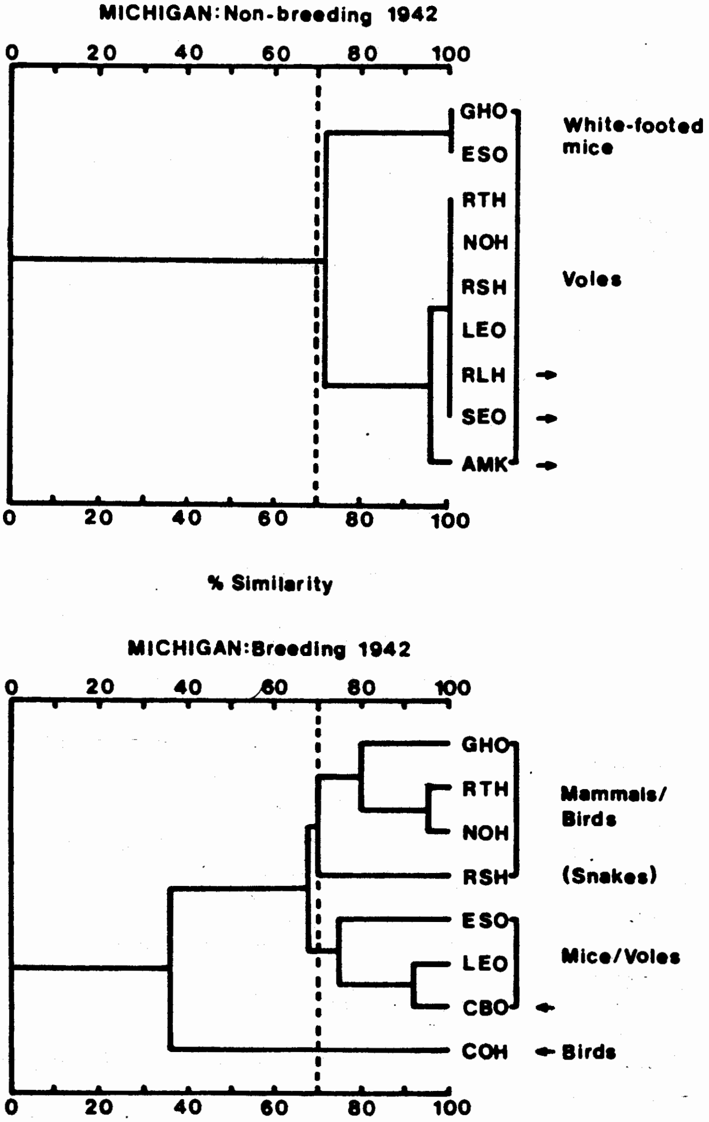

FIGURE 3 – Guild structure of raptors in Michigan, USA. Data from Craighead & Craighead (1956). Abbreviations as in Appendix.

On average, levels of diet similarity at which guilds formed were higher during the non-breeding season than during the breeding season (Mann-Whitney U-test; $P < 0.005$). Diet breadths were higher during the breeding season than during the non-breeding season, when all species were considered (Mann-Whitney U-test; $P < 0.005$) or when only year-round residents were considered (Wilcoxon signed-ranks test, $P = 0.01$).

DISCUSSION

The three localities represent a gradient in dynamics of guild structure. Chile demonstrated the least dynamic assemblage, even though the climate there is highly seasonal. The same species were present throughout the year, and guild structure did not vary. Minor changes in diet between the non-breeding and breeding seasons were not sufficient to shift node values of similarities or diet breadths, even though shifts occurred in the prey resource base (Jaksic, Jimenez & Feinsinger, unpublished data). The situation in Spain was intermediate. Guild structure remained quite stable throughout the year, even to the values of node levels. Guild membership changed because of an influx of migrants that bred in the locality during the prey-rich season, but no significant shifts among residents resulted. The most dynamic changes in guild structure between seasons occurred in Michigan. During the non-breeding season, raptors concentrated on specific resources, forming tight trophic guilds. During the breeding season, guilds broke down through species emigration and by the remaining guild members using more diverse prey. Immigrants also contributed to changes in guild membership. There was no evidence, however, that immigrants caused lateral displacements in the diets of residents; rather, residents broadened breeding-season diets in an apparently opportunistic response to a broader array of available prey (Craighead & Craighead 1956).

The lack of migratory dynamics in the Chilean raptor assemblage results from geography. Chile is enclosed by important barriers to raptor migration: the open ocean to the west and south, the high Andes to the east, and the Atacama desert to the north. No large pool of migrants exists at higher latitudes, simply because the area to the south is small. Most raptor migration within the country is short range, effected by only fractions of the populations (Jaksic & Jimenez 1986). In contrast, the North American continent poses no unsurmountable obstacles to raptor migration, and to the north of Michigan lies a vast region providing a large pool of seasonal migrants. Spain is in the middle of the important European-Saharan corridor of raptor migration through the Gilbraltar Strait, with large pools of potential migrants at higher latitudes.

Stability of trophic guild structure in terms of prey use is evident in both Chile and Spain. In both regions, many raptors appear to rely on mammals as staple prey during the non-breeding season, whereas during the breeding season they broaden their diets only slightly by exploiting alternate prey that are increasingly available (in terms both of numbers and activity), such as reptiles and birds, but without ceasing predation on mammals. Given these sites' geographical position at about 30° latitude, subjected to the moderating influence of the ocean and without snow, prey fluctuations may not be as pronounced as those in the truly continental, higher latitude setting of Michigan. Complete data are not currently available on seasonal changes in prey in these localities. Nevertheless, an indirect test of this hypothesis could be performed by studying guild dynamics in, for example, California, whose geographic and climatic features are more similar to those in central Chile and southern Spain than they are to Michigan. We expect that California guild structure should be less dynamic than that in Michigan.

A general picture emerges from scrutinizing guild dynamics under fluctuating levels of prey resources at these sites. In no case does niche separation increase under conditions of presumably limiting resources (the non-breeding seasons). Either there are no significant changes in levels of diet similarity (Chile and Spain), or the changes go in the opposite direction (Michigan) expected for competition-structured assemblages. We propose the following scenario: (1) During lean seasons, raptors emigrate from areas where resources become scarce, or alternatively, they converge upon the few resources that can be exploited. (2) During resource-rich seasons, raptors immigrate back into the same areas and/or opportunistically exploit a more varied supply of prey resources as these become available. Yet the immigrants, where these occur, do not appear to displace residents' diets in any discernible way, nor does emigration result in "competitive release" among the residents. If competition occurs among raptors in these assemblages through their common use of prey, it has no obvious links to diet shifts.

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APPENDIX

Raptor species found in the three study sites and their residence status. Scientific and vernacular nomenclature after Amadon et al. (1988).

A) CHILE. Residents: *Buteo polyosoma* (Red-backed Hawk, RBH); *Falco sparverius* (American Kestrel, AMK); *Geranoaetus melanoleucus* (Black-chested Eagle, BCE); *Parabuteo unicinctus* (Harris' Hawk, HAH); *Athene cunicularia* (Burrowing Owl, BUO); *Bubo virginianus* (Great Horned Owl, GHO); *Glaucidium brasilianum* (Ferruginous Pygmy Owl, FPO); *Tyto alba* (Common Barn Owl, CBO).

B) SPAIN. Residents: *Aquila heliaca* (Imperial Eagle, IME); *Milvus milvus* (Red Kite, REK); *Athene noctua* (Little Owl, LIO); *Strix aluco* (Eurasian Tawny Owl, ETO); *Tyto alba* (Common Barn Owl, CBO). Breeding visitors: *Buteo buteo* (Eurasian Buzzard, EUB); *Falco tinnunculus* (Old World Kestrel, OWK); *Milvus migrans* (Black Kite, BLK).

C) MICHIGAN. Residents: *Buteo jamaicensis* (Red-tailed Hawk, RTH); *Buteo lineatus* (Red-shouldered Hawk, RSH); *Circus cyaneus* (Northern Harrier, NOH); *Asio otus* (Common Long-eared Owl, LEO); *Bubo virginianus* (Great Horned Owl, GHO); *Otus asio* (Eastern Screech Owl, ESO). Breeding visitors: *Accipiter cooperii* (Cooper's Hawk, COH); *Tyto alba* (Common Barn Owl, CBO). Wintering visitors: *Buteo lagopus* (Rough-legged Hawk, RLH); *Falco sparverius* (American Kestrel, AMK); *Asio flammeus* (Short-eared Owl, SEO).