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TOWARD RAPTOR COMMUNITY ECOLOGY: BEHAVIOR BASES OF ASSEMBLAGE STRUCTURE

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ABSTRACT — Despite definite advantages in comparison to other model systems (e.g. assemblages of passerine birds and lizards), raptor community ecology is in its infancy. I discuss the adequacy of raptors as model predators for the study of the relationships between behavioral processes (agonistic interactions and hunting modes) and assemblage-level patterns (community structure).

Community ecology studies of animals can be equated with the identification and quantification of the niche axes along which sympatric species appear to separate in order to reduce co-use of resources in limited supply. Schoener (1974) identified habitat, food, and time as the axes that most frequently separate vertebrate predators (including arthropod consumers such as passerine birds and lizards, as well as carnivorous vertebrates). Indeed, the study of insectivorous passerine birds as model predators has contributed substantially to the development of community ecology, as attested by the pioneering studies of MacArthur (1972) and Cody (1974; Cody and Diamond 1975); (see Strong et al. 1984 for more recent views). Subsequently, lizards have gained considerable importance as model predators (see Huey et al. 1983 for an overview of past and current contributions of herpetologists to community ecology).

The early findings of Schoener (*op. cit.*), although disputed by some in terms of the underlying causes (see Strong et al. (*op. cit.*) for a confrontation of views), have by and large been held as verified. Both with passerine birds and lizards it has been shown that species often segregate along habitat (or microhabitat) dimensions. However, the data demonstrating food segregation among these organisms are suspect for reasons described below, and the adequacy of activity time as a niche difference is under serious questioning (e.g., Jaksic 1982; Huey and Pianka 1983, Carothers and Jaksic 1984). Adding to the confusion is the fact that the three niche axes are usually correlated (segregation along one of them leads to segregation along another),

thus making causality difficult to resolve. The reasons for these correlations are easy to infer. For example, the trophic structure (patterns of prey use) of sympatric assemblages, which is described on the basis of the diets of the component predators (taxonomic composition, diversity, interspecific similarity, mean prey size, etc.) is only the outcome of behavioral processes occurring at the level of the local population. These processes involve not only prey selection, but also habitat preferences by the individual predators, their activity times, foraging modes and efficiencies, as well as morphological, physiological, and ecological constraints.

The gap between the summary description of food-niche patterns in predator assemblages and the foraging mode of individual predator species has recently been bridged for passerine birds (Eckhardt 1979; Robinson and Holmes 1982) and lizards (Huey and Pianka 1981). In my view, however, these two groups of organisms, which seem to be very suitable for studies of habitat preferences and microhabitat partitioning, are less suitable for the study of prey selection and food segregation. First, prey in their diet often are identifiable only to the ordinal level, and with some difficulty (at least for ornithologists) to the familial level, which represents an important shortcoming. Greene and Jaksic (1983) have shown that in dietary studies of predators identification of prey at the ordinal level (customarily used in passerine and lizard diet studies) underestimates diet diversity and overestimates diet similarity calculated at the species level of prey identification. Further, Greene and Jaksic (*op. cit.*) have shown that these biases arise in unpre-

dictable fashion, so that no reliable correction factors can be introduced in the computation of dietary statistics and consequently the food-niche patterns so far documented for passerine birds and lizards are suspect.

A second shortcoming of using passerine birds and lizards as model predators is that they are subject to predation themselves. This renders it difficult to resolve whether they maximize some prey selection function or compromise the use of optimal prey by minimizing predation risks (an important consideration in terms of optimal foraging theory: see Pyke et al. 1977).

These two shortcomings become especially apparent if one's intention is to correlate food-niche statistics (for whole predator assemblages) with the foraging modes of the constituent species. It is unfortunate that this is so, because I think that the question of how foraging mode is reflected in the trophic structure of sympatric predators is an important one in community ecology. Provided that neither passerine birds nor lizards seem particularly adequate model predators for such an enquiry, I contend that raptors (Order Falconiformes and Strigiformes) may help clarify the relationships between "basal" behavioral processes and "epiphenomenic" patterns of assemblage structure. In the following sections I discuss the pros and cons of using raptor assemblages as models for behaviorally-based community analyses and propose the type of information to be gathered.

RAPTOR ASSEMBLAGES AS MODEL SYSTEMS

Until recently, raptors have been neglected as model predators in community ecology. Nevertheless they have much to offer toward the clarification of niche relationships among sympatric consumers. Segregation of raptors along the habitat axis has been documented both intra- and interspecifically (e.g., Newton 1979; Schmutz et al. 1980; Nilsson et al. 1982; Janes 1984), but this segregation does not clearly result in access to different prey populations. Consequently, reduction of exploitative competition seems an unlikely cause for such phenomenon, nor does use of the same hunting habitat lead to compensatory differentiation along the food axis (Schnell 1968; Baker and Brooks 1981; Steenhof and Kochert 1985) which may be interpreted as resulting from the functional response of essentially opportunistic raptors to high prey densities (Jaksic et al. 1981; Jaksic and Braker

1983; Erlinge et al. 1984). In my impression, where habitat separation is observed among raptors, the proximate cause lies on agonistic interactions — a claim for which both direct (Rudolph 1978; Janes *op. cit.*) and indirect evidence exists (see Newton 1979; Jaksic 1982; Mikkola 1983, for summaries of predation among raptors, an extreme form of agonistic interaction). Consequently, the use of exclusive ranges by raptors relate to reduction of interference rather than of exploitative competition.

Something similar may be said of the causes of temporal segregation. Jaksic (1982) documented that diurnal and nocturnal raptors do not differ enough in prey use (i.e., their diets are too similar) to justify the view that they reduce exploitative competition by differing in activity period (similar conclusions were reached by Huey and Pianka 1983). In fact, Jaksic (*op. cit.*), based on circumstantial evidence, contended that reduction of agonistic interactions was the likely target of such temporal segregation of activity. Carothers and Jaksic (*op. cit.*), have elaborated this point on more theoretical grounds, and for a variety of other organisms. Rudolph (*op. cit.*) documented temporal segregation between two sympatric owl species, mediated by predation of one upon the other. Notice, then, that where interspecific segregation of raptors along habitat and time dimensions has been reported, the proximate factor may well be aggressive exclusion rather than peaceful preemption of specific resources as accomplished by differential efficiencies in the exploitation of portions of the niche axes. The latter has been the general assumption underlying most studies of community ecology, and I think that the study of raptor assemblages can contribute greatly to the understanding of the alternative mechanism (interference competition) in generating the structure of communities.

What about food partitioning? Studies ranging in generality from selected pairs of species through small groups of related raptors to entire assemblages have rendered varied conclusions (e.g., Schmutz et al. *op. cit.*); Jaksic and Braker (*op. cit.*); Knight and Jackman 1984; Marks and Marti 1984). Results indicate that sometimes prey is partitioned via size differences between raptors (accipiters are good examples of this: see Storer 1966; Opdam 1975; Schoener 1984), and that sometimes raptors differing greatly in body size take essentially the

same prey (Schmutz et al. (*op. cit.*); Jaksic 1983; Jaksic and Braker (*op. cit.*)). There is a tendency, though, for particular raptor groups to "specialize" on certain general prey categories (e.g., kites and harriers on small mammals and birds, small falcons on insects, larger falcons on medium-sized mammals and birds, eagles on hares; buteonines appear very catholic in diet). These different groups of raptors share in common similar morphologies and hunting modes (*see* Jaksic and Carothers 1985), which leads me to suggest that the reported trophic structure of the few raptor assemblages so far quantified (*see* Jaksic 1982, 1983; and Jaksic and Braker (*op. cit.*)) somehow reflects those similarities. I do not exactly share the view of Ricklefs and associates (e.g., Ricklefs and Cox 1977; Bierregaard 1978; Ricklefs and Travis 1980) that it is not necessary to go to the field for studying community ecology: morphologic analyses suffice. Instead, I espouse the view (*see also* Steenhof and Kochert (*op. cit.*)) that the study of the hunting behavior of raptors will tell us much about the way assemblages are structured. That is, how behavioral processes result in community patterns.

In comparison to both passerine birds and lizards, the scrutiny of raptor food-niche relationships is facilitated by their greater conspicuousness and use of prominent roosting and nesting sites, where detailed information on their diet can be obtained. However, they also show some shortcomings as model predators. Despite the fact of generally being top predators in terrestrial ecosystems, raptors are not entirely free of predation. Some species are indeed frequently preyed upon by other raptors (*see* Newton *op. cit.*; Mikkola *op. cit.* for summaries), and thus the study of raptor assemblages does not completely eliminate the dual constraints of energy maximization and mortality minimization. But at least in comparison to passerine birds and lizards, raptor behavior should, on the average, be less affected by predation.

The problem of the taxonomic resolution of prey (Greene and Jaksic (*op. cit.*)) is important in raptors that prey primarily on insects; but essentially carnivorous raptors abound, and their vertebrate prey is easily identifiable to the species level, particularly if mammalian (*see* Errington 1930; Burton 1973, for examples). In comparison to passerine birds and lizards, then, accurate estimates can be made of raptor diet diversity (= breadth) and interspecific similarity (= overlap). In addition, open-terrain

raptors are relatively large, conspicuous birds whose time budget, hunting mode, and hunting success, can be quantified with minimal equipment (*see* Rudebeck 1950, 1951; Warner and Rudd 1975; Tarboton 1978; Wakeley 1978a, 1978b; Mendelsohn 1982; Rudolph 1982). Consequently, the proportional use that raptors make of differing hunting modes can be recorded and examined in light of their diets and hunting success in different habitat types. In sum, at least as compared to passerine birds and lizards, raptor assemblages are excellent candidates for the study of food-niche relationships of sympatric predators as related to the hunting behavior of the component species. In the following section I propose the type of information to be gathered for such an aim.

INFORMATION REQUIRED TO ASSESS
COMMUNITY-ECOLOGICAL CORRELATES OF RAPTOR
HUNTING BEHAVIOR

1. The use that sympatric raptors make of different hunting techniques. — Raptor hunting activities can be dichotomized as either perch- or aerial-hunting. Within this second category, at least four techniques can be recognized: a) hovering flight: a stationary flight that may or may not take advantage of the wind conditions; used by small falcons (e.g., *Falco sparverius*), small kites (e.g., *Elanus* spp.), and by the Burrowing Owl (*Athene cunicularia*); b) cruising flight: a high-speed, low-altitude flight; used by large falcons (e.g., *Falco mexicanus*) and accipiters (*Accipiter* spp.); c) quartering flight: a low-speed, to-and-fro flight; used by harriers (*Circus* spp.), and some owls (*Asio flammeus*, *Tyto alba*); and d) soaring flight: low-speed, high-altitude flight that takes advantage of either thermal or obstruction air currents; used by eagles (e.g., *Aquila* spp.) and buteonine hawks (*Buteo* spp.), among others. More detailed descriptions of these hunting flight techniques can be seen in Brown and Amadon (1968), Warner and Rudd (1975), Everett (1977), Tarboton (1978), Wakeley (1978b), Cade (1982), Rudolph (1982), Collopy (1983a), and Collopy and Koplin (1983). Recognition of these five techniques seems necessary because there are indications that they facilitate access to different habitats and prey types, and also because their energetic costs differ (*see* Jaksic and Carothers 1985 for a selective summary). The time allocated to the different hunting techniques by sympatric raptors should be evaluated and, noting the prey captured

with each, the ecological consequences of raptor use of differing techniques assessed.

2. The use that sympatric raptors make of different habitat types while hunting. — Here, it is necessary to evaluate the time spent by raptors hunting in different habitat types (see Wakeley 1978a; Bechard 1982, for examples), because it is likely that prey availabilities differ among habitats (see USDI 1979 et seq.; Baker and Brooks 1981; Bechard 1982, for such findings). Perhaps only broad categories of habitat use by raptors need to be recognized, depending on the physiognomy and landscape units that characterize the study site. For interesting examples of ad-hoc habitat categorizations see USDI (1979 et seq.).

3. The hunting success of sympatric raptors in different habitat types and in using different hunting techniques. — The hunting success can be estimated as the number of successful prey strikes over the total hunting time spent by the different raptors. Unsuccessful prey strikes also should be counted to determine the hunting efficiency (successful strikes/total strikes with known outcome) of raptors using different hunting techniques (Collopy 1983a; Collopy and Koplin (*op. cit.*)). The prey captured ideally should be identified to the species level with the aid of adequate viewing devices. Direct observations are possible especially during the breeding season, when birds can be tracked to the nest after a successful prey strike, and the prey can be identified there if not at the capture site (e.g., Collopy 1983b). By focusing attention on open-terrain raptors, the prey captured in different parts of the habitat can be identified (e.g., Mendelsohn (*op. cit.*)).

4. The presumable clues that sympatric raptors use in choosing hunting habitats. — This is undeniably the most difficult part of the proposed research protocol. Judging from recent studies (e.g., Jaksic et al. 1981, 1982; Jaksic and Braker (*op. cit.*); Erlinge et al. (*op. cit.*)), generalist raptors appear to take prey in about the order of their respective availabilities in the field. Within characteristic upper and lower size thresholds scaled to the sizes of the individual raptor (whatever their abundance, hares are unavailable prey for American Kestrels the same way that grasshoppers are for Golden Eagles). Because prey are taken by raptors on a one-by-one basis, numerical estimates of the abundance of individual prey may well serve as a crude estimate of their availability in the different habitat

types recognized in the study site (see Baker and Brooks 1981; and Bechard 1982, for cautionary notes). Many techniques exist that can be used (e.g., Giles 1971), and examples of their applicability and relative success can be found in USDI (1979 et seq.). An additional characteristic of the prey species which may be important in affecting their selection by — or vulnerability to — raptors is their mobility (e.g., Huey and Pianka 1981). This feature can be evaluated as the average displacement in meters per activity period, with the specifics of the measurement depending on the type of prey. Ideally, a vulnerability index for the different prey species at the study site could perhaps be devised by combining prey characteristics such as density, spatial distribution (clumped, random, regular), micro-habitat use, mobility, size, conspicuousness, etc. How to compute such a complex index I cannot figure out, because vulnerability is not an inherent feature of the prey and should vary relative to raptor characteristics (size, habitat preferences, and hunting mode).

CONCLUDING REMARKS

The study of assemblage-level correlates of hunting behavior in raptors should prove illuminating for a number of important questions in community ecology: To what extent does the trophic structure of predator assemblages reflect the hunting behaviors of the component species?, and — more specifically — provided that falconiforms and strigiforms replace each other during the daily cycle, is the similar trophic structure of these raptor assemblages (Jaksic 1983) based on behavioral similarities in the hunting modes of their respective constituent species? To what extent do the differing hunting modes of sympatric predators facilitate their coexistence through reduction of co-use of food resources (exploitative competition)? What is the influence of interspecific agonistic interactions (interference competition) in the selection of hunting habitats and of hunting modes by sympatric raptors?

Autecological studies of raptors are abundant (see Clark et al. 1978 for a bibliography; Bunn et al. 1982, and Watson 1977, for specific studies), and raptor population ecology has long reached its maturity (see Newton 1979; Mikkola 1983, and references therein). However, community ecology of raptors is still in its infancy (see Jaksic and Braker 1983 for a cursory review). Given that raptors com-

pare more than favorably to other organisms (passerine birds, lizards) as model predators, I think the time is ripe for exploring this much neglected aspect of raptor ecology.

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