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# The Guild Structure of a Community of Predatory Vertebrates in Central Chile

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**Summary.** The trophic ecology of eleven predator species (Falconiforms: *Buteo polyosoma, Elanus leucurus, Falco sparverius, Geranoaetus melanoleucus, Parabuteo unicinctus;* Strigiforms: *Athene cunicularia, Bubo virginianus, Tyto alba;* Carnivores: *Dusicyon culpaeus;* Snakes: *Philodryas chamissonis, Tachymenis peruviana*) in two nearby localities of central Chile is analyzed. The localities exhibit the typical climate (hot-dry summers, cold-rainy winters), and vegetation (chaparral), of mediterranean ecosystems. Densities of the staple prey (small mammals) were estimated by seasonal trapping during two years in both open and dense patches of chaparral.

The trophic parameters examined are: 1) proportion of diurnal, crepuscular, or nocturnal prey found in the predators' diet; 2) relationship between abundance of different mammalian prey in the predators' diet, and in both open and densely vegetated habitat patches; 3) mean weight and variance of weight of small mammal prey consumed; 4) average weight of the predators; 5) food-niche breadth of the predators; 6) relationship between average weight of predators and mean weight of mammalian prey taken, its variance, and food-niche breadth; 7) overlap in food-niche between all the predator species; 8) guild packing of the predators. Parameters 1) and 2) are used to assess the importance of temporal and habitat segregation of the predators, respectively; parameters 3), 4), 5), and 6) provide information on the possibilities of partitioning the prey resources among the predators; parameters 1), 2), 7) and 8) are used to investigate the organization of the community in terms of guilds.

Three niche dimensions seem to be important in determining the structure of the predator community: 1) hunting activity period (diurno-crepuscular, nocturno-crepuscular), 2) hunting habitat (open, or both open and dense patches), and 3) mean prey size taken. Segregation along these three axes results in generally low food niche overlaps ($<54\%$ in 47 of the 55 pair-wise comparisons) among the predators, but it is not possible to determine whether this was produced by competitive interactions or stochastic differences. Three guilds (niche overlap $>90\%$ in pair-wise comparisons) can be recognized: a) the carnivorous-insectivorous guild formed by the diurnal raptors *A. cunicularia* and *F. sparverius,* which tend to hunt in open habitat patches; b) the herpetophagous guild formed by the diurnal snakes *P. chamissonis* and *T. peruviana,* which presumably hunt in open habitat patches; c) the carnivorous guild (highly specialized in the capture of two rodent species) formed by the diurnal raptors *B. polyosoma, G. melanoleucus, P. unicinctus,* and the carnivore *D. culpaeus,* which hunt in open habitat patches. The diurnal raptor *E. leucurus* is not clearly associated with any guild, and the only two nocturnal raptors in the community (*B. virginianus* and *T. alba*) exhibit marked differences in their trophic ecology.

## Introduction

The structure of natural communities can be reasonably well described by the utilization of habitat, food resources, and activity time of the component organisms (Schoener 1974). These three factors, if they are not correlated (interdependent), can be considered as orthogonal axes of the niche-hypervolume generated by the component organisms of the community (Hutchinson 1957), thus making possible the use of quantitative methods for its analysis (Colwell and Fuentes 1975). Consequently, it may in principle be possible to analyze separately these three dimensions, because the selection of a particular habitat may not be related at all with the food resources that thus become available, in much the same way that a monophagous predator might search its preferred prey in different habitats, or predators with different activity times might consume the same prey if it is available throughout the day. However, if niche dimensions are not independent (segregation along one axis leading to segregation on another and vice versa), the possibilities of resource partitioning decrease and segregation is attained either along one dimension or another rather than on both simultaneously. For this reason, habitat and diet are frequently complementary dimensions of the niche as specified, suggesting that for coexistence to be possible organisms compensate for similarities in habitat utilization by differential use of food resources (Schoener 1974; Fuentes 1976; Fuentes and Jaksić 1979).

The habitat axis of the niche is usually perceived as a non-continuous dimension by vertebrate-sized organisms, which during their life span generally travel through different habitat patches, and are thus potentially capable of discriminating and choosing the most appropriate habitats (Levins 1968). The food resource axis is sometimes a continuous dimension, particularly in the case of granivorous, insectivorous, and carnivorous organisms, because the size distribution of food types such as seeds, insects, and small vertebrates is generally of an overlapping nature (MacArthur 1972). Exceptions to this are organisms specialized in the consumption of particular taxonomic categories, like the predators of ants and termites (even though such predators could partition this prey by size, e.g., Huey and Pianka 1974). The activity time of organisms is essentially a continuous variable, but temporal segregation of the organisms in the community has an important role only when it involves relatively extensive time intervals (e.g., diurnal, crepuscular, nocturnal, or seasonal activity periods) (Schoener 1974). Also, differences in the activity time of the components of the community lead to their coexistence only when causally related to differential availability of other resources (food, habitat). If a predator eats the members of the same prey population during the day that another predator

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consumes at night, they are still exploiting the same prey resource. Conversely, if the temporal availability of prey species is fairly discontinuous (i.e., there is no overlap in their activity times), the number of predator species in a given habitat could potentially be increased as long as they also have distinct activity times. Another possibility is that syntopic predators can coexist despite using the same limited resources if the renewal rate of the resources is high enough, but this probably does not apply in the case of the prey of carnivorous predators.

Although by conventional definition communities are composed of organisms of all trophic levels, the difficulty of completely analyzing the interactions among all the components has led to a more restricted, operational, meaning of the term community. The most common restriction involves the recognition of communities of related organisms at the class or lower taxonomic levels. There have been studies on communities (*sensu lato*) of birds (Cody 1973), carnivores (Rosenzweig 1966), and lizards (Fuentes 1976), among many other examples. In our opinion, these "communities" could more usefully be called taxonomic assemblages (cf. Pianka 1974a:235). Recently, a new operational unit has been used in the study of communities: the "guild", a group of species exploiting the same class of environmental resources in a similar manner (Root 1967) which can in principle contain members of several taxonomic assemblages. Although there are objective means to determine the extent to which a given community is organized in guilds (Inger and Colwell 1977; Landres and MacMahon 1980), most authors have just assumed organization in guilds based on general patterns of resource utilization (see for example Phelan and Robertson 1979; Blaustein 1980). Whichever method is used, in a given community (*sensu stricto*) one or more guilds could be recognized, and each one of these guilds could comprise organisms belonging to different taxonomic assemblages. The danger in examining the ecology of assemblages is that by restricting the study to a group of related organisms, other taxonomically distant but otherwise ecologically similar ones are excluded and their possible importance ignored. The studies of Brown and Davidson (1977), and Davidson et al. (1980) on competition between rodents and ants for seeds provide a good example of how distantly related organisms affect each other's ecology more than taxonomically closer ones. Another problem with this kind of approach is that it does not take into account that the behavior of one trophic level is influenced by higher levels, sometimes dramatically. A classical example is the presence of zones denuded of herbs around shrubs in the California chaparral. By focusing only in plant interactions, Mueller et al. (e.g., 1964, 1968) concluded that the phenomenon was due to the allelopathic effects of shrubs upon neighboring herbs. Bartholomew (1970), by considering the consumer trophic level, realized that herbivory by small mammals accounted for the same fact. Furthermore, the concentration of small mammalian activity beneath and close to the shrubs was probably due to the effect of yet another trophic level, that of predators (Bartholomew 1970).

One way to surmount the shortcomings of ecological studies of assemblages is to examine thoroughly complete trophic fractions of the community (*sensu stricto*) (e.g., decomposers, herbivores, predators), and include organisms in the other trophic levels that are likely to interact with, and have important effects upon, the group chosen (a similar approach has been proposed by Cohen 1978, for the study of food webs). Although this involves a somewhat arbitrary decision, it is more so to assume that the only significant interactions in a community are within taxonomic assemblages. For the type of analysis that we propose, the structure of a community of small mammals would require not only the assessment of the importance of food, habitat, and activity time as dimensions of the niche that may allow reduced overlap among potentially competing species, but also the assessment of the role of predators in affecting the expression of these factors (see Bartholomew 1970; Fuentes and Le Boulengé 1977; Jaksić et al. 1979; Jaksić and Soriguer 1980; for some examples of the effects of predation upon small mammals). Therefore, if the distinction between the ecology of taxonomic assemblages and communities is accepted, there are clear advantages in studying communities of predators, because they are the less likely to be affected by predation itself by being at the top of the trophic pyramid (Elton 1927; see also Cohen 1978).

Our aim is to analyze the structure of a community of vertebrate predators in a small area of central Chile. This analysis has two main restrictions: 1) only predators continually residing and breeding in the area are included; 2) only essentially carnivorous predators are studied, thus disregarding insectivores (most of the birds and all of the lizards in the area), and carrion-eaters (some falconiforms). (See Materials and Methods for species excluded from this analysis.) Despite these limitations, our study has two clear advantages: 1) to our knowledge, this is the first quantitative-statistical analysis of the structure of a complex terrestrial community of vertebrate predators, consisting of four orders of three vertebrate classes (Horn and Fitch 1942, Valverde 1967, and Craighead and Craighead 1969 seem to be the only researchers that have used a similar, although less quantitative approach to the study of vertebrate predators; Cohen 1978 gives examples on food-web studies involving other kinds of predators); 2) the abundance of the most important prey (small mammals) in two habitat types of the same locality is presented, along with a reasonable understanding of the ecology and activity times of the prey species. On the bases of this information – and an awareness of its limitations – we describe the structure of the predator community in terms of component guilds, and evaluate the segregation of the predators along the corresponding niche dimensions of habitat, diet, and activity time. We also explore some relationships between the predators' size, their food-niche breadth, and prey size. Finally, we comment on the concept of ecological "guilds" and on the likelihood that time, habitat, and food are orthogonal resource axes for vertebrate predators.

## Materials and Methods

*Study Sites.* La Dehesa (33°21′ S, 70°32′ W; 875 m elevation; 20 km NE of Santiago), and Los Dominicos (33°23′ S, 70°31′ W; 950 m elevation; 20 km E of Santiago) are located in the foothills of the Cordillera de los Andes, about 5 km apart, map distance. Vegetational physiognomy is very similar, characterized by an association of evergreen shrubby species known as matorral in Chile, very similar to the chaparral in California. Due to the effects of human disturbance (grazing, agricultural practices, extraction of firewood; see Aschmann and Bahre 1977; Fuentes and Hajek 1979), two types of habitat patches are readily recognized: 1) open patches, produced by past disturbance, containing pure stands of the shrubs *Acacia caven, Baccharis rosmarinifolia,* and *Muehlenbeckia hastulata,* interspersed with *Colliguaya odorifera, Lithraea caustica,* and *Trevoa trinervis*; average height of the shrubs varies between 1 and 2 m, and cover between 20% and 60%; 2) dense patches, relatively undisturbed, with higher cover (between 80% and 100%), and taller shrubs (average between 2 and 4 m), including *Cryptocarya alba, Lithraea caustica,* and *Quillaja saponaria* as dominant species, with *Drimys winteri* and *Kageneckia oblonga* in lesser abundance.

*Sampling Techniques.* Between 1973 and 1979 F. Jaksić, J. Yáñez, and R. Schlatter collected 939 regurgitation pellets of five species of falconiforms, 1019 pellets of three species of strigiforms, 289 feces of one species of carnivore, and 9 individuals of two species of snakes. This information (except that on snakes) has been published separately; a list of the raptor and carnivore predators in the area follows, with the corresponding references that describe their diet in detail. Falconiforms: *Buteo polyosoma* (Schlatter et al. 1980a), *Elanus leucurus* (Schlatter et al. 1980b), *Falco sparverius* (Yáñez et al. 1980), *Geranoaetus melanoleucus* (Schlatter et al. 1980a), *Parabuteo unicinctus* (Jaksić et al. 1980c). Other falconiforms seen in the area, that are not permanent residents, are *Circus cinereus, Coragyps atratus, Falco femoralis, Falco peregrinus,* and *Vultur gryphus* (Schlatter 1979). Although *Milvago chimango* is a permanent resident, it is not included in this study because it is fundamentally an insect and carrion-eater (Schlatter 1979). Strigiforms: *Athene cunicularia* (Schlatter et al. 1980c), *Bubo virginianus* (Jaksić and Yáñez 1980), *Tyto alba* (Jaksić and Yáñez 1979, 1980; Herrera and Jaksić 1980). *Glaucidium brasilianum* is found in the area but does not reside continually (Schlatter 1979). Carnivores: *Dusicyon culpaeus* (Fuentes and Jaksić 1979; Jaksić et al. 1980a). *Felis guigna* and *Grison cuja* may be present in the area (Miller and Rottmann 1976), but we failed to confirm this.

*Philodryas chamissonis* and *Tachymenis peruviana* are the only snake species in the area (Donoso-Barros 1966), and are in fact locally preyed upon by *F. sparverius, G. melanoleucus, P. unicinctus,* and *D. culpaeus* (see references cited above). Of the five *P. chamissonis* examined, one contained a frog (*Pleurodema thaul*) and another a lizard (*Liolaemus* sp.); of the four *T. peruviana* examined, two contained one *P. thaul* each. Because these sample sizes are so small, we included in the community matrix of La Dehesa-Los Dominicos data collected at other localities, assuming that the food habits of the two snake species do not change greatly from place to place. Greene and Jaksić (unpublished) found that both species prey primarily on frogs and lizards, small mammals being consumed only occasionally by the largest individuals of *P. chamissonis.* It appears, then, that the snakes fill the niche of lizard- and frog-eaters in the community under study. As documented in Appendix 1, they can potentially compete with *F. sparverius* and *A. cunicularia* for lizard and frog prey, respectively, but their abundances in the area and their metabolic rates are presumably low. Thus, in comparison with endotherms, the impact of snakes upon prey populations should be sufficiently small as to not significantly affect our analysis of prey relationships in the study area. Considering these characteristics of the snake population, and the heterogeneous origin of the food sample studied, we do not include snake data in the analysis of habitat, food, and time segregation in La Dehesa-Los Dominicos, but we do so in the quest for the guild structure of the predator community in the area.

Because the food resources more heavily utilized by all the predators in the area were small mammals, we conducted systematic trapping in Los Dominicos all year round during 1976 and 1978. This allowed us to learn the number of small mammal species present in the area, and estimate both their absolute and relative abundances in open and dense matorral patches; these estimates were strikingly different between-habitats but not between-years (Jaksić et al. 1980b; see also Le Boulengé and Fuentes 1978). Yáñez (unpublished) conducted trappings in La Dehesa, and his results are very similar to those obtained in Los Dominicos; we regarded, therefore, the figures drawn from this latter site as an adequate estimate of the abundances of small mammal species in the area as a whole.

*Quantitative and Statistical Techniques.* Based on the published information cited above, we constructed a rectangular matrix of prey *x* predators (or trappers, in the case of population estimates of small mammals), standardizing all the information to proportions of the total prey caught by either predators or trappers (Appendix 1). Based on these data, we calculated the following parameters: 1) Proportion of actively diurnal, crepuscular, or nocturnal prey found in the diet of the predators (excepting snakes). The description of activity patterns of small mammals in central Chile was taken fundamentally from Glanz (1977), and modified according to Mann (1978); the activity periods of the remaining prey were determined on the basis of personal observations in the area by F. Jaksić and J. Yáñez. 2) Relationship between abundance of mammalian prey species in the diet of predators (except snakes) and their abundance in both open and densely vegetated habitat patches, as estimated with the Spearman rank correlation coefficient (Sokal and Rohlf 1969:538). If predators consume prey in roughly the proportion that prey species are present in the field, it is expected that predators hunting in open or dense habitat patches exhibit high correlation between the abundance of prey in their diet and the abundance of prey in one of the two habitat types. These expectations would obviously not be met if predators take their prey under criteria other than relative availability. 3) "Mean weight" (in g) of small mammal prey taken by each predator species (except snakes), and its variability as estimated by the standard deviation of the parameter. "Average weights" of adult-sized individuals (no dispersion statistic reported) of each species of small mammals were obtained mainly from Glanz (1977); some exceptions to this procedure are detailed in the Appendix 1. 4) "Average weight" of predator species (no dispersion statistic available), in grams, as documented by Jaksić and Soriguer (1980); snakes are excluded. 5) Food-niche breadth, using Levins' (1968:43) modification of Simpson's diversity index, which gives values ranging from 1 to N (for N equally used resources or for uniform utilization over an interval of length N and no outside utilization.) 6) Relationship between average weight of the predator species (except snakes) and: a) mean weight of mammalian prey in their diet; b) standard deviation of this latter parameter; c) food-niche breadth. Spearman rank correlation coefficient was used to evaluate these relationships. 7) Overlap of food-niches of different predator species (including snakes), using the symmetrical equation described by Pianka (1974b), which renders values ranging between 0 and 1 (null to complete overlap). For this purpose we constructed a square matrix of predators *x* predators, and calculated the overlap between all the pairs. 8) The technique described by Inger and Colwell (1977:243–245) was used to determine the guild structure of the community. This statistical procedure involves first the computation of the overlap (food, habitat, etc.) between each species and its first, second, ⋯ *i*th nearest neighbor (see Pielou 1969); secondly, the computation of the mean overlap for the whole set of first, second, ⋯ *i*th nearest neighbors. Because the expected distribution of distance between *i*th nearest neighbors for randomly placed points in n-space as well as the standard deviation, is known to be monotonic on *i*, the presence of peaks of standard deviation at any point of nearness order indicates organization of guilds at approximately that nearest neighbor level (see Inger and Colwell 1977 for detailed explanations). Parameters 1) and 2) allow us to assess the importance of temporal segregation, and differential utilization of the habitat by the predators, respectively. Parameters 3), 4), 5), and 6), render information about the possibilities of partitioning the prey resources among the predators. The set of parameters 1), 2), 7), and 8), allow us to investigate the structure of the community in terms of component guilds.

## Results and Discussion

*Temporal Segregation.* Six predator species include essentially diurnal prey in their diet, one consumes mainly crepuscular prey, and two prey fundamentally on nocturnal species (Table 1). In none of these cases, however, do the predator species consume only diurnal, or crepuscular, or nocturnal prey. In fact, most of these predators consume prey which are active during all three periods (the exception is *F. sparverius,* which does not seem to prey on nocturnal species). This is probably related to two factors, operating singly or in combination: 1) Diurnal and nocturnal predators may extend their hunting periods to crepuscular hours, thus having access to prey active at dusk and dawn. 2) Prey species of any activity period may extend their activities in the field, exposing themselves to predators of different hunting periods. Personal observations in the study area suggest that the first factor operates, but that it is of lesser importance than the second. It has been shown that the activity periods of some prey species in the area change according to both the season -probably associated with the onset of breeding and later dispersal of juveniles (Le Boulengé and Fuentes 1978;

**Table 1.** Hunting activity period of nine predator species in central Chile, as estimated by the contribution of prey of different activity times to their diet. Predators' body weight increases from the upper to the lower part of the table. $N$ = number of prey of known activity period identified in the sample

| Predators | % Diurnal Activity | % Crepusc. Activity | % Nocturn. Activity | $N$ |
|---|---|---|---|---|
| *Falco sparverius* | *90.7* | 9.3 | 0.0 | 378 |
| *Athene cunicularia* | *83.4* | 8.7 | 7.9 | 3,038 |
| *Elanus leucurus* | 10.6 | *88.1*[a] | 1.3 | 151 |
| *Tyto alba* | 14.0 | 28.1 | *57.9* | 599 |
| *Parabuteo unicinctus* | *70.5* | 8.7 | 20.8 | 172 |
| *Buteo polyosoma* | *61.2* | 11.5 | 27.3 | 391 |
| *Bubo virginianus* | 11.4 | 43.0 | *45.6* | 114 |
| *Geranoaetus melanoleucus* | *63.0* | 26.5 | 10.5 | 164 |
| *Dusicyon culpaeus* | *51.5* | 31.6 | 16.9 | 319 |

[a] See text for discussion

**Table 2.** Hunting habitat of nine predator species in central Chile, as evaluated with Spearman rank correlation coefficient ($r_s$) between the abundance of mammalian prey in predators' diet and their abundance in both open and dense habitat patches. Generic name of the predators as in Table 1. $P$ = significance level

| Predators | Open habitat | | Dense habitat | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| *F. sparverius* | *0.603* | < 0.07[a] | 0.279 | > 0.40 |
| *A. cunicularia* | 0.439 | > 0.18 | 0.382 | > 0.25 |
| *E. leucurus* | 0.318 | > 0.34 | 0.418 | > 0.20 |
| *T. alba* | 0.312 | > 0.34 | 0.403 | > 0.22 |
| *P. unicinctus* | *0.600* | < 0.07[a] | −0.130 | > 0.69 |
| *B. polyosoma* | *0.761* | < 0.03 | −0.085 | > 0.79 |
| *B. virginianus* | −0.433 | > 0.19 | 0.148 | > 0.65 |
| *G. melanoleucus* | *0.858* | < 0.01 | −0.091 | > 0.78 |
| *D. culpaeus* | *0.833* | < 0.02 | -0.267 | > 0.42 |

[a] Regarded as marginally significant in the text

Mann 1978; Jaksić et al. 1980b)- and population densities (Péfaur et al. 1979; Schlatter et al. 1980b). These two factors render temporal segregation rather inefficient as a mechanism for clear-cut differential utilization of prey resources by the predators. However, some subtle but significant differences between diurnal and nocturnal predators can be seen at the species level of prey (Appendix 1). The nocturnal *T. alba* and *B. virginianus* consume more of the nocturnal *A. bennetti* and *M. elegans* than any other predators in the area. In addition, *B. virginianus* is the only predator that preys to such a great extent (19.3% of its diet) on *R. rattus*, another nocturnal species. Therefore, differences in the hunting periods have an observable correlate at the level of prey species consumed, but they do not suffice to preclude the exploitation of most of the prey resources by both diurnal and nocturnal predators in the study area.

That six of nine predator species concentrate their hunting activities in the diurnal period contrasts with the lower number of nocturnal predators (two species). This could be the result of the smaller densities attained by nocturnal small mammals in the area, as compared to diurnal ones (Jaksić et al. 1980b). *Elanus leucurus* appears characterized as a crepuscular predator, which constitutes the only discrepancy between the method used to evaluate hunting periods and our personal observations. This raptor is in fact diurnal but with activity peaks at dawn and dusk; Schlatter et al. (1980b) discussed the relationship between its hunting activity time and its available prey in central Chile.

*Habitat Segregation.* Five of nine predator species in the area seem to concentrate their hunting activities in open habitat patches; four species do not exhibit habitat preference (Table 2). The great number of species seemingly hunting exclusively in the open may be related to the high density of small mammals in this type of habitat, which on the average is seven times greater than in dense patches (Jaksić et al. 1980b). This suggests that predators in the area concentrate their hunting activities in habitats where the abundance of small mammal prey is greatest. It is interesting to note that all the predator species that hunt in the open are diurnal; this is probably due to the fact that the most abundant small mammals in open patches are either diurnal or crepuscular (Jaksić et al. 1980b).

The lack of significant correlation between relative availability of different prey in either open or dense patches, and the abundance of those prey in four predator diets (*A. cunicularia, E. leucurus, T. alba, B. virginianus*) suggests that they hunt in both habitat types, that is, that they may be habitat generalists. We must not forget, however, that if these predators hunted in only one habitat type, but took their prey in proportions different than the availability in that habitat patch, the result would be the same: no correlation. On the other hand, the significant or marginally significant correlations found between consumption and availability in five out of the nine cases analyzed (*F. sparverius, P. unicinctus, B. polyosoma, G. melanoleucus, D. culpaeus*), strongly suggest that at least these five predators are not selective in their food habits. That is, once a hunting habitat is chosen (open patches in this case), the predators tend to consume the different prey species in approximately the same proportions as their relative availability in the hunting habitat (which in turn suggests that they are approximately equally catchable, and that none of them is neglected on basis of their size). This hypothesis is certainly more parsimonious than one requiring predators to be prey-selective and not to choose habitat patches of high prey abundance. It is worth noting that the two nocturnal predators, *T. alba* and *B. virginianus*, seemingly hunt in both habitat types. This is associated with their high consumption of three species that are more abundant in dense habitats (*P. darwini, R. rattus, M. elegans;* see Appendix 1; Glanz 1977), which suggests that the nocturnal predators parallel the diurnal, allocating hunting efforts in different patches according to the prey yields.

*Food Segregation.* There are significant, positive correlations between the average weight of predator species and the mean weight of small mammal prey taken ($r_s = 0.97$; $P < 0.001$); between average weight of predator species and variability – as estimated by the standard deviation – of prey weights consumed ($r_s = 0.92$; $P < 0.001$); and between average weight of predator species and food-niche breadth ($r_s = 0.53$; $P < 0.02$) (Table 3). These results are coincident with those reported by other authors working with different predator species (for reviews see Hespenheide 1973; Wilson 1975). It is clear, then, that in comparison with smaller-sized predators the larger ones consume larger prey on the average. This is probably related to their greater killing and handling capabilities, which allow them to safely manipulate larger prey species. Although one fraction of the increased variability in prey sizes included in the diet of large predators is associated with the greater representation of large-sized prey, another important fraction is accounted for by the fact that large predators also prey on small-sized prey. The smaller preda-

**Table 3.** Average weight of nine predator species in central Chile, with corresponding mean size of mammalian prey taken, and food-niche breadth. Generic name of the predators as in Table 1. $\bar{x} \pm$ SD $(N)$ = mean ± standard deviation (sample size)

| Predators | Average weight (g) of predator $\bar{x}$ | Mean weight (g) mammal prey $\bar{x} \pm$ SD | $(N)$ | Niche breadth |
|---|---|---|---|---|
| *F. sparverius* | 120 | 28.1 ± 9.0 | (20) | 2.234 |
| *A. cunicularia* | 250 | 64.5 ± 37.3 | (465) | 1.679 |
| *E. leucurus* | 300 | 50.4 ± 24.3 | (138) | 3.593 |
| *T. alba* | 310 | 109.0 ± 78.2 | (583) | 5.173 |
| *P. unicinctus* | 890 | 214.8 ± 63.0 | (151) | 2.263 |
| *B. polyosoma* | 960 | 213.0 ± 108.3 | (373) | 2.684 |
| *B. virginianus* | 1,500 | 265.8 ± 325.6 | (95) | 6.900 |
| *G. melanoleucus* | 2,000 | 308.2 ± 208.5 | (149) | 2.622 |
| *D. culpaeus* | 8,600 | 337.4 ± 302.2 | (261) | 4.230 |

tors of the community (*F. sparverius*, *A. cunicularia*, *E. leucurus*, *T. alba*), tend to segregate in the mean size of mammalian prey taken (Table 3). On the contrary, the larger predators (*P. unicinctus*, *B. polyosoma*, *B. virginianus*, *G. melanoleucus*, *D. culpaeus*) consume very similar mean prey size. This might at first seem surprising, because the most distinct predators in the smaller group differ by a ratio of 2.6 (310 g/120 g); in the group of larger predators this factor is 9.7 (8,600 g/890 g = ), a ratio almost four times greater. However, the explanation seems to be simple: the mean prey size taken by the larger predators coincides approximately with that of the rodents *Octodon degus* (230 g), and *Abrocoma bennetti* (219 g), which are consumed in high proportions by all of them. Statistically, this contribution causes the mean weight of the small mammal prey taken by *P. unicinctus*, *B. polyosoma*, *B. virginianus*, *G. melanoleucus*, and *D. culpaeus* to be similar in the study area. This will be discussed further in the following section.

*Guilds.* We have already gained some insight about the number and identity of predators utilizing the same environmental resources (either time, habitat, or food), in a similar manner. Hunting time is not a resource that can be partitioned unless it is associated with differential availability of prey resources (Schoener 1974). Because such availability seems to change with time of day in the study area it is possible to distinguish two sets of predator species that hunt at different periods: one is composed of the diurno-crepuscular *F. sparverius*, *A. cunicularia*, *E. leucurus*, *P. unicinctus*, *B. polyosoma*, *G. melanoleucus*, and *D. culpaeus*; another is that of the nocturno-crepuscular *T. alba* and *B. virginianus*. Because it is rather difficult to learn if both diurnal and nocturnal predators have access to crepuscular prey due to the extension of their hunting periods, or to the extended activity periods of crepuscular prey, we prefer to group the predators into these two categories only.

Considering habitat as a resource susceptible to partitioning, a set of predators utilizing open habitat patches can be distinguished, consisting of *F. sparverius*, *P. unicinctus*, *B. polyosoma*, *G. melanoleucus*, and *D. culpaeus*. The rest of predators apparently utilize both open and dense habitat patches and can be considered part of a set of habitat generalists.

In terms of prey resources, two sets of predators are readily recognized: those of small size (120 g–310 g) that apparently segregate in the mean prey size taken; and those of larger size (890 g–8,600 g) that concentrate their predation on a very similar mean prey size and in particular, on two prey species.

The intersection among all these sets of predators (recognized on the bases of their similarity in utilization of temporal, habitat, and food resources), may be regarded as a description of the internal organization of the predator community in terms of guilds. However, resource partitioning along either temporal or habitat dimensions of the niche is possible only if prey species also segregate along these axes. As we have discussed, these three axes are nearly orthogonal in the community studied, because there is not a complete turnover in the composition of prey resources, neither between habitats nor between activity periods. This is not unexpected, because of the relatively low renewal rates of mammalian prey resources in the area (see Jaksić et al. 1980b). The situation is even more confounded by the lack of clearcut habitat segregation and hunting periods of the predators. Therefore – since there are no good correlations between the food, habitat, and time axes – it is completely reasonable to try to recognize predator guilds solely on food-niche overlap patterns, because the activity times and habitat selection of both predators and prey are thereby implicitly included. In the subsequent analysis, the two snake species are considered.

Three categories of food-niche overlap may be arbitrarily distinguished: low (0.00–0.33), medium (0.34–0.66), and high (0.67–1.00). Table 4 shows that out of 55 overlap measurements, 40 can be regarded as low, 7 as medium, and another 8 as high overlap. How should we assess whether this pattern presents an excess of low and medium categories, thus suggesting a response to interspecific competition? One way would be to make a random matrix by stochastically reassigning the proportions of different prey in the diet of each predator (therefore, not changing their food-niche breadth), then calculating the niche overlaps again. By repeating this whole process 99 times, it would be possible to determine whether the pattern observed with actual data is one of the five presenting the highest number of low

**Table 4.** Food-niche overlaps between nine predator species in central Chile. Values near 0 indicate minimum overlap (very dissimilar diet), values near 1 indicate maximum overlap (very similar diet). Generic name of the predators as in Table 1

| Predators | *A. cunicularia* | *E. leucurus* | *T. alba* | *P. unicinctus* | *B. polyosoma* | *B. virginianus* | *G. melanoleucus* | *D. culpaeus* | *P. chamissonis* | *T. peruviana* |
|---|---|---|---|---|---|---|---|---|---|---|
| *F. sparverius* | *0.971* | 0.058 | 0.033 | 0.043 | 0.039 | 0.073 | 0.041 | 0.053 | 0.138 | 0.116 |
| *A. cunicularia* | – | 0.068 | 0.074 | 0.049 | 0.056 | 0.026 | 0.045 | 0.050 | 0.017 | 0.006 |
| *E. leucurus* | | – | 0.439 | 0.186 | 0.212 | 0.210 | 0.176 | 0.219 | 0.049 | 0.000 |
| *T. alba* | | | – | 0.431 | 0.537 | 0.413 | 0.348 | 0.430 | 0.015 | 0.000 |
| *P. unicinctus* | | | | – | *0.983* | 0.129 | *0.951* | *0.904* | 0.054 | 0.048 |
| *B. polyosoma* | | | | | – | 0.188 | *0.951* | *0.923* | 0.020 | 0.005 |
| *B. virginianus* | | | | | | – | 0.168 | 0.390 | 0.078 | 0.000 |
| *G. melanoleucus* | | | | | | | – | *0.975* | 0.037 | 0.009 |
| *D. culpaeus* | | | | | | | | – | 0.049 | 0.000 |
| *P. chamissonis* | | | | | | | | | – | *0.954* |

and medium niche overlaps (or simply the lowest mean overlap). Then, if $P < 0.05$, the null hypothesis of a random arrangement of niche overlaps would be rejected (we thank R.K. Colwell for suggesting this; see also Pianka et al. 1979). Although ingenious, this method would be time-consuming, given the amount of information that must be processed to obtain the matrix overlaps. It is worth noting that this method assumes that all prey items are equally catchable by any predator – which is probably not realistic in many cases. At any rate, without doing so we cannot conclude at present that the predator community in the study area tends to minimize food-niche overlap by segregating along any of the niche axes described. The observed segregation may well be the result of stochastic differences among the predators.

At this point, it may be more interesting to discuss how it is possible that eight pairs of predator species (involving eight different species) can coexist despite having food-niche overlaps greater than 90% (Table 4). The pair *F. sparverius-A. cunicularia* appears to constitute a guild of diurnal carnivore-insectivore raptors that otherwise tend to differ in their habitat utilization pattern (Table 2) and mean size of small mammal prey taken (Table 3), the latter probably associated with their different body size. The pair of snakes *P. chamissonis-T. peruviana* separates from the other predators in their herpetophagous habits, thus forming another feeding guild. They are diurnal (Donoso-Barros 1966), but their habitat preferences are not known, although personal observations suggest that they utilize open habitat patches more frequently than dense ones. A possible food-niche difference between the two species could be caused by the larger size attained by *P. chamissonis,* which allows this species to hunt larger prey items when adult-sized (Greene and Jaksić, unpublished). However, food overlap seems to be extensive when considering similarly-sized snakes of both species (Greene and Jaksić, unpublished). Clearly, more research is needed on the ecological partitioning (if any) of these snakes in central Chile.

Four species, the falconiforms *P. unicinctus, B. polyosoma, G. melanoleucus,* and the carnivore *D. culpaeus,* present very high food-niche overlaps. All have diurno-crepuscular activity periods, hunt in open patches, and take a similar mean prey size. Also, all of them prey heavily on *O. degus* and *A. bennetti* (see Appendix 1, and Jaksić et al. 1979, 1980a, 1980b, 1980c, Schlatter et al. 1980a). In combination, these two rodents comprise 77.3%, 69.6%, 65.3%, and 52.8% of the total prey of the above predators, respectively. With the exception of rabbits (*Oryctolagus cuniculus*), the two rodent species are the largest prey in the area. Hence, their importance as energetic resource of these predators is even greater than suggested by their numerical representation. *Octodon degus* is demonstrably the most abundant of the mammalian prey in the study area (Le Boulengé and Fuentes 1978; Yáñez and Jaksić 1978; Jaksić et al. 1980b), and it is likely that *A. bennetti* also reaches high densities. Jaksić et al. (1980a) pointed out that *A. bennetti* is extremely trap-shy and Fulk's (1976) results also suggest that this rodent is much more easily seen than trapped. This indicates that the usual trapping techniques tend to underestimate the density of *A. bennetti* in the field. Consequently, the combined high abundances of both *O. degus* and *A. bennetti* in the study area might cause some raptors and carnivores to hunt diurnally in the open habitat patches occupied by these rodents, and to prey heavily on them, given that the predators are large enough to kill and handle them. Thus, the raptor and carnivore species involved constitute a tight guild whose packing not only occurs along the food dimension of the niche, but also along the habitat and activity time axes. No evident segregation in the utilization of these resources occurs, leading to the conclusion that the abundance of certain prey resources of profitable size favors the convergence of a group of differently-sized predators to hunt in the same habitat type, during the same time period, on the same basic prey.

Only three of the eleven predators in La Dehesa-Los Dominicos do not appear to form guilds. It is noteworthy that two of these are the only nocturnal species in the area, the owls *B. virginianus* and *T. alba.* Jaksić and Yáñez (1980), based on the same data presented here, concluded that these two species exhibit low food-niche overlap because of the larger size of *B. virginianus,* which allows this owl to prey on the heavier small mammals available (particularly on rabbits, never found to be prey of *T. alba* in central Chile), and perhaps also because of different hunting habitats and activity times. *Bubo virgianus* is a known predator of *T. alba* in other regions (Herrera and Hiraldo 1976; Rudolph 1978), and it has been documented that this latter species avoids the former by shifting its activity period (Rudolph 1978). Consequently, the differences in food between *B. virginianus* and *T. alba* might not be the result of competition, but rather of different body sizes coupled with predation interactions. The third predator, *Elanus leucurus,* again appears as a unique raptor (see above), which may be related to its peculiar hunting behavior (Meserve 1977; Schlatter et al. 1980b).

Ecologists interested in species diversity questions (e.g., MacArthur 1972) have typically considered the number of species in a community, the distribution of individuals among these taxa, the total niche space (usually in terms of habitat, time, and food), and the amount of niche overlap (usually in terms of summary statistics). Colwell (1979) emphasized that the degree to which species are organized into guilds represents an additional structural parameter of communities, and he stressed that the detailed study of these functionally integrated units is likely to further clarify patterns of species richness in time and space, ecological and coevolutionary dynamics, the origin and integration of multispecies assemblages, and other community phenomena (see also Pianka et al. 1979). A key requirement for such an analysis is that the guilds be recognized by quantitative, nonapriori methods (rather than as taxonomic assemblages). Our application of Inger and Colwell's (1977) technique indicates that the community of vertebrate predators in La Dehesa-Los Dominicos includes guilds averaging three species each (there is a definite peak in the standard deviation of mean food-niche overlap with the third nearest neighbor), that these guilds are actually composed of two or four species, and that overlap is extremely high within each guild (>90%). The quantitative assessment of guild structure coincides with our more qualitative judgement based on Tables 1–4. It is worth emphasizing that these results are not consistent with theoretical predictions regarding the limiting similarity of species along a resource axis (MacArthur and Levins 1964, 1967), and that they would not have been evident in a simple expression of mean overlap or even mean guild size. Our results suggest further questions: To what extent and under what conditions *is* food directly limiting as a resource for vertebrate predators? How prevalent is the type of organization we describe, and does "guildiness" vary among communities? Quantitative studies of other objectively defined guilds in a variety of environments would clearly be valuable.

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**Appendix 1.** Percent by numbers of prey categories in the study area. Open and dense patch columns refer to trapping results; columns under predators refer to dietary results. Predators are ordered from left to right by increasing size

| Prey categories | Activity period | Weight (g) | Open patch | Dense patch | *Falco sparverius* | *Athene cunicularia* | *Elanus leucurus* | *Tyto alba* | *Parabuteo unicinctus* | *Buteo polyosoma* | *Bubo virginianus* | *Geranoaetus melanoleucus* | *Dusicyon culpaeus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mammals | | | | | | | | | | | | | |
| *Abrocoma bennetti* | N | 219 | 1.6 | 0.0 | 0.0 | 0.3 | 0.0 | 18.5 | 12.8 | 12.0 | 18.4 | 7.6 | 11.6 |
| *Akodon longipilis* | C | 76 | 0.0 | 27.3 | 0.0 | 0.7 | 10.0 | 4.8 | 1.2 | 0.0 | 16.7 | 0.0 | 0.0 |
| *Akodon olivaceus* | C | 40 | 8.9 | 0.0 | 1.1 | 3.5 | 34.4 | 6.0 | 1.2 | 2.6 | 0.8 | 0.0 | 4.1 |
| *Marmosa elegans* | N | 40 | 1.1 | 36.4 | 0.0 | 0.4 | 0.0 | 6.7 | 0.0 | 1.0 | 3.5 | 0.0 | 0.0 |
| *Octodon degus* | D | 230 | 80.1 | 0.0 | 1.8 | 3.2 | 8.6 | 12.0 | 64.5 | 57.6 | 0.0 | 57.7 | 41.2 |
| *Oryctolagus cuniculus* | C | [a] | prst[b] | abst[c] | 0.0 | 0.1 | 0.0 | 0.0 | 1.2 | 6.1 | 15.8 | 18.8 | 19.7 |
| *Oryzomys longicaudatus* | C | 45 | 2.4 | 27.3 | 2.4 | 2.8 | 37.1 | 16.4 | 0.0 | 1.8 | 4.4 | 0.6 | 0.0 |
| *Phyllotis darwini* | N | 66 | 5.9 | 9.0 | 0.0 | 4.0 | 1.3 | 32.7 | 7.0 | 14.3 | 4.4 | 2.9 | 5.3 |
| *Rattus rattus* | N | 158 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 19.3 | 0.0 | 0.0 |
| *Spalacopus cyanus* | C | 112 | prst[d] | abst[e] | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Unidentified | C | – | – | – | 5.8 | 1.6 | 6.6 | 0.7 | 5.1 | 1.0 | 5.3 | 7.1 | 7.8 |
| Birds | | | | | | | | | | | | | |
| Unidentified passeriform | D | – | – | – | 12.7 | 1.0 | 2.0 | 2.0 | 1.2 | 3.3 | 11.4 | 1.2 | 3.4 |
| Unidentified egg | D | – | – | – | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 2.2 |
| Reptiles | | | | | | | | | | | | | |
| *Liolaemus* spp. | D | – | – | – | 8.2 | tr[f] | 0.0 | 0.0 | 3.4 | 0.3 | 0.0 | 0.6 | 0.0 |
| *Philodryas chamissonis* | D | – | – | – | 1.1 | 0.0 | 0.0 | 0.0 | 1.2 | 0.0 | 0.0 | 3.5 | 4.7 |
| *Tachymenis peruviana* | D | – | – | – | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| Amphibians | | | | | | | | | | | | | |
| *Bufo chilensis* | N | – | – | – | 0.0 | 1.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pleurodema thaul* | N | – | – | – | 0.0 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Insects | D | – | – | – | 64.8 | 76.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Arachnids | D | – | – | – | 0.2 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Chilopods | D | – | – | – | 1.9 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Crustaceans (Isopoda) | D | – | – | – | 0.0 | 1.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total by No. | – | – | 371 | 110 | 378 | 3038 | 151 | 729 | 172 | 391 | 114 | 164 | 319[g] |

[a] Kittens (< 1 month), 80 g; juveniles (3–6 months), 534 g; adults (> 9 months) 1,300 g

[b] Present; assessed by sightings and signs; traps used were inappropriate for its capture; assigned rank 9 in abundance (second highest)

[c] Absent; no sightings, no signs of its presence; assigned rank 3.5 (lowest possible for the tied group with zero abundances)

[d] Present; assigned rank 3 in abundance (second lowest possible)

[e] Absent; assigned rank 3.5 in abundance (see *c*)

[f] Trace; representation in the sample less than 0.1%

[g] This fox includes berries in its diet, but they are not considered as prey here

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