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Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America

Relaciones depredador-presa entre vertebrados terrestres: una revisión exhaustiva de estudios realizados en el cono sur sudamericano

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ABSTRACT

We review the available information on predator/prey relationships among southern South American terrestrial vertebrates, as dichotomized into two topics: effects of predators upon their prey, and effects of prey on their predators. We describe what is known (and to what extent) and not known of predation-related phenomena in southern South America. We identify different trends and emphases, as well as current gaps of knowledge. By following the recent course of predation-related research in Chile, we provide a study case from an historical perspective. Finally, we describe potentially fruitful avenues of inquiry and suggest prospects for future research on predator/prey relationships.

Key words: Predation, predators, prey, amphibians, reptiles, birds, mammals, South America, Chile, Argentina.

RESUMEN

Revisamos la información disponible sobre relaciones depredador-presa en vertebrados terrestres del cono sur sudamericano, dicotomizada en dos tópicos: efectos de depredadores sobre sus presas y efectos de presas sobre sus depredadores. Describimos lo que se sabe (y en qué medida) y no se sabe sobre fenómenos predatorios en el cono sur sudamericano. Identificamos diferentes tendencias y énfasis, así como áreas de desconocimiento actuales. Siguiendo el curso de investigaciones sobre depredación en Chile, proveemos un estudio de caso desde una perspectiva histórica. Finalmente, describimos avenidas de investigación potencialmente fructíferas y sugerimos nuevas líneas a seguir en el estudio de las relaciones depredador-presa.

Palabras claves: Depredación, depredadores, presas, anfibios, reptiles, aves, mamíferos, Sudamérica, Chile, Argentina.

INTRODUCTION

We understand predator/prey relationships as a two-way interaction. Predators may have direct effects on prey individuals (e.g., causing them loss of fitness, injury, or death), and indirect effects on population structure (e.g., selecting particular phenotypes) and on assemblage organization (e.g., reducing the number of potential competitors). Concomitantly, the prey base may affect its predators in several ways. For example, by directly determining the presence and abundance of particular predators, and by indirectly providing a resource axis along which predators may aggregate (forming multispecific guilds) or segregate (effecting resource partitioning). In this latter case, the prey level may indirectly affect the diversity and relative species abundances of the predator trophic level.

With this conceptual framework we review the available information about predator/prey relationships among South American terrestrial vertebrates, as dichotomized into two major topics: effects of predators upon their prey, and effects of prey on their predators. Our aim is to describe what is known (and to what extent) and not known of predation-related phenomena in southern South America. We attempt to identify different trends and emphases, as well as current gaps of knowledge. By following the recent course of predation-related research in Chile, we provide a study case from an historical perspective, and discuss what we consider has been the scientific contribution of Chilean ecologists to studies

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of predation. Finally, we describe what we think are potentially fruitful avenues of inquiry and suggest prospects for future research on predator/prey relationships.

LIMITATIONS & DISCLAIMERS

Four limitations and one disclaimer deserve clarification. 1) Owing to our limited expertise (terrestrial vertebrates), we have considered as prey only the terrestrial members of the Classes Amphibia, Reptilia, Aves, and Mammalia. Similarly, we have considered as predators only those terrestrial members of the Classes Reptilia (snakes), Aves (hawks and owls), and Mammalia (carnivores) that prey mainly on live vertebrates. We have disregarded those predators that feed largely or exclusively on carrion or insects. 2) Because of our limited familiarity with the regional literature (southern South America) we have restricted our geographic coverage to neighboring Chile and Argentina. 3) Although we examined literally hundreds of primary literature sources, restrictions of space do not allow listing of all the publications consulted. However, they may be traced from the bibliographies of those actually listed in this review. 4) We ended our literature search in August 1986; consequently our review reflects the state of the art up to this date. 5) Although we use the term "effect of predators (or prey) on" quite profusely, it should be understood that what is implied is "presumed effect on".

METHODS

We examined all the primary literature sources to which we had access, scanning for claims on aspects of predator/prey relationships ranging from sheer speculation through casual observation to quantitative documentation. We accommodated all this information into two major categories: effects of predators on prey, and of prey on predators. Within the first category we distinguished effects: 1) at the prey individual level (in terms of habitat use, time use, and phenotype – including morphology and behavior), 2) at the prey population level (including age structure, demography, breeding biology, and life history tactics), and 3) at the prey assemblage or taxocene level (including species richness and relative abundance).

Within the category of effects of the prey on the predators, we also recognized the same three major subdivisions, although considering phenomena that are more peculiar to predators. 1) At the predator individual level we considered such phenomena as functional response, prey-switching, optimal foraging, and hunting mode. 2) At the predator population level we considered the phenomenon known as numerical response (including migration), and 3) at the assemblage level that of interspecific segregation (implying competition for prey), and aggregation (implying opportunistic use of abundant prey) along the prey resource axis.

I) *Effects of Predators on Prey*

In what follows, the presumed effects of predation by whichever vertebrate predator or group of predators are examined under headings that identify the prey by Class, and information from Chile and Argentina is presented in the same sequence.

Amphibians

Habitat Use:

No references are available on predation effects in either Chile or Argentina.

Time Use:

No references are available on predation effects in either Chile or Argentina.

Morphology & Behavior:

In Chile, Cei (1962) has considered the skin secretion of frogs in the genera *Bufo, Batrachyla* and *Hylorina* as deterrent to predators. Indeed, the owl *Athene cunicularia* kills but does not eat the toad *Bufo chilensis* or the frog *Pleurodema thaul,* the owl rejects these anurans after tasting their seemingly unpalatable secretion (Schlatter *et al.* 1980c). Díaz *et al.* (1983) reported that the frog *Insuetophrynus acarpicus* jumps into the water when disturbed, and seeks shelter under rocks. Anecdotal information refers the escape of the southern frog *Rhinoderma darwini,* which jumps into water courses belly-up and lets itself be passively transported down the course when approached by potential predators. Although the dorsum of this frog is green, its belly is a mixture of yellowish and dark-bluish patches, thus conveying to the observer the impression of dead leaves floating on a stream (M. Sallaberry, personal communication). The frog *Caudiverbera caudiverbera,* however, adopts a threatening posture when disturbed (Donoso-Barros 1972).

In Argentina, Gallardo (1979) and Bucher (1980) have deemed aposematic the coloration of the frogs *Leptodactylus laticeps* and *Melanophryniscus stelzneri,* suggesting that it advertises their toxic secretion. Mares *et al.* (1977: 115) reported that the frog *Pleurodema nebulosa* jumps into the water when disturbed. Numerous notes on the natural history of Argentine amphibians, some of which may be interpreted as anti-predator adaptations, have been reported by Cei (1980).

Population Structure:

Low (1976) has proposed that predation is a major factor influencing life-history tactics of amphibians. She specifically cited the Chilean frog *Rhinoderma darwini* as exhibiting traits related to reduction of predation risks during vulnerable stages, referring that males guard the eggs, and later provide protection to their tadpoles by carrying them in the vocal sac. However, studies of anuran adaptations to life in the Monte Desert (Argentina), failed to consider predation as a selective force (Blair 1976, Mares *et al.* 1977).

Assemblage Structure:

Analyses of the assemblage structure of both high Andean (Duellman 1979, Péfaur & Duellman 1980) and Monte Desert (Mares *et al.* 1977) herpetofaunas (frogs and reptiles included), do not mention predation as an influencing factor of the patterns detected.

Summary:

Several morphological, behavioral, and life-history traits of amphibians have been interpreted as predation-related phenomena, but the causal relationships have not been demonstrated. The impact of predation on habitat and time use, and on assemblage structure remains to be evaluated. Most of the information available is either anecdotal or descriptive. No advantage has been taken of correlational or comparative methods. Neither field nor natural experiments have been used at all.

Reptiles

Habitat Use:

In Chile, predation has been considered to be an important force in determining the habitat use of several lizards. The evidence from four studies conducted in central Chile is as follows. 1) The rock/sand segregation of *Liolaemus nigromaculatus* and *L. platei* is associated with the former being territorial, conspicuously colored (*i.e.*, highly detectable by visually-oriented predators), and restricted to potential shelters (rocks); the latter being non-territorial, cryptically colored, and ubiquitous in open sand (Fuentes & Cancino 1979). 2) The rock/ground segregation of *L. fuscus* and *L. lemniscatus* is correlated with dark coloration and longers legs in the former, and lighter color and shorter legs in the latter. Whereas the former escapes by jumping and hiding among dark rocks, the latter runs into grass patches, where its coloration appears cryptic (Jaksić & Núñez 1979). 3) The geographical replacement of the relatively long-legged, bare-ground dweller *L. platei* by the shorter-legged dweller of grassy fields *L. lemniscatus* occurs along a gradient of herb density. *Liolaemus platei* is considered to be ill-fitted to escape predators in grassy areas because of its longer legs; the opposite applying to *L. lemniscatus* (Fuentes & Jaksić 1980). 4) *Liolaemus kuhlmanni* restricts its spatial activity to the vicinity of shrubs, associated to high predation risks in open areas (Simonetti & Ortiz 1980). Moreover, this lizard does not behave optimally if thermoregulation is the process to be maximized by microhabitat selection; apparently, a compromise is reached in terms of minimizing predation risks (Simonetti 1984).

In a different vein, Jaksic & Fuentes (1980) documented the incidence of regenerated tails among 12 species of *Liolaemus* lizards, and reported that it is not correlated with the degree of sexual dimorphism (an estimate of territoriality and aggressive behavior), or with size (an estimate of life span) but with the degree of use of conspicuous perches. They interpreted this latter phenomenon as reflecting lizards' successful escapes from visually-hunting predators, and proposed that the incidence of regenerated tails should be positively correlated with predator inefficiency but not with predation pressure. Tests of this hypothesis in California and Spain showed that the incidence of regenerated tails in local lizards is actually uncorrelated with predation pressure (Jaksić & Busack 1984, Jaksić & Greene 1984), thus providing support to Jaksić & Fuentes' (1980) contention.

In Argentina, the habitat use of Monte Desert reptiles was described by Mares *et al.* (1977), but without reference to predation.

Time Use:

Although daily and seasonal shifts in activity time of lizards have been documented in Chile, these findings have been considered as a response to climatic variables and associated changes in food supply (*e.g.*, Fuentes 1976). Predation effects have not been considered.

In Argentina, information on activity time of reptiles is available, but no attempt has been made to relate it to predation (see Mares *et al.* 1977).

Morphology & Behavior:

In Chile, territorial, dimorphic (in both size and color) lizards are restricted to microhabitats that seemingly offer adequate shelter from predation; *i.e.*, they are sit-and-wait. On the contrary, dwellers of open spaces tend to be neither dimorphic nor territorial; *i.e.*, they are wide-foragers (Donoso-Barros 1960, Fuentes 1977, 1981, Fuentes & Cancino 1979, Manzur & Fuentes 1979). Open-space dwellers apparently are subject to heavy predation: Webb & Greer (1969) reported that pasture-dwelling (wide-foraging) lizards were frequent prey of raptors in Malleco, in contrast to sympatric forest lizards of presumably sit-and-wait habits. Similarly, in California and Spain wide-foraging lizards are more frequent in predator diets than sit-and-wait lizards (Jaksić & Greene 1984, Jaksić & Busack 1984). As noted above (Habitat use), the different escape response of *Liolaemus fuscus* and *L. lemniscatus* was attributed to predation (Jaksić & Núñez 1979).

Jaksić & Schwenk (1983) suggested that the higher prevalence of the greyish morph of *Liolaemus magellanicus* in sandy areas of Tierra del Fuego, and of the greenish morph in grasslands, was due to predation. They implied that these morphs were cryptic in the respective habitats. Fuentes & Ipinza (1979) described that *Liolaemus monticola* is not only strictly myrmecophagous, but eats ants in essentially one genus. Unlike myrmecophagous lizards in the genera *Phrynosoma* (North America) and *Moloch* (Australia), *L. monticola* is a rock-dweller and has the generalized morphology of a typical *Liolaemus.* They proposed that the bizarre morphology of *Phrynosoma* and *Moloch* may have more to do with reducing predation risks in open habitats than with myrmecophagy *per se.* Interestingly, Jaksić *et al.* (1982b) showed that predation pressure appears lighter on six central Chilean lizards studied (as compared to lizards in California and Spain) and discussed that this comparatively reduced predation had affected more clearly behavioral (such as habitat use, territoriality), rather than morphological traits in *Liolaemus* (see also Sage 1973).

Mares *et al.* (1977: 129), in the context of ecological convergence, described the matching of species analogs between the U. S. Sonoran Desert and Argentina's Monte Desert. They reported that "In *Homonota* [an Argentine gecko] the tail is thinner than in *Coleonyx* [a U. S. gecko] and the lizards do not exhibit the marked functioning as a caudal lure behavior characteristic of *Coleonyx,* and the tails break off less easily". Mares *et al.* (1977) thus suggested that predation pressure upon *Homonota* was smaller than upon *Coleonyx.*

Population Structure:

Almost no documentation exists regarding the role of predation in reptile age-structure, demography, breeding biology, or life-history traits. Fuentes (1977), analyzing the "clutch" sizes of different populations of *Liolaemus nigromaculatus* along a north-south gradient, suggested that large "clutch" sizes and long pre-reproductive periods were associated with reduced predation pressure.

No reference is made by Mares *et al.* (1977) to the potential impact of predation on population phenomena of Argentine reptiles.

Assemblage Structure:

Sage (1973) provided the first overview of assemblage structure of five central Chilean *Liolaemus* within the framework of ecological convergence in mediterranean-type ecosystems. He did not, however, make any reference to predation, but concentrated on patterns of niche segregation and associated morphological attributes. Fuentes (1976) also emphasized the role of competition for resources (mainly food and microhabitat) as a force providing structure to lizard assemblages in Chile (nine species in three sites) and California, but later he (Fuentes 1977, 1981) conceded that the role of predation had not adequately been examined, indicating that it affected the ecology of several species, including *L. nigromaculatus, L. platei, L. tenuis,* and *Callopistes maculatus.* Jaksić *et al.* (1982b), finding low levels of predation upon lizards in Chile, as compared to Spain and California, speculated that the low generic diversity of the central Chilean herpetofauna was associated with this phenomenon.

In Argentina, Mares *et al.* (1977) examined niche patterns of Monte Desert reptiles, but failed to relate them to predation. Similarly, Duellman (1979) and Péfaur & Duellman (1980) analyzed assemblage structure of high Andean herpetofaunas, including Argentine localities, but did not consider predation as a potential modifier of the patterns detected.

Summary:

Observational and correlational evidence (largely based on Chilean data, usually presented within a comparative framework) suggests that habitat use, morphology, behavior, and assemblage structure of lizards are influenced by predation. Predation effects have also been suspected to affect some life-history tactics, but the evidence is weak. Nothing is known about its potential effect on time use by lizards. Generally, good advantage has been taken of the comparative approach and of natural experiments. Perhaps field experimentantion could be put to work in order to corroborate some of the findings.

Birds

Housse (1945) provided colorful accounts on the natural history of Chilean birds, which he interpreted in an adaptationist context, usually in anthropocentric terms. Potentially useful information of predation effects on morphological, ecological, and behavioral traits (including escape tactics) is thus marred by the loss of credibility attained through sheer story-telling. In the words of Peters (1947: 46) "There are many valuable original observations, but there also seems to be included a certain amount of hearsay and it is not always simple to tell where the original part ends and the hearsay begins". Although we may be making a grave injustice to Housse (1945), we have chosen not to rely on his accounts. Buckley *et al.* (1985) edited a volume on Neotropical ornithology that includes three papers (Skutch's, Powell's, and Robinson's) that have as a major focus the potential effects of predation on the biology or interspecific relationships of Neotropical birds, but dealt with countries other than Chile and Argentina. Other papers in the same volume, that specifically refer to birds in these two countries are discussed below.

Habitat Use:

Habitat use of Chilean birds (mainly passerines) was studied extensively by Cody (*e.g.*, 1970, 1973, 1974), but he emphasized ecological segregation as mediated by competition for resources (mainly food, as attained through segregation in habitat, microhabitat, and foraging tactics). Actually, Cody (1974: 213-214), when recognizing that predation may affect niche patterns of birds, failed to cite a single bird example. Simonetti *et al.* (in press) reported that in northern Chile the insectivorous *Anairetes parulus, Leptasthenura aegithaloides, Tripophaga humicola,* and *Troglodytes aedon* all concentrate their foraging activities to *Eulychnia* cacti. Despite being less abundant than other shrubs, *Eulychnia* seems to afford better protection to birds against predators, as well as more insect food.

Ralph (1985), in southern Argentina, and Vuilleumier (1985), in Chile-Argentina Patagonia, studied diversity, abundance, and distributional patterns of forest and steppe birds in relation to structural features of the habitats they inhabited. In neither case was bird distribution mentioned to be potentially modified by predation.

Time Use:

No references are available on predation effects in either Chile or Argentina.

Morphology & Behavior:

No references are available on predation effects in either Chile or Argentina.

Population Structure:

Myers *et al.* (1985) discussing why sanderlings (*Calidris alba*) winter in high numbers in Chile and Peru, but not in California, proposed predation as a possible underlying factor (predation pressure on sanderlings may be lower in the southern hemisphere). They admitted, however, that with the available data this hypothesis could not be tested.

In Argentina, Murton *et al.* (1974) described that the dove *Zenaidá auriculata* nests in thornscrub habitats at a height corresponding to that affording maximum cover, presumably as a defence against predators. Interestingly, the same species nests on the ground in thornscrub areas of northeastern Brazil, where it is subjected to heavy predation (Bucher 1982). Bucher interpreted this paradox as natural selection maximizing a short breeding season (60 days) synchronized with the transient period of abundant food supply (seeds). Synchronized ground-nesting minimizes the time lost in building an aerial nest, and may saturate local predators by not allowing the build-up of their population numbers in such a short time.

According to Mares *et al.* (1977) Monte Desert birds appear to be influenced by predation pressure in using spiny shrubs as nesting places (so minimizing egg and nestling mortality), despite the greater availability of non-spiny shrubs (see the next heading). Humphrey & Livezey (1985), referring to Steamer Ducks (*Tachyres* spp.), Mason (1985), to passerines, and Escalante (1985), to Royal Terns (*Sterna maxima*), all reported on these birds' losses to predators (mainly of eggs, secondarily of nestlings). However, they did not elaborate on what effects predation had in the population structure of the birds studied.

Assemblage Structure:

Cody (1970, 1973, 1974) interpreted assemblage structure of Chilean passerines as emerging from exploitative competition for food resources. This competition resulted in macro- and micro-habitat segregation, complemented by differential foraging tactics. He did not consider predation as a force likely to influence bird assemblages. On the other hand, Jaksić (1982) analyzed food-niche relationships of sympatric hawks and owls in several regions (including central Chile), and proposed that the observed structure emerged as a result of gaps in resource space. He also stated that if any interactions aided in producing structure, they were more likely of the interference-type, not of the exploitative-type. Jaksić (1982) considered predation among hawks, among owls, and between hawks and owls to be an important –if extreme– form of interference competition.

In Argentina, Myers (1980) studied interactions between Nearctic and Neotropical shorebirds (Charadriiformes). He also emphasized the role of interference interactions (interspecific predation included) in producing niche patterns.

In a different vein, Mares *et al.* (1977: 142) analyzed ecological convergence in habitat use between bird assemblages in U.S. and Argentina deserts. They reported that "This convergence reflects strong predation pressure on nesting desert birds and the poor protection provided by the dominant sclerophyll desert shrubs". Orians & Solbrig (1977: 244) reported that the number of bird species in the two deserts could be predicted from measures of foliage height diversity (which is what Cody 1973, 1974, found in Chile and California). But they also noted that in the deserts studied"the addition of just a few individuals of a spinescent shrub, for instance, may increase bird species diversity more than its effect on foliage height diversity would suggest". This because "Birds of both deserts make extensive use of cacti and spinescent shrubs for nesting sites, including species that forage primarily or entirely on other substrates. Therefore, these data indicate a real convergence in desert bird community structure toward a pattern distinct from that found in more mesic habitats" (referring to Cody's matorral/chaparral study sites).

Apparently, then, convergence not only may result from competitive segregation over food resources in short supply, as postulated by Cody (1973, 1974), but may also be caused by similar predation pressures, and resulting patterns of refuge use.

Summary:

Virtually nothing is known about the potential effects of predation on habitat and time use by birds, or on their behavior and morphology. Comparative evidence suggests that some life history tactics (particularly those associated to breeding) could be influenced by predation. Assemblage structure also appears to be affected by predation – or by competition of the interference type. Cody's views of bird assemblage structure as resulting exclusively from competition-mediated resource partitioning need to be re-examined. The comparative approach has been widely applied, but perhaps natural experiments could be used more extensively.

Mammals

Housse (1953) provided interesting accounts on the natural history of Chilean mammals, but for the same reservations expressed above about his bird accounts, we prefer not to use this reference. Mann (1978) was a more reliable source, although he tended to assign adaptive value to phenotypic traits, based on deductive logic and on archaic notions of the "psychic" capabilities of small mammals. Castillo *et al.* (1978) provided a succint account of which species of rodents have been recorded as prey of Chilean and Argentine predators. Mares & Genoways (1982) edited a volume with a wide array of contributions to the knowledge of mammalian biology in South America. Chilean and Argentine mammals were referred to in a variety of contexts, but predation effects on their biology and interspecific relationships were not explicitly dealt with. On the other hand, Simonetti & Otaíza (1982) made a state-of-the-art review on the ecology of central-Chilean small mammals, explicitly assessing the role of predation in affecting their population dynamics, habitat and time use, and niche segregation. Simonetti (1986a) specifically tested hypotheses associating predation to habitat use. Jaksić (1986b) discussed the correlations, and presumable causes and consequences of predation upon small mammals in Chile and Argentina. These three recent reviews summarized most of what is known about predation effects on southern South American mammals. Under this circumstance, below we discuss only specially relevant examples whose details may be found in either of the reviews, or examples that were not included in either.

Habitat Use:

Restricted habitat use as a consequence of predation has been documented by several authors working in central Chile. Fulk (1976b), Glanz (1977), Mann (1978), Jaksić *et al.* (1979), and Meserve *et al.* (1984) suggested that as a consequence of the high predation pressure it experiences, the rodent *Octodon degus* restricts its activities to the vicinity of potential shelters such as bushes, burrows, and rock piles. In addition, Fulk (1976b), Mann (1978), Yáñez & Jaksić (1978), and Le Boulengé & Fuentes (1978) proposed that as a means of reducing predation risk, *O. degus* moves between neighboring shelters minimizing the distance covered (and presumably the time spent) in open areas, thus generating conspicuous, straight-line surface runways. Yáñez & Jaksić (1978) further suggested that, when the distance between two neighboring patches of habitat or shelters is too long, *O. degus* builds short, shallow underground tunnels for use as intermediate, temporary refuges.

Restricted habitat use as related to predation pressure has been documented in five other Chilean studies: 1) Mann (1978) reported observations similar to those referred above for *O. degus* in the rodents *Microcavia australis* and *Lagidium viscacia* of southern and central Chile, respectively. 2) Péfaur *et al.* (1978) showed that feral *Mus musculus* in a central Chilean grassland were most frequently trapped in tall grass rather than in short grass patches, and attributed this phenomenon to their avoidance of patches where they may be more vulnerable to owl predation. 3) Murúa & González (1982) attributed the differential microhabitat selection of the rodents *Akodon olivaceus* and *Oryzomys longicaudatus* in southern Chile to predation pressure. According to them, the former species "is associated with vegetational variables that provide greater cover from above" (implying avoidance of aerial predators?). The latter is associated to scrub's "dense areas with understory that offer protection from a horizontal viewing" (implying higher predation risks from terrestrial predators?).

4) Simonetti *et al.* (1985) reported restriction of spatial activity close to potential shelters (shrubs, burrows, and boulders) by two montane rodents of central Chile, *Akodon andinus* and *Phyllotis xanthopygus.* When shrubs were cut and subsequently placed elsewhere, rodents disappeared from previously used areas, and appeared where the shrubs were relocated, in areas where no rodent had been previously captured. They also documented that neither rodent was present in grassy areas, but both occurred in pastures where burrows of the rodent *Spalacopus cyanus* provided shelters. 5) Simonetti (1986a) reported that *Akodon longipilis, A. olivaceus, Marmosa elegans, Oryzomys longicaudatus* and *Phyllotis darwini,* all used areas under shrub canopies more often than open areas between shrubs. In a series of field and laboratory experiments he showed that predation pressure was one of the four factors that determined micro-habitat use by the five small mammals studied.

In Argentina (Buenos Aires Province), Rood (1969, 1970) studied the ecology and behavior of the rodent *Microcavia australis* and found that it concentrates its activities near bushes, and that it also develops straightline runways between potential cover or shelters and excavates short, shallow tunnels. In Buenos Aires Province (according to Crespo 1966), and in Uruguay (according to Barlow 1969), high predation upon *Cavia aperea* forces it to be active close to potential cover or shelters (terrain taluses, vegetation clumps). *Cavia* also builds short underground tunnels, surface galleries through dense vegetation, and surface runways. Similar observations in terms of restricted habitat use have been reported for the rodent *Lagostomus maximus* by Llanos & Crespo (1952) in Entre Ríos Province, by Bucher (1980) in the Chaco region, and by Mares *et al.* (1981) in Salta Province. Pearson & Pearson (1982) reported that in southern Argentina the rodent *Akodon longipilis* gains protection against owl predation by living near brushy places or under large bushes.

The effects of reduced predation pressure upon mammals have been studied mainly on introduced rabbits, *Oryctolagus cuniculus,* in both Chile and Argentina. In central Chile, *O. cuniculus* is scarcely preyed upon (Jaksić *et al.* 1979) and then mostly on its juvenile cohorts (Simonetti & Fuentes 1982). Low predation on adult rabbits has been attributed to the lack of behavioral adaptation of native predators to hunt for this historically recent prey (Jaksić *et al.* 1979). The different predation pressure on these two small mammals is clearly reflected in their respective patterns of habitat use: whereas *O. degus* of all ages concentrate their activities close to shrubs, adult *O. cuniculus* are found in the open areas between shrubs (Jaksić *et al.* 1979; but see Simonetti 1986a). Although the information is scanty, some reports (Howard & Amaya 1975, Amaya & Bonino 1980, Jaksić & Yáñez 1983, Bonino & Amaya 1984) indicate that this conclusion also applies to *O. cuniculus* in Argentina. It is interesting to note that in Chile juvenile *Oryctolagus,* which are much more strongly preyed-upon than are adults, also restrict their activities to the vicinity of shrubs (Simonetti & Fuentes 1982). Similarly, Jaksić & Soriguer (1981) and Jaksić & Ostfeld (1983) have shown that native rabbits in Spain and California are more strongly preyed-upon than introduced rabbits in Chile, and that the former behave similarly to Chilean *O. degus* in their use of cover and shelters.

Time Use:

Mann (1978) noted that *Tadarida brasiliensis* is the first bat to become active at dusk in Chile. He related this finding to the bat's high-aspect wings and fast flight, thus affording it easy escape from diurnal raptors hunting at dusk. Simonetti and Otaíza (1982) suggested that the nocturnal habits of most central Chilean mammals were an ancestral character. Therefore, they should not be interpreted as resulting from temporal avoidance of diurnal predators, given that they are more numerous than nocturnal predators.

Iriarte (1986), using stopwatches attached to live traps, showed that the peak of small mammal activity in central Chile occurs between 7 PM and 4 AM. Small mammals in the diet of the fox *Dusicyon culpaeus* correspond to those species with earlier (4 to 10 PM), crepuscular activity periods. Whether some small mammals shift their activity period to later hours of the night in response to fox predation needs assessment, provided that foxes are not the only predators in the study area (several nocturnal raptors are present).

No information is available from Argentina.

Morphology & Behavior:

In Chile, Bullock (1931) documented that *Akodon olivaceus* displays a "freezing" behavior when approached by a potential predator. Simonetti (1986a) reported that both *Akodon longipilis* and *A. olivaceus* exhibit "freezing" behavior when subjected to overhead raptor silhouettes in laboratory experiments. Neither *Marmosa elegans* nor *Oryzomys longicaudatus* or *Phyllotis darwini* displayed that behavior. All five species were reported by Simonetti (1986a) to escape more often to shelters when the overhead silhouette was of a large raptor than when it was of a small one. Yáñez & Jaksić (1978) reported experiments using field pens stocked with *Octodon degus,* above which the cardboard-made representations of two types of Chilean raptors (kestrel size and buteo size) were passed overhead hanging from a cable. Circles of the same area as the raptors' figures were also passed. The rodents responded (by taking refuge and emitting shrill alarm sounds) to the two larger-sized figures (raptor and circle), but not to the small ones. Kestrel-sized raptors in Chile very rarely prey on *Octodon,* but buteo-sized ones frequently do. Yáñez & Jaksić (1978) interpreted their results as escape behavior of the rodents in response to predation. They also discussed that *O. degus* appeared more attentive when foraging in the open (lifting its head more frequently and sitting on its hindquarters, with fore legs raised, apparently watching and listening intently) than when under shrubs.

According to Mann (1978), the rodents *Octodon degus, Octodon bridgesi, Abrocoma bennetti, Lagidium viscacia,* and *Myocastor coypus,* all utter alarm calls when approached by predators; it is interesting that all these species tend to be colonial. Mann (1978), noting that most carnivores in the Puna hunt for the edentate *Chaetophractus nationi,* commented on the remarkable speed of this species at escaping by digging. He also reported that, on account of its long hind legs, the rodent *Oryzomys longicaudatus* is able to escape predators by jumping away into open fields. In contrast, he observed, the short-legged rodents *Phyllotis* spp. and *Akodon* spp., make only short, quadrupedal, runs toward the nearest shelter. Glanz (1982) reported that, among central Chilean small mammals, only the marsupial *M. elegans* and the rodents *A. bennetti* and *O. longicaudatus* climb shrubs as an escape response. Simonetti (1986a) showed that central Chilean nocturnal small mammals are more active and use open areas more often during moonless nights. He attributed this phenomenon to reduced predation risks derived from the less efficient hunting by owls under low light intensity. However, he found no correlations between morphological traits and use of open microhabitats (high predation risk).

Henkel (1938) documented "autotomy" of the tail in the rodent *Octodon degus* when the appendage is firmly grasped, and Ipinza *et al.* (1971) interpreted the phenomenon as a means to escape predation. Tail "autotomy" has also been observed in *Phyllotis darwini* and *P. rupestris* (Jaksić, Simonetti, pers. obs.). This phenomenon is not like that shown by lizards: only the tegument covering the tail is lost, no bleeding is observable, and the denuded tail vertebrae and associated tissue soon mummify and are apparently gnawed away by the rodent itself. Mann (1978) claimed that the Chilean marsupials *Marmosa elegans* and *Dromiciops australis* enjoyed protection from predators by their strong musky odor. Greer (1965), however, failed to notice any disagreeable odor when handling live *Marmosa* in southern Chile.

Courtin *et al.* (1980) documented that after a puma (*Felis concolor*) entered a small island in southern Chile, pudu deer (*Pudu pudu*) started avoiding open areas and even paths within the forest, habitats which they normally use when pumas are absent. In the same island, the introduced red deer (*Cervus elaphus*) reacted the opposite way, abandoning the forest and congregating in a single herd in open areas.

In Argentina, Pearson *et al.* (1968) detected differences in pelt coloration of *Ctenomys talarum* inhabiting areas with different soil color. The matching was as expected in terms of crypsis, but the differences between the two populations were slight; Pearson *et al.* (1968) concluded that predation pressure was not high enough to act as an efficient selective agent. Rood (1969) reported that *Galea musteloides, Microcavia australis,* and *Cavia* *aperea* (*pamparum* in the original) differ in their reponse to predators: whereas the first two species are dwellers of short-grass scrub and race into their burrows on the approach of predators, the latter freezes in its usual tall-grass habitat. In addition, *Microcavia* utters alarm calls, whereas *Galea* does not. Dalby (1975), quoting Barlow (1969), commented on the strong odor of *Oxymycterus rutilans* as serving to discourage potential predators, and also reported that this species is capable of tail "autotomy". Miller & Anderson (1977) reported body proportions of Uruguayan rodents (most of them shared with neighboring Argentina) as associated to their locomotory habits and habitat selection, but failed to relate morphology to predation.

Population Structure:

Claims about excessive killing of predators resulting in increases of small mammal populations abound. In Chile, suffice it to cite Greer (1965: 98), who mentioned that in Malleco Province "The constant hunting pressure on the chilla and culpeo (*Dusicyon* spp.) probably has contributed to the increase of the European rabbit (*Oryctolagus cuniculus*) and European hare (*Lepus europaeus*), to the detriment of crops". In Argentina, Llanos & Crespo (1952) stated that the snake *Constrictor constrictor* was a major predator of the rodent *Lagostomus maximus*, and that heavy commercial hunting of the snake was responsible for the population increase of the rodent and consequent damage to pastures and agricultural plots. In a more positive vein in Argentina, Cabrera (1953: 84) commented that "According to recent reports, it is apparent that the marra [*Dolichotis patagonum*] is becoming more abundant in some coastal areas of Chubut, to the south of Golgo Nuevo, a fact which, in the opinion of my informers, is due to the intense persecution which the foxes have been suffering for the last fifteen or twenty years" (Spelling errors in the original).

Few studies have analyzed which segment of a mammal population is more affected by predation proportionally to its numerical representation. Two types of such studies may be recognized: those (type-one) that examine the size, age, or sex composition of prey in the diet of predators as related to that in the field; and those (type-two) that infer predation from population losses between consecutive sampling or censusing periods.

Among Chilean studies of the first type we will mention three. 1) Fulk (1967a), in northern Chile, compared the age structure of the rodents *Akodon olivaceus* and *Phyllotis darwini* in the field and in owl pellets of *Tyto alba* and *Asio flammeus.* He showed that juveniles of *A. olivaceus* were over-represented in the pellets, whereas the opposite was true for *P. darwini.* In comparison to these two species *Akodon longipilis* was scarcely preyed-upon, and had a much higher survivorship between trapping sessions than did the former species. He also discussed that when significant differences were detected between sex ratios in the field and in the pellets, they were biased toward higher representation of males of the two former species in the pellets. Indeed, females of *A. olivaceus* showed higher survivorship than males. 2) In an area nearby Fulk's, Péfaur *et al.* (1977) studied the diet of the owl *Athene cunicularia* (*Speotyto* in the original) and found that it preyed on juvenile and adult *P. darwini* in the same proportion as these two age classes were available in the field. The owl, however, preyed more frequently on adult than on juvenile *A. olivaceus.* 3) Schlatter *et al.* (1980c) showed that in central Chile *A. cunicularia* preyed only on juvenile *O. degus* and *O. cuniculus,* not on adults. Results from these studies suggest that for some mammals the juvenile stage, with its associated smaller size and relative inexperience, may be an important bottleneck in the process of recruitment into the adult segment of the population.

Studies of the second type (population losses between consecutive trapping periods) abound in Chile (see Simonetti & Otaíza 1982 for a review), but owing to the field techniques used (mainly live-trapping in small areas), losses due to predation cannot be separated from those caused by emigration. Only occasionally metal ear-tags are recovered from pellets or scats of predators (Yáñez & Jaksić, pers. obs.), thus unequivocally indicating disappearance due to predation.

In Argentina, three type-one studies deserve mention. 1) Pearson *et al.* (1968)

found that the owl *Athene cunicularia* (*Speotyto* in the original) preyed heavily on the young of the rodent *Ctenomys talarum* and not at all on adults. 2) Bellocq & Kravetz (1983) compared the age and sex composition of rodents available in the field with that in the diet of *A. cunicularia.* They found that the owl did not prey on the youngest cohorts of *Akodon azarae* and *Calomys laucha,* and that it preyed disproportionately more on males of *A. azarae* and of *Oligoryzomys flavescens,* whereas it took males and females of *C. laucha* in the proportion that they were available in the field. 3) Although not documented quantitatively, Massoia & Fornes (1964) reported that during the peak of recruitment for small mammals, the owl *Tyto alba* preyed heavily on young of the relatively large *Holochilus, Cavia, Lutreolina,* but mainly on adult of the smaller *Scapteromys, Akodon, Oryzomys, Oxymycterus, Marmosa, Dasypterus, Reithrodon, and Eptesicus.*

Population losses of Argentine small mammals between trapping periods (type-two studies) have been reported by many authors, but only two have assessed the importance of dispersal as compared to predation. 1) Rood (1970) attributed mortality of *Microcavia australis* as mainly caused by predation, as opposed to dispersal. 2) On the contrary, Dalby (1975) disregarded predation as a major factor causing population losses of *Akodon azarae, Oryzomys nigripes,* and *Oxymycterus rutilans.*

Assemblage Structure:

Comparing small mammal assemblages in central Chile and southern California, Glanz (1977) found that Chilean small mammals showed a more restricted use of the available habitats. There was a clear association with potential shelters (crevices, burrows, shrubs), suggesting that predation may be heavier on Chilean than on California small mammals. Glanz (1977) suggested that coexistence was attained in Chilean mammal assemblages through segregation along the food axis, provided that the habitat axis was truncated by predation pressure.

In a similar comparison between the Argentine Monte Desert and the U.S. Sonoran Desert, Mares (1975, 1976) found that the small mammal assemblage in Sonora had several bipedal, granivorous rodents, whereas none was present in the Monte. He speculated that until late Pliocene the bipedal, and probably granivorous Argyrolagid marsupials were the ecological analogs of the Sonoran Heteromyid rodents. Mares (1975, 1976) further suggested that the Pleistocene influx of northern-hemisphere predators (canids, felids, mustelids) into the Monte may have caused the demise of the Argyrolagids; this because they were unfamiliar with the new host of predator species with varied hunting styles.

Summary:

Except for time use, evidence of the effects of predation on most facets of mammalian ecology has been abundantly reported. The major part of the evidence is based on observational-correlational protocols, usually within comparative contexts. In general, studies of small mammal ecology have proceeded more rigorously than those conducted on other vertebrates (except perhaps for those on lizards), by taking better advantage of natural experiments. The time seems ripe for making definite advances in performing field experiments of the type initiated by Simonetti *et al.* (1985) and Simonetti (1986a).

II) *Effects of Prey on Predators*

We consider that the profile of prey resources (species richness, associated body sizes, and relative abundances) may influence the predators in three major ways: 1) Determining which prey taxa are eaten in preference to or regardless of others (functional response, including prey selection, prey-switching, optimal foraging, and hunting mode). 2) Determining how many predators will congregate in a given area (numerical response, including migration). 3) Determining how many and which predators will coexist in an area (assemblage structure, including niche segregation and guild structure). With this optic, we scrutinized the literature on the three major vertebrate predator groups: snakes (suborder Serpentes), raptors (orders Falconiformes and Strigiformes), and carnivores (order Carnivora). We do not discuss mere accounts on the diets of predators, but analyze those in which interpretation is made of the data collected in terms of some of the three general categories referred to above. We do not consider behavioral studies of South American predators kept in captivity, or anecdotal accounts on the ways predators search, detect, pursue, handle, and/or ingest prey in the field.

Snakes

The Chilean snake fauna is extremely depauperate, with essentially two species in the whole country, which is in striking contrast with similarly situated areas in North America (Cody *et al.* 1977). Despite this interesting ecological context, except for anecdotal accounts (*e.g.*, Housse 1953, Donoso-Barros 1966), no references are available about the trophic ecology of Chilean snakes. A paper on the diet and feeding behavior of Chilean snakes has been in preparation for seven years now (H.W. Greene, pers. comm.). A snake assemblage consisting of two species is almost a misnomer, but Jaksić *et al.* (1981) reported that a central Chilean predator assemblage (including two snakes, eight raptors, and one carnivore) contained a trophic guild made up by the two local snakes (*Philodryas chamissonis* and *Tachymenis peruviana),* which concentrated their predation on lizards and frogs. Jaksić & Delibes (1987) compared the structure of this snake assemblage with that of its trophic analog in southern Spain, finding that the latter is composed of dietarily more specialized snakes.

No information is available from Argentina.

Raptors

Between 1926 and 1938, R. Housse published in the Revista Chilena de Historia Natural a series of papers dealing with the biology of the different species of Chilean raptors, including observations on what we here call functional and numerical responses. He consolidated these species accounts into a single book "Las aves de Chile..." (Housse 1945). However, for reasons stated in the first section of this review, we have preferred not to rely on his field observations. A more reliable author was R. Barros, who between 1950 and 1967 published in the Revista Universitaria (subtitled "Anales de la Academia Chilena de Ciencias Naturales") a new series of accounts on Chilean raptors. However, his field observations also were of an anecdotal nature. More rigorous natural history notes on Chilean raptors may be found in Johnson (1965, 1967), but they are lacking in quantification. We direct the interested reader to these early accounts, but the analysis that follows is based on more quantitative information reported by contemporary authors. Jaksić (1986a) summarized comparative research on predation conducted in mediterranean-type ecosystems of Chile, United States, and Spain.

Functional Response & Related Phenomena:

The functional response of raptors has been addressed mainly by comparing the taxonomic, age, size, and/or sex composition of the prey found in pellets as compared to that obtained with simultaneous trapping. For example, Fulk (1976a) showed that in the diets of the sympatric owls *Tyto alba* and *Asio flammeus* in northern Chile some small mammals were over-represented, whereas others were under-represented, as contrasted to results obtained through simultaneous trapping. In a nearby locality, Péfaur *et al.* (1977) reported similar findings, this time for the owl *Athene cunicularia* (*Speotyto* in the original). In central Chile, the same phenomenon has been reported for the owls *T. alba* (Jaksić & Yáñez 1979, Simonetti & Walkowiak 1979), *A. cunicularia* (Schlatter *et al.* 1980c), and *Bubo virginianus* (Jaksić & Yáñez 1980), and for the hawks *Parabuteo unicinctus* (Jaksić *et al.* 1980a), *Elanus leucurus* (Schlatter *et al.* 1980b), *Geranoaetus melanoleucus* and *Buteo polyosoma* (Schlatter *et al.* 1980a), *Falco sparverius* (Yáñez *et al.* 1980), and *Milvago chimango* (Yáñez *et al.* 1982). Similar findings have also been reported for the owl *B. virginianus* in southern (Reise & Venegas 1974), and southernmost Chile (Jaksić *et al.* 1986).

In Argentina, Dalby (1975) reported both under- and over-representation of particular rodents in comparisons involving trapping results and concomitant collections of pellets and scats of local predators. Indeed, Dalby (1975) documented the functional response of the owl *Asio flammeus,* which shifted predation on *Akodon azarae* in favor of *Cavia aperea* when the latter greatly increased in numbers (see Numerical Response). Two mammalian predators did the same (see below). Although not documenting his trapping results, Massoia (1983) states that the owls *Tyto alba, Bubo virginianus,* and *Athene cunicularia* preyed on small mammals out of the proportions they were represented in traps.

These observations in Argentina and Chile suggest prey selection, functional response, and perhaps optimal foraging by raptors, but it should be taken into account that what they in fact reflect is the different way raptors and traps sample the same mammal populations. But using this same technique of analysis, several counterexamples suggesting opportunistic use, rather than selection, of prey by raptors have been reported. Jaksić *et al.* (1981) performed correlation analyses of the incidence of small mammal prey in the diets of nine sympatric predators (five hawks, three owls, and one carnivore), against the composition observed in trappings conducted in both open and dense scrub of central Chile. Correlation coefficients were high and significant in five cases, all with the small mammal composition in the open scrub. Jaksić *et al.* (1981) proposed that those five predators first chose their hunting habitat, and then preyed on small mammals in about the proportions they were available in that habitat. A similar conclusion was reached by Bellocq & Kravetz (1983). They studied the diet composition of the owl *Athene cunicularia* in Buenos Aires Province, correlated it with the availability of small mammals in agricultural plots and bordering uncultivated areas, and detected a higher correlation with the latter. Jaksić *et al.* (1981) and Bellocq & Kravetz (1983) attributed the corresponding choices of hunting habitat as dictated by the higher densities that small mammals reached in the respective habitats.

Some authors have made more detailed analyses of predator/prey relationships by discriminating prey in the raptors' diets according to the age/size distribution of those species' populations in the field (as assessed by trapping). In Chile, differences between age/size composition in the diet and in the field have been reported for the owls *T. alba* and *A. flammeus* by Fulk (1976a), and for the owl *A. cunicularia* by Péfaur *et al.* (1977), and Schlatter *et al.* (1980c). In Argentina, the same has been shown for *T. alba* by Massoia & Fornes (1964), and for *A. cunicularia* by Bellocq & Kravetz (1983). However, the interpretation of these data is marred by the little that is known about the factors that may render some age/size cohorts more susceptible to predation and/or trapping.

The hunting modes of Chilean and Argentine raptors have been described mainly on an anecdotal basis (see Housse 1945, Johnson 1965, 1967, Vigil 1973, Hudson 1984). More rigorous observations have been conducted by McNutt (1981) on southernmost Chilean *Falco peregrinus,* by Vasina & Straneck (1984) on Argentine *F. peregrinus,* by Jaksić *et al.* (in press) on Chilean *Elanus leucurus,* and by Jiménez (in prep.) on three central Chilean buteonines. At a broader level, Jaksić & Carothers (1985) examined morphological and trophic correlates of the hunting behavior (dichotomized as "active search" and "sit-and-wait") of hawks and owls. They found that active searchers had lighter wing loadings than sit-and-wait hawks or owls, but no other consistent correlation was reported.

Numerical Response & Migration:

The numerical response of raptors is usually reported in connection with rodent outbreaks. However, although Fulk (1975, 1976a), Péfaur *et al.* (1979), and Fuentes & Campusano (1985) assessed and/or commented on the rodent outbreak of 1973 in northern Chile, they failed to report whether raptors (or any other predator) congregated in the irruption areas. It is sad that this natural experiment passed unnoticed in terms of predation research.

In Argentina, Crespo (1966) mentioned that the periodic irruptions of the rodent *Cavia aperea* (*pamparum* in the original) resulted in conspicuous concentrations of raptors, particularly of the owl *Asio flammeus* and the hawk *Milvago chimango.* Despite their massive congregation at the site of the irruption, these raptors become so overwhelmed by the *Cavia* numbers that they kill but do not eat many of them. Dalby (1975), similarly reported finding dead cavies after their irruption occurred in his study area, as well as a high concentration of raptors.

In Chile, Meserve (1977) mentioned that *Elanus leucurus* populations from the south migrate to the central part of the country, apparently in search of better food supply levels and/or better weather for hunting. In Argentina, Vigil (1973) reported that *Elanoides forficatus* is a wanderer, that *Circus cinereus, Milvago chimango, Falco sparverius,* and *Asio flammeus* migrate from the southern to the central or northern provinces during winter, and also reported on the yearly arrival of the Nearctic *Pandion haliaetus* and *Falco peregrinus.* Hudson (1984) documented the local migrations or wanderings of same raptors, plus *Buteo albicaudatus, Falco femoralis,* and *Rostrhamus sociabilis.* Vasina (1975), contrary to Hudson (1984), stated that Argentine *Falco peregrinus* migrate from the southern provinces to the northern ones during winter. In Patagonia (which is shared between Chile and Argentina), Vuilleumier (1985) reported that *Accipiter bicolor, Polyborus* (= *Milvago*) *chimango,* and *Glaucidium nanum* migrate north during the winter. None of these authors provided an explanation for these migrations, although unfavorable weather was implied. Tracking of prey resources is implicit in several works, though (*e.g.*, Liebermann 1935, Vigil 1973, Hudson 1984, Vasina & Straneck 1984, Olrog as cited in Vuilleumier 1985: 290). Jaksić & Jiménez (in press) made a summary review of raptor migrations between North and South America, analyzing Chilean, Argentine, and Patagonian localities among others. They attributed some cases of migration to seasonal changes in prey supply levels between the two hemispheres.

Assemblage Structure:

Jaksić (1981, 1983, in press) and Jaksić & Braker (1983), have studied food-niche relationships and trophic guild structure of owl, and hawk plus owl assemblages in Chile, as compared to that of similar assemblages in North America and Europe. A pervading feature of all these assemblages is that hawks and owls do not spread evenly along the prey resource axis, but form multispecific guilds that include both diurnal and nocturnal raptors. This latter fact calls into attention the inadequacy of temporal segregation between hawks and owls as a means to reduce overlap in the exploitation of prey resources (Jaksić 1982). Indeed, Jaksić (1982, 1985) proposed that interference interactions (including resource depression) played a major role in structuring raptor assemblages.

No information is available from Argentina, but Jaksić & Jiménez (in press) provide a preliminary analysis of diet and size features of one raptor assemblage in an Argentine locality.

Carnivores

Housse (1953) provided plenty of natural history notes on all Chilean carnivores, which we disregard for the sake of conservatism. Miller & Rottmann (1976) provided reliable accounts on Chilean carnivores, but we failed to find descriptions of the phenomena of our interest. For Argentine carnivores, Cabrera & Yepes (1940) reported rather general accounts which we cannot judge in terms of their accuracy, and consequently prefer to ignore. Langguth (1975) gave a general overview of the ecology and evolution of South American canids, including Chilean and Argentine foxes. In the same volume, Crespo (1975) provided a cursory review of his own investigations on the ecology of Argentine foxes. Because these two authors only summarized information reported by primary sources, below we discuss those original sources rather than their overviews.

Functional Response & Related Phenomena:

Jaksić *et al.* (1980b) reported that central Chilean populations of the foxes *Dusicyon culpaeus* and *D. griseus* shift their diet to consumption of berries when rodent populations decline during winter. Atalah *et al.* (1980) reported that the population of *D. griseus* in Tierra del Fuego is opportunistic in its food habits, shifting its diet toward a broader variety of energetically less-rewarding prey during winter, in response to reduced prey densities. Interestingly, Simonetti *et al.* (1984) detected the same phenomenon in northern Chile. In a similar vein, Jaksić *et al.* (1983) showed that mainland (Magallanes) and island (Tierra del Fuego) populations of both foxes feed on different prey according to geographic variations in availability. Iriarte (1986) showed in central Chile that *D. culpaeus* preys on the rodent *Octodon degus* in proportion to its abundance in the field (as assessed by live-trapping), whereas the rabbit *Oryctolagus cuniculus* and the rodent *Abrocoma bennetti* are over-represented in the fox's diet during fall and winter, and under-represented during spring and summer. Simonetti (1986b) reported that *D. culpaeus* takes advantage of the increased rabbit availability provided by the snare-trapping activities of humans. Apparently, then, the two fox species display functional response, at least in terms of prey selection and prey switching, and perhaps also in terms of optimal foraging.

Courtin *et al.* (1980) reported observations of puma (*Felis concolor*) predation on pudu deer (*Pudu pudu*) in southern Chile, which are consistent with optimal foraging tactics: one puma stayed in a small island until the pudu population declined below a threshold that apparently rendered it unprofitable for the puma to stay there. Yáñez *et al.* (1986) remarked on the dietary differences, as related to prey availability, between pumas in neighboring natural and livestocked ranges in southernmost Chile. Also in southernmost Chile, Wilson (1984) described the hunting mode of the puma, and found that it preyed on adult female guanacos (*Lama guanicoe*) in about their proportion in the field, whereas adult males were preyed upon less, and young twice as much than their respective field proportions.

In Argentina, Crespo & de Carlo (1963) reported several aspects of the ecology of the fox *Dusicyon culpaeus* in the western part of the country. Functional response is reflected in the proportional increase of introduced European hares (*Lepus capensis*) and native rodents in the diet of the fox, coincident with the yearly march of abundance of these small mammals in the field. When these prey decline during winter, the fox switches predation to sheep. A different fox, *Dusicyon gymnocercus,* was studied by Crespo (1971) in eastern Argentina. From a historical perspective, this fox shows a functional response to the introduction of European hares and the pest control effected on native vizcachas (*Lagostomus maximus*). Prior to these events, the fox preyed mainly on vizcacha, but now preys mainly on hare. Dalby (1975) reported that in Buenos Aires Province the predatory marsupial *Lutreolina crassicaudata* and the mustelid *Galictis cuja* switch prey from mainly *Akodon azarae* to almost exclusively *Cavia aperea,* following the population increase of the latter.

Numerical Response & Migration:

Jaksić & Yáñez (1983) reported what may be considered a numerical response of *D. griseus* when first introduced to Tierra del Fuego in 1951: the original 24 foxes greatly increased in abundance through reproduction and high survivorship, nowadays probably representing the densest population of this fox in the whole country (Durán *et al.* 1985). The introduction in 1940 of two pregnant coaties *Nasua nasua* into then predator-free Robinson Crusoe Island resulted in the explosive increase of its population. By 1976 there were 4,000 individuals thriving on ground-nesting seabirds (Miller & Rottmann 1976).

In Argentina, Crespo & de Carlo (1963) reported that the fox *Dusicyon culpaeus* greatly increased in number following the introduction of the European hare (*Lepus capensis*) and the initiation of sheep ranching activities. Indeed, a fraction of the population of foxes follows hares and sheep in their summer altitudinal migration to pastures, and back to the lowlands during the fall. Crespo (1971) failed to notice any numerical response of *Dusicyon gymnocercus* to fluctuations in its prey resources, although he remarked that individuals removed from his study area were quickly replaced by immigrants. Crespo & de Carlo (1963) also mentioned that the intensive pest control measures applied to this species (170,000 foxes were eliminated in six years from La Pampa Province) were fruitless, given its enormous potential for population increase. Rood (1970) reported that his main study population of *Microcavia australis* was eliminated by grisons *Galictis cuja.* Apparently, the grisons settled in the area of high *Microcavia* abundance, and produced three young, which contributed to the demise of the local *Microcavia* population. Perhaps *Galictis* searchs for and congregates in places with high prey abundance, staying there until the prey supply is depleted, then moving away.

Assemblage Structure:

Fuentes & Jaksić (1979) reported that the foxes *Dusicyon culpaeus* and *D. griseus* are of similar size in central Chile but diverge in size according to a gradient of increased sympatry toward the south of the country, apparently exploiting contrasting segments of the broadened array of prey sizes available in southern Chile. They interpreted these results as depicting compensation of niche dimensions, with increased sympatry leading to decreased diet overlap via character displacement in body size. Indeed, Jaksić *et al.* (1983) showed that dietary similarity between allopatric central Chilean foxes was higher than that between sympatric foxes in Tierra del Fuego.

In Argentina, Crespo & de Carlo (1963), and Crespo (1975) implied that interspecific competition for food resulted in the scarcely overlapping ranges of *Dusicyon culpaeus* (western Argentina), *D. gymnocercus* (eastern), and *D. griseus* (southern). Langguth (1975) also comented on the habitat separation exhibited by these and related foxes. None of these authors, however, provided quantitative evidence for their claims.

Multi-Class Predator Assemblages

Analyses of the structure of taxonomic assemblages of vertebrate predators, such as those discussed above, may be technically sound but we think they are biased. Predators of vertebrates usually interact with predatory species in different orders and even classes. With this hardly novel idea in mind, Jaksić *et al.* (1981) made the first (and so far only) study analyzing the time, habitat, and food axes of the niche of eleven sympatric Chilean predators (two snakes, three owls, five hawks, and one carnivore). Disregarding snakes, their results show that six predators are diurnal, one is crepuscular, and two are nocturnal. Five hunt exclusively in open scrub whereas four others hunt in both open and dense scrub. Diet overlaps are often very high (above 90%). Jaksić *et al.* (1981) also showed that three trophic guilds can be recognized: an insectivorous one formed by one owl and one hawk, a herpetophagous guild formed by two snakes, and a carnivorous guild, formed by three hawks and one fox. Jaksić *et al.* (1981) actually showed that this latter trophic guild emerges in response to the high population levels of a single prey in the locality, the rodent *Octodon degus*.

Jaksić & Delibes (1987) analyzed a multi-class predator assemblage in Spain, detecting similar patterns of guild structure. In fact, the emergence of at least one trophic guild in the Spanish locality can be ascribed to the high abundance of rabbits. With these data, plus similar information reported from several other localities in North America and Europe, Jaksić and co-workers have proposed that predator assemblages in general seem not to be structured on the basis of exploitation competition for food-resources, but that their structure emerges as an epiphenomenon of opportunistic responses to prey supply levels. These responses are in turn determined by a peculiar set of characteristics of each predator, including size, hunting mode, and sensory adaptations.

III) *Trends in the Study of Predator/Prey Relationships*

A quantification of the studies that have reported presumable effects of predation on vertebrate prey in Chile and Argentina is presented in Table 1. Considering all prey groups, Chilean studies represent nearly two thirds (62% of the references) of the total production as quantified. Description of predation phenomena affecting amphibians, birds, and mammals is quantitatively similar between the two countries, but there is a ratio of twenty to one in the detection of predation effects upon reptiles in Chile as compared to Argentina. Consequently, most of the difference in production between these countries is accounted for the heavier emphasis on reptile studies in Chile.

The number of studies reporting predator responses to prey levels (Table 2) in Chile again represents nearly two-thirds (66% of the references) of the regional production. But now this difference is consistently spread among all predator groups. Apparently, there has been more interest in studying predators in Chile than in Argentina.

Because we are more familiar with the history of ecological research in Chile

TABLE 1

Number of published studies that have reported presumable effects of predation on vertebrate prey in Chile and Argentina. Only reliable references that addressed predation explicitly are listed; those that failed to address the topic are not considered. Numbers before and after the slash represent studies conducted in Chile and Argentina, respectively.

Número de estudios publicados que han documentado presuntos efectos de la predación sobre presas vertebradas en Chile y Argentina. Sólo referencias confiables que han considerado explícitamente la predación aparecen listadas; aquellas que omiten consideración del tópico no aparecen listadas. Los números antes y después de la línea diagonal representan estudios realizados en Chile y Argentina, respectivamente.

Predation Effects:	Amphibians	Reptiles	Birds	Mammals	All groups
Habitat Use	0/0	6/0	0/0	14/12	20/12
Time Use	0/0	0/0	0/0	2/0	2/0
Morphology & Behavior	4/4	11/1	0/0	7/4	22/9
Population Structure	1/0	1/0	1/3	5/5	8/8
Assemblage Structure	0/0	2/0	1/3	1/2	4/5
All categories	5/4	20/1	2/6	29/23	56/34

TABLE 2

Number of published studies that have reported presumable responses of vertebrate predators to prey resources in Chile and Argentina. Only reliable references that relate prey levels to predator responses are listed; those that failed to notice any relationship between these trophic levels are not considered. Numbers before and after the slash represent studies conducted in Chile and Argentina, respectively.

Número de estudios publicados que han documentado presuntas respuestas de predadores vertebrados a sus recursos de presas en Chile y Argentina. Sólo referencias confiables que relacionan los niveles de presas con las respuestas de los predadores aparecen listadas; aquellas que omiten relacionar estos dos niveles tróficos no aparecen listadas. Los números antes y después de la línea diagonal representan estudios realizados en Chile y Argentina, respectivamente.

Predator Responses:	Snakes	Raptors	Carnivores	All groups
Functional & Related	0/0	18/6	8/3	26/9
Numerical & Migration	0/0	3/10	2/3	5/13
Assemblage Structure	2/0	8/0	2/0	12/0
All categories	2/0	29/16	12/6	43/22

(rather than with that of Argentina), below we document the trends observed in Chilean studies of predator/prey relationships, hoping to shed light on the features that characterize such research as practiced by native ecologists.

Chile: a Case Study

Reading Table 1 vertically, it can be seen that on a taxon by taxon basis, the number of references to predation effects is by far higher for mammals (52% of the total), then for reptiles (36%) distantly followed by those for amphibians (9%) and birds (3%). The sample size is made up of 56 references.

"Modern" ecological studies of Chilean mammals may be said to have started the early seventies with G. Fulk (a U.S. citizen), and since then both Chilean and U.S. investigators have been pursuing vigorous field research for more than a decade. Interestingly, the former (*e.g.*, E. Fuentes, F. Jaksić, J. Simonetti, J. Yáñez) have been more concerned with predation as an important factor affecting small mammal ecology, whereas the latter (*e.g.*, W. Glanz, P. Meserve) have been more interested in resource partitioning (competition-oriented) studies.

Contemporary reptile ecology, has been dominated by Chilean researchers (*e.g.*, E. Fuentes, F. Jaksić, H. Núñez, J. Simonetti), with U.S. herpetologists becoming active only as of lately (J. Carothers, S. Fox). The publication of ecological studies of Chilean lizards boomed between 1976 and 1982, and it was oriented to answering theoretical questions. Although an early emphasis on resource partitioning is evident in that production, predation became an important theme during subsequent stages.

In comparison to ecological trends in mammalogy and reptile-herpetology, the opposite extreme is represented by Chilean ornithology. Whereas most mammalogists and herpetologists had some formal training in biology, early (1930's to mid-1960's) ornithologists were bird-watchers from all ranks of society (*e.g.*, R. Housse, R. Barros, A. Johnson). These amateur ornithologists produced a wealth of natural history notes on Chilean birds, but without any reference to conceptual frameworks. The first theoretically-oriented ornithologist appeared during the early seventies (M. Cody, a U.S. citizen), and focused on patterns of resource partitioning among Chilean birds. During the late seventies and early eighties, a group of Chilean researchers (F. Jaksić, H. Núñez, R. Schlatter, J. Simonetti, J. Yáñez) produced a series of studies on food-niche relationships of raptor assemblages, and placed emphasis in opportunism, as opposed to competitive segregation, in the use of prey resources. So far, nobody has re-examined Cody's conclusions, which were based mainly on passerine birds.

Amphibian-herpetology has been dominated by systematists ever since J. Cei (an Italian citizen who arrived via Argentina) started his work in Chile. This lack of ecologists studying Chilean frogs has resulted in the low number of publications dealing with predation, competition, or related phenomena. The recent paper of Díaz & Valencia (1985) may be signaling a welcomed change of emphasis on amphibian studies.

Reading Table 1 horizontally, it appears that two topics have attracted much attention of Chilean ecologists: habitat use (36% of the references) and morphology/behavior (39%). Population structure ranks third (14%), with assemblage structure (7%) and time use (4%) lagging behind. Observations on habitat use by mammals and reptiles have usually been made under the assumption that predation played a role, and consequently they very often have been coupled with observations on phenotypic traits of the organisms under study. Indeed, these two categories of analysis are frequently reported in the same paper. Different is the case of studies on population structure, where the preoccupation of the researchers has been to relate the age/size/sex composition of the mammal prey found in pellets or scats of predators, with that which is available in the field. Studies of the effect of predation on assemblage structure have been conducted in all groups except for amphibians, whereas time use as affected by predation has been reported only for mammals.

The quantification of presumable responses of Chilean vertebrate predators to prey resources, based on 43 references, is presented in Table 2. Reading the table vertically (taxon by taxon), the largest number of studies corresponds to raptors (67%), then to carnivores (28%), and snakes (a meager 5%).

The heavier emphasis on raptors has its basis on the continuing sequel of quantitative reports on the diets of Chilean raptors (mainly by F. Jaksić, H. Núñez, R. Schlatter, J. Simonetti, J. Yáñez). The fact that most of these researchers had done ecological work on mammals and/or reptiles allowed them to interpret the composition of raptor diets in light of the ecology and behavior of the prey. With the diets of many sympatric raptors quantified, as related to local prey levels, different combinations of these researchers have proceeded with studies of assemblage structure, which they have compared with that of North American and European raptors. These comparative studies (with, *e.g.*, E. Braker, H. Greene, C. Marti, all U.S. citizens, and M. Delibes, C. Herrera, R. Soriguer, all Spaniards) have given much vigor to Chile-based raptor research, thus explaining in part its productivity.

Carnivore studies have mainly focused on the two most common species of foxes, whose trophic ecology has been studied all along Chile. Because they constitute puzzling subjects in terms of zoogeography and ecology, their study has attracted much interest among Chilean ecologists, perhaps hindering progress in the understanding of the ecology of other carnivores.

Snakes have been almost completely neglected by Chilean students of predation. This situation is sad, because Chile presents a broad latitudinal succession of different habitats and prey levels which are exploited by only two snakes living in sympatry. This ecological context is indeed unique in the world.

Horizontal reading of Table 2 indicates that functional and related responses have been abundantly reported for raptors, less for carnivores, and not at all for snakes. This type of predator response has been reported in 60% of the references, and its high incidence is related to the fact that many studies of raptor and carnivore diets have been made on a yearly basis (noting seasonal differences) or on a comparative basis (for allopatric populations of the same species). It is curious that the numerical response of Chilean predators has been reported much less frequently (12% of the references). Being an easily observable phenomenon, and given that small mammal irruptions are not infrequent in Chile, its low incidence may reflect the fact that studies of prey populations in the country have mainly been short-term. Apparently, small mammal irruptions take two or three years to build up, so that counting of local predators should be done concomitantly in order to notice whether there is indeed a "response" to the irruption. That 28% of the references deal with assemblage structure speaks to the activity of community ecologists in Chile.

From the information above, it appears that contemporary Chilean ecologists show some interesting features: They have invaded the fields of mammalogy, reptile-herpetology, and ornithology, carrying across these taxonomic boundaries their empirical knowledge of different organisms, but also their theoretical conceptions. An emphasis on detecting the presumable effects of predation rather than those of interspecific competition may indeed reflect their own biases rather than the prevalence of the first phenomenon among southern South American vertebrates. Another feature is their treatment of predator assemblages as including snakes, owls, hawks, and carnivores, and their emphasis on guild structure as emerging from opportunistic responses to prey levels rather than as mandated by diffuse competition. That these biases have been applied by some Chileans to analyses of northern hemisphere predator/prey systems is indeed a refreshing change in the usual course of interactions between South- and North-Americans.

IV) *Prospects for Future Research & Collaboration*

So far, most of the patterns of the prey level that have been attributed to the action of predation, are based on correlative-comparative evidence. Although natural experiments have been used to infer the importance of predation as opposed to other ecological interactions, virtually no field experiments have been attempted (but see Simonetti *et al.* 1985; Simonetti 1986a). Detection of pattern may be considered a first and necessary step in the understanding of a particular system, and we feel that the patterns so far documented warrant further examination through field manipulation. We envision that a potentially fruitful avenue in the study of vertebrate prey involves field experiments with those organisms that lend themselves best for manipulations, for example, lizards and small mammals.

At the predator level, we think that emphasis on pattern detection has also been heavy, but use of the comparative method of research has provided some interesting hypotheses about the structure of predator assemblages. However, most of the studies so far conducted have provided static pictures of average conditions of the predator/prey system. We think that much effort is needed to study the coupling of the prey level dynamics with the presumably changing niche relationships of predators according to the prey dynamics. Vertebrate predators do not lend themselves to field manipulation for ethical or logistic reasons. But concomitant studies evaluating the march of abundances of prey populations and the functional, numerical, and assemblage-level responses of sympatric predators should fill important gaps in our knowledge.

We think that collaborative research between South and North Americans, ideally involving comparative studies in matched sites of both hemispheres, with adequate exchange of visits to those matching areas, should accelerate the bridging of gaps referred to above. We also think that the days of the "ugly American" doing hit-and-run research in South America are gone, and that the time is ripe for initiating collaboration on an equal intellectual basis.

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