COMMENTARY

Predator-prey interactions in terrestrial and intertidal ecosystems: Are the differences real?

Interacciones predador-presa en ecosistemas terrestres
e intermareales: ¿Son reales las diferencias?

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ABSTRACT

Studies of intertidal invertebrates indicate that predators can determine the abundance and diversity of prey. The opposite seems to occur in vertebrate predator-prey interactions in terrestrial ecosystems. This apparent contrast results from the research protocols followed by intertidal and terrestrial ecologists, their differing emphasis, and the mobility characteristics of the organisms studied.

Key words: Predation, keystone predator, species diversity, relative mobility, research protocols.

RESUMEN

Estudios realizados en invertebrados intermareales indican que los predadores son capaces de determinar la abundancia y diversidad de sus presas. Lo opuesto parece ocurrir en interacciones predador-presa en ecosistemas terrestres. Este aparente contraste se debe a los distintos protocolos de investigación seguidos por ecólogos terrestres e intermareales, a sus diferentes énfasis y a las características de movilidad de los organismos estudiados.

Palabras claves: Predación, predador clave, diversidad de especies, movilidad relativa, protocolos de investigación.

INTRODUCTION

One of the most often stated generalizations in community ecology is that predators, by preferentially preying on a competitively superior species (potentially the most abundant), keep it at a density low enough for other species to coexist. Removal of such "keystone" predators shifts the balance of competitive interactions among the prey, thus reducing overall biotic diversity in the community (Paine 1966, 1980, Connell 1975). Furthermore, as predator density increases, prey species diversity varies from low —the superior competitor monopolizes the resources in short supply— to peak and then to low diversity again —because only those species extremely resistant to predation persist (Menge & Sutherland 1976). So far, most of the supporting evidence of a community-organizing role for predators comes from experimental studies conducted with invertebrates in intertidal ecosystems. In addition, the same phenomena have been documented for intertidal herbivores "preying" on algae (Lawrence 1975, Lubchenco 1978, Lubchenco & Gaines 1981).

Do predators in terrestrial ecosystems play a similar "keystone" role to that observed in intertidal ecosystems, or is the "keystone" predator concept only a special case rather than a broad generality? If predators in these two ecosystems do not play the same role, what characteristics of the two systems might explain the differing role of predators? The available evidence indicates that effects similar to those of intertidal predators on their prey are not demonstrable in terrestrial ecosystems. I argue that these effects more closely resemble those observed in terrestrial herbivore-plant and not in terrestrial predator-prey interactions, being linked to prey mobility. In fact, a different network of causal relationships with respect to com-

munity structure appears associated to the two predator-prey systems. In intertidal ecosystems the effect of predators on their prey has been clearly shown, but the outcome of the reverse interaction is not known. In terrestrial ecosystems it has been shown that the prey level strongly influences the structure of the predator level, whereas the reverse is not clearly understood (Table 1).

TABLE 1

Features and results that characterize intertidal and terrestrial studies of predator-prey interactions.

Características y resultados de estudios sobre interacciones predador-presa en ecosistemas terrestres e intermareales.

FEATURES	TERRESTRIAL ECOSYSTEMS	INTERTIDAL ECOSYSTEMS
Organisms studied	Vertebrates	Invertebrates
Research protocol	Correlational	Experimental
Scale of studies	Many thousands m^2	A few m^2
Prey/predator mobility	High	Very low
Effects of prey on predators:		
— Increased predator diversity	Apparently	Unknown
Effects of predators on prey:		
— Increased prey diversity	Unknown	Yes
— Local extinction of prey	No (few exceptions)	Yes
— Restricted prey space use	Yes	Perhaps

Are these difference real? To what extent do they reflect contrasting research protocols in intertidal and terrestrial studies (Jaksić 1985a), differing emphases, or differences in the characteristics of the organisms studied? I discuss these topics in the light of comparative studies that my colleagues and I have conducted on predator-prey interactions among some vertebrates in terrestrial ecosystems. Although our major research thrust has been in mediterranean-type habitats (see di Castri et al. 1981), data from other habitat types reveal that the phenomena to be discussed below are pervasive in terrestrial ecosystems.

Effects of prey on predators

In this section I report research that my colleagues and I have conducted on terrestrial vertebrate predators (avian raptors, mammalian carnivores, and snakes) at three levels of ecological resolution: the population, the assemblage, and the community.

We have analyzed the trophic ecology of twelve populations of owls in the genera *Tyto, Athene,* and *Bubo,* that occur in mediterranean-type habitats of Chile, Spain, and California (Jaksić & Marti 1981, 1984, Jaksić et al. 1982a). We found that the owls respond opportunistically to their food supply, and that marked differences occur among allopatric —but congeneric— populations in diet breadth and mean prey weight. Diet breadth appears determined by the total number of prey species locally available, ease of capture of those prey (in terms of size), and their relative abundance. The mean weight of prey in the owls diets also appears to be determined by the prey catchability and abundance. Surprisingly, these two diet metrics show no clear relation to geographic variation in body size of the owls, which is conspicuous in some cases. Congeneric but allopatric owls of similar size usually take different ranges of the prey weights locally available, coinciding with that of the most abundant prey within catchable range. It is clear that the owls take differently sized prey without regard to any fixed "optimal" prey size. Rather, they eat whatever prey is more abundant, as scaled to the size (and presumably energetic demands) of the owls themselves.

In sum, the local profile of prey species abundance, as weighted by the corresponding prey sizes (or by the species com-

position because size is a species characteristic), strongly affects the owls' trophic ecology. Similar findings have been reported for other avian raptors (Korschgen & Stuart 1972, Newton 1979, Mikkola 1983, and references below), mammalian carnivores (Clark 1972, Brand *et al.* 1976, Nellis & Keith 1976, Beasom & Moore 1977), and snakes (Kephart & Arnold 1982).

We have also analyzed the structure of assemblages of both diurnal (order Falconiformes) and nocturnal (order Strigiformes) raptors in Chile, Spain, Michigan, Wisconsin, and Utah (Jaksić 1982, 1983, Jaksić & Braker 1983). We found that assemblage structure emerges from species-specific responses of the raptors to the prey population levels and prey size configuration locally available. Different raptor species frequently have broadly overlapping diets because they prey on the most abundant species in a given locality.

Provided that raptors differ in size, the "most abundant prey" has to be scaled to the raptor considered. For example, for falcons and small owls, invertebrates constitute abundant prey that is energetically rewarding. Larger raptors instead concentrate their predation on locally abundant vertebrates, neglecting invertebrates (Jaksić 1985b).

Counter to the theoretical expectation that raptor species should spread out in the use of prey resources in order to minimize competition, we found that raptors actually concentrate on just a few prey types (usually one or two prey species), forming feeding guilds of variable size (see Jaksić 1981). These guilds build up on the polymodal distribution of prey sizes, with a few prey species (of similar size) being the basis for each feeding guild. We usually detected three such guilds in every locality studied, based on the following prey groups: 1) arthropods, reptiles, and small-sized mammals such as mice and shrews; 2) birds and medium-sized mammals such as rats and ground squirrels; and 3) relatively-large-sized mammals such as rabbits and hares. Independent assessments of the abundance of prey populations in the study sites reveal that the raptors take whatever prey is more abundant, provided it is large enough to render a positive energy balance to the predator, and small enough to be subdued and ingested (Jaksić 1985b).

In sum, the abundance of prey species of a given size determines the presence and significantly affects the abundance (and reproductive performance) of particular raptor species (see also Rusch *et al.* 1972, Smith & Murphy 1973, 1979, Hamerstrom 1979, USDI 1979, Thurow *et al.* 1980, Baker & Brooks 1981). Where rabbits and hares are abundant, large raptors are present, abundant, and prolific; as these relatively large prey disappear, so do the large raptors. Similar findings have been reported for assemblages of mammalian carnivores (Rosenzweig 1966, McNab 1971), and of snakes (Arnold 1972, Brown & Parker 1982, Fitch 1982, Reynolds & Scott 1982).

At the community level, our findings in Chile are essentially the same as those reported for raptor assemblages above (Jaksić *et al.* 1981a). Greater generality is provided by analysis at this level because predators in three different classes (birds, mammals, and snakes) are included. The community structure of a group of 11 Chilean predator species can be understood in terms of their individual ecologies. The snakes form a herpetophagous guild that exploits the small and abundant lizards and amphibians in the locality. Birds of prey are split into a carnivorous-insectivorous guild formed by the smaller raptors that eat mice and insects, and a strictly carnivorous guild formed by the large raptors and the only mammalian carnivore in the locality, all of which prey mainly on one medium-sized rat species. We will soon be reporting similar findings in a richer (25 species) predator assemblage of southern Spain (Jaksić & Delibes, ms.), and in an 11-predator species assemblage in California (Jaksić, ms.). In sum, the guild structure of these predatory communities appears based on the high and sustained abundance of some small mammal species, and that of some insects, amphibians, and lizards.

As a general summary for this section, it appears that at the population, assemblage, and community levels of resolution, terrestrial vertebrate predators behave opportunistically —exploiting whatever prey is most abundant in relation to their own body size. Because large eagles cannot subsist on a diet of caterpillars (energetically unrewarding), or small falcons on one of hares (impossible to subdue), it is the size and abundance configuration of the local prey resources that affects the size (or species) composition of the predator level,

rather than the opposite. The energetic demands of vertebrate predators are usually large, and their prey is often highly mobile and difficult to catch and subdue. Vertebrate predators probably cannot afford to stay in a place where certain prey sizes (as weighted by their corresponding abundance) are not present. Because vertebrate predators themselves are highly mobile, they can choose places where their energetic demands are met. In this way the prey influences which predator species (or sizes), and in which abundance, are found at a given place.

Because intertidal ecologists have mainly analyzed the effects of predators on its prey, the complementary phenomenon discussed above for terrestrial ecosystems is yet poorly explored. Apart from the trivial case of lack of prey causing the absence of predators, intertidal ecologists have neglected the influence of the number, abundance, and size composition of the prey on the predator level. Perhaps intertidal and terrestrial ecosystems are comparable in terms of the effects of the prey level on its predators, but the study of their similarities has been hindered by the emphasis that intertidal ecologists have placed on only one half of the predator-prey interaction.

The different emphases made by intertidal and terrestrial ecologists may reflect a tactical and philosophical difference in the research protocols followed for studying the respective ecosystems (Jaksić 1985a). Intertidal ecologists identify a unit of space (say, $0.1 - 3.0$ m^2), manipulate one or two species on it, observe the outcome, and emphasize the results of experimentally having changed the interaction network. Terrestrial ecologists use as a study site thousands of square meters, focus on the diets of some chosen vertebrate predators, and relate their diets to the local prey supply. In this case, there is no experimental proof of any dynamic coupling between predators and prey. The evidence produced is circumstantial and of a correlational nature, where cause and effect is often difficult to resolve. Although the difference in approach between intertidal and terrestrial students of predation may hamper the comparison between the two ecosystems, data of a more comparable nature are available for considering how predation influences prey populations, as I now discuss below.

Effects of predators on prey

Here I analyze information on prey abundance and spatial distribution in the same localities where my colleagues and I conducted the predator studies. In terrestrial ecosystems vertebrate predators do not seem capable of forcing their prey to local extinction, as is commonly the case in intertidal ecosystems. The presumed regulation of terrestrial prey by their predators has for years been a subject of controversy (Errington 1946, Blondel 1967, Andersson & Erlinge 1977), particularly with reference to cycling rodents (Chitty 1960, Pearson 1966, 1971, MacLean et al. 1974, Boonstra 1977, Beacham 1979). There is no doubt that in some situations vertebrate predators can greatly reduce rodent populations (Pearson 1964, Baker & Brooks 1982), but even in these extreme cases the rodents soon recover and build up their numbers again.

The continuous presence of sizable prey populations is verified in most of the localities that we surveyed with respect to predators (and in many others; see Blondel 1967, Korschgen & Stuart 1972, Rusch et al. 1972, Andersson & Erlinge 1977). In Chile, the rodent *Octodon degus* is intensely preyed upon by almost all the local predators (Jaksić et al. 1981a), but nonetheless maintains high population densities throughout the year (Jaksić et al. 1981b). In Spain most predators consume large numbers of the rabbit *Oryctolagus cuniculus*, but its abundance remains at high levels (Jaksić & Soriguer 1981, Jaksić & Ostfeld 1983). In Wisconsin and Michigan raptors prey extensively on the vole *Microtus pennsylvanicus*, forcing it to yearly low densities that nonetheless become high again the next growing season (Errington 1932, 1933, Craighead & Craighead 1969). In Utah the jackrabbit *Lepus californicus* is the staple prey of most raptors, and though it fluctuates widely in numbers from year to year it does not ever disappear (Smith & Murphy 1973, 1979). The conclusion I draw from these examples is that although vertebrate predators may prey strongly on some species, with few exceptions they do not seem capable of driving prey resources to the point of local extinction. In fact, prey species usually recover in the presence of their predators and persist as their staple prey indefinitely.

What then is the main effect of terrestrial vertebrate predators on their prey? Our studies show that a major effect is to restrict the prey's spatial activity patterns. In Chile the staple prey of local predators (*O. degus*) stays near shrubs, not venturing into open spaces where predation risks are presumably higher (Jaksić *et al.* 1979). In Spain rabbits (*O. cuniculus*) are restricted to areas close to shrubs in dense scrub (Jaksić & Soriguer 1981), which is also the case for rabbits (*Sylvilagus* spp.) in California (Orr 1940, Bartholomew 1970, Jaksić & Ostfeld 1983). In both Spain and California rabbits suffer high mortality from predation, in contrast to rabbits introduced in Chile (*O. cuniculus*), which are scarcely preyed upon (Jaksić *et al.* 1979, Jaksić & Soriguer 1981, Jaksić & Ostfeld 1983). The latter are not restricted to the vicinity of shrubs, choosing sparser scrub than their conspecifics in Spain (Jaksić & Soriguer 1981). Although voles in North America are found in exposed habitats such as grasslands, where they may be easy prey (Baker & Brooks 1982), they use grass clumps as refuges against predation (Taitt & Krebs 1983, Pearson 1985).

Other instances of restricted habitat use associated with vertebrate predation have been documented for lizards in Chile, Spain, and California (Jaksić *et al.* 1982b). Although in general little has been done regarding the effects of predation on the behavior of lizards (Jaksić & Núñez 1979, Schall & Pianka 1980, Bauwens & Thoen 1981, Huey & Pianka 1981), its influence on habitat preferences of this prey type may not be negligible (Jaksić *et al.* 1982b).

In summary, at any given place, terrestrial vertebrate predators do not seem to affect drastically the continuing presence of their prey despite intensive removal. This is probably because a certain number of prey individuals are able to escape predation, building up population numbers later on. Escape of a remnant number of prey is facilitated by vertebrate predators usually moving away from areas where their food supply has become too rarefied to pay staying there. Alternatively, vertebrate predators may stay in the same area and start eating less "preferred" prey, thus decreasing the pressure upon their main prey. Even if all prey are killed at a site, dispersal from neighboring areas aids in replenishing the exhausted prey populations and starts a new build-up. Escape of prey from predators may occur in both time and space. Escape in time seems rather ineffective in terrestrial ecosystems because vertebrate predators are long-lived and can hunt all day, with diurnal species being replaced by nocturnal ones (e. g., hawks by owls). Escape in space seems a better alternative, although by restricting their habitat use prey species may be left with less food supply. Predators await outside, though, and seem to be efficient agents of natural selection in forcing their prey to restricted habitat use. In short, terrestrial vertebrate predators seem to affect behavioral patterns of particular prey species more strongly than their presence or absence.

Do terrestrial vertebrate predators foster higher biotic diversity by consuming the potentially most abundant, and presumably superior competitor, prey species? This well worked aspect of the predators' effect on intertidal prey has not been addressed in terrestrial ecosystems. There are obvious reasons for this neglect. Vertebrate predators are both relatively scarce and highly mobile. Maintenance of an experimental area with reduced (or null) predation would require a continual removal of predators that would soon reach unethical proportions (Jaksić 1985a). Enclosure of an area large enough to preserve all the biotic diversity at a site would probably be prohibitive in terms of the funds required. Use of "natural experiments" such as islands with no predators or fewer predators than comparable mainland areas is hampered by the compound effects of predation and island-biogeography phenomena.

None of these problems seems to be important in intertidal studies, where several experiments can be mounted on a few square meters. Demonstration of a "keystone" role for predators seems to be closely tied to the use of experimental protocols using invertebrates as focal organisms. Specifically devised tests of the "keystone predator" hypothesis have not been performed with predators in the terrestrial environment, for reasons explained above. But even if experiments of such nature could be conducted, I doubt the "keystone predator" hypothesis could be verified. There is a factor that has to be taken into account: the different mobility of prey relative to predators in terrestrial and intertidal systems.

I emphasize here that if intertidal predators can keep the competitively superior prey in check (thus fostering increased biotic diversity) it is because that prey cannot often escape by moving away. The prey's defense normally rests on alternatives such as outgrowing its predator, being physically or chemically inedible, living in microhabitats inaccessible to its predator, or colonizing areas temporarily devoid of predators. There is a striking similarity between this situation and that faced by plants in terrestrial ecosystems, the link between the two systems being the immobility of the "prey" relative to that of its "predators" (plants and herbivores in the terrestrial environment, respectively). Competitively dominant terrestrial plants may be locally exterminated by herbivores, and provided the latter are absent they can monopolize all the space thus excluding weaker competitors and consequently reducing the biotic diversity at a site (Harper 1969, 1977). Should intertidal ecologists center their attention on mobile prey, perhaps the apparent differences between intertidal and terrestrial predation would fade away. It may well be the case that the real ecological counterparts of terrestrial vertebrate predators are fishes (mobile consumers) that prey on mobile prey such as crabs (see Edwards *et al.* 1982, and Menge 1982 for an interesting controversy on the importance of high-and low-movility intertidal predators). Although my knowledge of the fish literature is scanty, I think that some interesting parallels between marine and terrestrial predatory vertebrates have been reported by Hobson (1978), Harmelin-Vivien (1978), and Choate (1982, and references herein). A study of the predatory tactics and effects of fishes on mobile prey populations, to test the findings reported above for terrestrial predators, may prove illuminating indeed.

CONCLUSIONS

An influential part of the work on the role of predation in structuring communities has been conducted in intertidal ecosystems (Paine 1966, 1980, Connell 1975, Menge & Sutherland 1976). The finding that predators usually are major determinants of the structure of those communities by affecting the abundance and di-

versity patterns of the prey has subsequently permeated the general ecological literature, conveying the impression that terrestrial predator-prey systems behave as their intertidal analogues (Krebs 1972, MacArthur 1972, Emlen 1973, Ricklefs 1973, Begon & Mortimer 1981, Pianka 1983; but see Remmert 1980). I question this extrapolation from intertidal to terrestrial ecosystems. Predators in the former environment may well have similar effects as do herbivores in the latter, because most intertidal predators "graze" essentially stationary prey and can potentially deplete a patch of a given prey species.

Terrestrial vertebrate predators have to deal with highly mobile prey that can escape predation with a much richer array of behaviors. This major difference, in part, may account for terrestrial predation being less effective as a controlling agent of prey population numbers. In fact, vertebrate predators depend on the prey populations' ability to reach a certain threshold density that allows the predators to survive or thrive on the surplus. The body sizes of the most abundant prey types subsequently determine which predator species can reside continuously in an area. How superabundant a certain prey type is, in turn, determines how many predators form the feeding guild that relies on that prey as the staple food. Concomitantly, vertebrate predators act as selective agents by limiting the activities of their main prey to microhabitats where prey mortality is minimized.

The finding reported here on terrestrial vertebrate predation —that the profile of abundances and the species (size) composition of the prey level in combination affect the presence and abundance of their predators— has not been tested in intertidal ecosystems. Conversely, the finding of intertidal ecologists, that predation is a major structuring agent of communities, is not yet evident in terrestrial ecosystems (unless herbivory is equated with predation). In fact, population levels of terrestrial vertebrate predators seem to be more affected by those of their prey than the opposite. It has yet to be shown that these predators determine the biotic diversity of their prey.

As discussed above, the contrasts documented for predator-prey interactions in terrestrial and intertidal ecosystems are likely to result from the different research protocols followed (correlational versus experimental, respectively), the emphasis

applied (predators' dependence on the prey level, versus "keystone" predation), and the mobility characteristics of the prey relative to predators (highly mobile versus nearly stationary).

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