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COMMENTARY

Predator-prey interactions in terrestrial and marine ecosystems: a reappraisal

Interacciones depredador-presa en ecosistemas terrestres y marinos: una reevaluación

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ABSTRACT

A critical analysis of Jaksić (1986) and López & Buschmann (1988) commentaries on predator-prey interactions in terrestrial and marine ecosystems shows that the evidence presented and discussed by these authors is in some cases inappropriate, at best incomplete, and rather confusing as to enable drawing any valid conclusion about the ecological processes operating in these two ecosystems.

Key words: Predation, mobile predators, prey vagility, intertidal ecosystems, research protocols.

RESUMEN

Un análisis crítico de los comentarios de Jaksić (1986) y López & Buschmann (1988) sobre las interacciones depredador-presa en ecosistemas terrestres y marinos muestra que la evidencia presentada y discutida por estos autores es, en algunos casos inapropiada, en todo caso incompleta y bastante confusa como para permitir extraer alguna conclusión válida sobre los procesos ecológicos que operan en estos dos ecosistemas.

Palabras claves: Depredación, depredadores móviles, movilidad de presas, ecosistemas intermareales, protocolos de investigación.

Comparisons of community patterns and organization models between different ecosystems (*e.g.*, between marine and terrestrial) have recently become of great interest to ecologists because they represent an important analytic approach to our understanding of concepts, models, and generalizations in community ecology theory (see for example Orians & Paine 1983, Steele 1985, Fuentes & Jaksić 1988). In one of these recent comparisons, dealing with predator-prey interactions in terrestrial and intertidal ecosystems, Jaksić (1986) concluded that the finding that intertidal predators can significantly affect the abundance and diversity of their prey, in constrast to the opposite finding in terrestrial predators, may be due to: (a) the different research protocols followed by intertidal and terrestrial ecologists (of a correlational nature in terrestrial ecosystems and mostly experimental in intertidal ecosystems), and (b) the differences in the mobility characteristics of the prey relative to predators (primarily sessile in intertidal versus highly mobile prey in terrestrial ecosystems). These conclusions received strong criticisms by López & Buschmann (1988), who argued that the apparent contrast between marine intertidal and terrestrial ecosystems is only due to the fact that it has not been possible to determine in intertidal habitats the real effects of predators upon their mobile prey. In this paper I will argue that the basic assumptions used by Jaksić (1986) and López & Buschmann (1988) were too weak to give support to their conclusions.

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First, it is necessary to point out that most of the marine evidence reviewed by Jaksić (1986) refers exclusively to the situation commonly observed in *rocky* intertidal ecosystems of temperate waters. This author did not explicitly state this

point, which is regrettable, because most of the temperate intertidal ecosystems of the world are made up of systems of a very different physical nature (*e.g.*, hard versus soft bottoms). This distinction is important because it is well known that marine landscapes are strongly influenced by the nature of the physical environment (see for example Dayton & Oliver 1980, Dayton 1984). Therefore, any valid criticism of Jaksić's conclusions must be made in the context of evidence proceeding from rocky intertidal systems. As I will discuss later, a major flaw in López & Buschmann's commentary is their failure in recognizing this point.

A second problem in Jaksić's paper concerns the spatial scales he used to compare predation processes occurring in marine and terrestrial ecosystems. The effect of terrestrial predators, for instance, was analyzed at very large spatial scales (*i.e.*, at the geographical scale) such as regions in Spain, Chile and California for owls, and in Michigan, Wisconsin, and Utah for diurnal raptors (Jaksić 1986). In sharp contrast, marine cases were analyzed at a very local scale that usually did not exceed a couple of square meters in the intertidal zone. Is this a valid comparison? I do not think so. Marine intertidal communities are highly variable and complex systems, and most marine ecologists accept today that the importance of the ecological processes operating in such systems may drastically change over very small spatial scales (*e.g.*, within meters) (Hawkins & Hartnoll 1983). Further, we should keep in mind that most common highly mobile predators found in intertidal habitats, such as fish and crabs, are animals of often relatively large sizes with foraging activity ranges that greatly exceed the size of the experimental plots studied in rocky intertidal systems. What does this mean? Simply, that in most cases the extent of the spatial scale has not been adequate for estimating the real effects of these predators in rocky intertidal habitats. Thus, in order to carry out an equivalent comparison in terrestrial and rocky intertidal systems, it will be necessary first to scale or standardize the spatial extent of the experiments with respect to both predator body sizes and their associated vagilities. This concern is also valid when comparing temporal dynamics of the two ecosystems (Steele 1985).

In their critique of Jaksić's (1986) paper, López & Buschmann (1988) argued that to date it has not been possible to determine the real effects of intertidal predators upon their mobile prey. This conclusion is vague and meaningless because these authors did not specify what did they mean by predators' "real effects". Certainly, predators can affect their prey populations in very different fashions. At the community level, for example, they can modify diversity patterns (Paine 1966, Paine & Vadas 1969, Lubchenco 1978; but see Jaksić 1986 and Fuentes & Jaksić 1988), whereas at the population level they may affect prey local distribution or prey abundance (see Taylor 1984 for a review). Regarding species richness and diversity patterns, the existing evidence is convincing in showing that both intertidal predators and terrestrial herbivores may drastically affect diversity patterns of sessile organisms in both systems (intertidal benthic prey and terrestrial plants respectively) (Jaksić 1986, Fuentes & Jaksić 1988). A different and confusing picture, however, emerges when we contrast the effect of highly mobile predators upon mobile (non-sessile) prey. The experimental evidence analyzed by Jaksić (1986) and Fuentes & Jaksić (1988) on this topic indicates that terrestrial mobile predators, in constrast to marine ones, do not affect to any larger extent the abundance or diversity patterns of their mobile prey. However, Parmenter & MacMahon (1988) in an interesting experimental study, have recently documented that rodent predation can significantly affect both the abundance and diversity (richness) patterns of ground beetles in a shrub-steppe ecosystem. The study of Parmenter & MacMahon (1988) provides opposing evidence to the views of Jaksić (1986) and also proves that experimental removals of predators are quite feasible in terrestrial ecosystems.

To give support to their conclusions, López & Buschmann (1988) utilized as evidence four experimental studies where birds and fish did not affect prey abundan-

ces. I should point out, however, that none of these studies was conducted in rocky intertidal systems: Reise's studies, for example, were carried out in soft bottoms or mudflats (Reise 1977, 1978, 1985), whereas that of Raffaelli & Milne (1987) was conducted in estuaries dominated by sandy bottoms. Similarly inappropriate in López & Buschmann's paper is the use of Choat & Kingett's (1982) work, because this study refers to a phenomenon observed in a rocky *subtidal* system of New Zealand. As I previously noted, it is not correct to treat different marine systems (*e.g.*, rocky intertidal and mudflast) as if they were organized in a similar fashion (see Dayton & Oliver 1980). Putting it another way, this is like treating tropical forests and semi-arid deserts as conforming only one ecosystem! López & Buschmann's (1988) incorrect use of the literature is a serious flaw that invalidates their arguments against Jaksić's conclusions.

There are other serious problems in the analysis of López & Buschmann as well. These authors concluded that "birds and fish significantly affect invertebrate populations of restricted mobility" (López & Buschmann 1988: 19). Quammen (1984), however, suggests in his study (pp. 534 and 535) that shorebirds can be important predators on invertebrate communities of sand and mudflats but physical and biological factors such as predator preference and prey availability must be known to predict the effects of predation. Further, Schneider (1978) observed that shorebird predation in a Massachusetts estuary repeatedly levelled off the relative abundance of invertebrate prey species but did not affect their presence or absence.

López & Buschmann (1988) also concluded that the observed differences regarding the effect of predators on mobile and sessile prey are due only to an operational problem (lack of effective control over mobile prey) and not to differences in prey vagility. This, because mobile prey were thought to be able to redistribute spatially, thus obscuring the real effect of their predators. Quammen (1984: 534), however, showed that such effect might well be due to a rapid in-situ recovery of local prey populations when predators (birds) were absent, which is quite a different explanation from that of López & Buschmann (1988). I also think that their explanation is rather confusing because even if we accept their argurment of a spatial redistribution of prey, we should recognize, therefore, that it is precisely the mobility of prey the factor obscuring the "real effects of predators".

Although it is important to consider that the are substantial numbers of mobile prey (*e.g.*, amphipods, isopods) in the intertidal zone, as López & Buschmann (1988) correctly pointed out, it is worth noting that this system is to a large extent dominated by dense stands of macroalgae and of sessile invertebrates (*e.g*, barnacles, mussels). These species often occupy most of the primary substrate, representing a significant proportion of the primary and secondary productivities of such ecosystems. The extensive ecological literature on the intertidal zone (*e.g.*, Stephenson & Stephenson 1972, Moore & Seed 1986) clearly shows that these sessile organisms support a heavy impact by mobile predators (Edwards *et al.* 1982). In addition to this, intertidal macroalgal stands and mussel beds play an important role in structuring significant populations of small-sized mobile organisms such as amphipods, providing not only food but also refuge against predation (Moore 1977, Gunnill 1982, Wakabara *et al.* 1983, Jacobi 1987, Johnson & Scheibling 1987). What seems clear from these studies is that mobile predators do affect distribution patterns of mobile intertidal prey, in a similar fashion as documented for terrestrial ecosystems (Jaksić 1986).

In summary, despite the attempts of Jaksić (1986) and López & Buschmann (1988), comparisons of predator-prey interactions in terrestrial and intertidal ecosystems seem, at this point, premature for two reasons: First, because a more thorough and critical analysis of the evidence is needed. Second, because these consumer relationships have been only scarcely explored in intertidal habitats (see Edwards *et al.*, 1982). These two shortcomings militate against drawing any valid conclusion about

the ecological processes operating in these two ecosystems.

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