Revista Chilena de Historia Natural
62: 13-17, 1989

COMMENTARY

Predator diets, guild structure and human disturbance: a rebuttal to Meserve's criticisms

Dieta de depredadores, estructura de gremios y perturbación humana: una réplica a las críticas de Meserve

JAVIER A. SIMONETTI

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

ABSTRACT

Simonetti (1988) advanced the hypothesis that the carnivorous guild of central Chilean predators resulted from the human alteration of the predator's food base. Meserve (1988) questioned this hypothesis as illogical and untestable, but concomitantly offered empirical evidence which supposedly falsified it. I analyze Meserve's criticisms and conclude that the hypothesis is logically correct and testable. The empirical evidence offered by Meserve as a refutation is considered necessary but insufficient to actually falsify Simonetti's (1988) hypothesis.

Key words: Chile, guilds, human disturbance, indirect effects, predators.

RESUMEN

Simonetti (1988) postuló la hipótesis que el gremio de depredadores carnívoros de Chile central es el resultado de la modificación humana de la disponibilidad de alimentos consumidos por los depredadores. Meserve (1988) criticó esta hipótesis por ser ilógica e irrefutable, pero al mismo tiempo ofreció evidencia empírica que refutaría dicha hipótesis. Un análisis de las críticas de Meserve permite concluir que la hipótesis no adolece de problemas de lógica y es refutable. La evidencia empírica ofrecida por Meserve como refutación es considerada necesaria pero insuficiente.

Palabras claves: Chile, efectos indirectos, gremio, perturbación humana, depredadores.

INTRODUCTION

Predator/prey relationships among central Chilean vertebrates have received considerable attention in recent years (see Jaksić & Simonetti 1987 for a review). Regarding predator assemblages, Jaksić *et al.* (1981, but *not* Simonetti 1988 as implied by Meserve 1988; see also Jaksić & Braker 1983, Jaksić & Delibes 1987) advanced the hypothesis that a carnivorous guild, formed by three hawks (*Buteo polyosoma, Geranoaetus melanoleucus* and *Parabuteo unicinctus*) and one fox *(Dusicyon culpaeus)* emerged as an epiphenomenon of the opportunistic response of these predators to the high abundance of a single prey, the degu rat (*Octodon degus*). Because high abundances of degus seem associated with human–disturbed shrublands, I hypothetized that: "If the guild structure of predatory species of central Chile depends upon their opportunistic response to prey supply levels [read: degu] which in turn results from the human degradation of the vegetation, it can be argued that the guild based on the exploitation of *O. degus* results directly from the human alteration of the food supply *via* habitat modification. Therefore, human disturbance may be regarded as the ultimate factor governing guild structure of predatory assemblages in central Chile" (Simonetti 1988: 24).

Recently, Meserve (1988) questioned this hypothesis on logical, epistemological, and empirical grounds. Here, I respond to Meserve's criticisms, attempting to demonstrate that the hypothesis I advanced has neither logical nor epistemological faults, and that the empirical evidence presented by Meserve is necessary but insufficient to falsify my hypothesis.

(Received 28 April 1989. Accepted 15 June 1989).

Unwarranted logical steps?

According to Meserve (1988), the proposition that predator diets are affected by human disturbance is an unwarranted leap in logic. No further argument is offered. In Meserve's words: "..., if factor A [predator diet] is determined by B [food supply], and B by C [disturbance], Simonetti is concluding that A is determined by C (*i.e.*, predator diets by human disturbance)" (Meserve 1988: 159). To consider my statement illogical involves two misconceptions. First, Meserve is assuming logical transitivity for a relationship that is biologically intransitive (Carnap 1958). In logical terms, Meserve assumes that (A)(B)(C) (RAB. RBC $\supset$ RAC)' or, more simply, $R^2 \subset$ R'. However, the relationship is biologically intransitive, because neither predator diets nor guild membership determine disturbance levels. Therefore, the relationship $R^2 \subset \sim R$' holds (Carnap 1958). Consequently, only if Meserve assumes logical transitivity is the hypothesis incorrect. As stated, my hypothesis is logically correct, provided that no causal relationship is implied or required between diet or guild membership as determinants of disturbance levels.

Second, and far more important, Meserve (1988) ignores the difference between proximate and ultimate causal factors in biology in general, and ecology in particular (Mayr 1961, Orians 1962). The variable tracked by predators, that is, the proximate factor affecting their choice about what to eat, and by extension determining their guild affiliation, is prey abundance (Jaksić *et al.* 1981). Factors affecting prey supply levels should be regarded as ultimate agents. These factors should directly affect the prey resource spectrum, and consequently, should also affect predator's choice. Here, human disturbance should be considered the ultimate agent determining guild structure, provided that prey supply levels are modified by the alteration introduced into the shrublands by human activities (Simonetti 1988; see also Simonetti 1986a, 1986b). Therefore, Meserve's criticisms seem invalid, as a basic distinction between proximate and ultimate factors has been ignored.

Further, the effect of human disturbance on guild membership can be regarded as an indirect effect of the reduction of shrub cover. Actually, the statements involved in Simonetti's (1988) hypothesis are analogous to the trophic-linkage type of indirect effect proposed by Miller & Kerfoot (1987; see also Wilson 1986). Here, species C affects species A by modifying the abundance of species B (Miller & Kerfoot 1987). Conceptually, this type of indirect effect does not differ from the relationship between disturbance, prey abundance and predator diets, and by extension, guild membership.

Indirect effects of human subsistence activities seem to be more common than previously recognized (Simonetti 1988[1]) and should be properly considered if we truly attempt to understand population and community structure and dynamics (*e.g.*, Godoy & Moreno 1989).

Is it unfalsifiable?

According to Meserve: "Simonetti's suggestion falls into the realm of an *ad hoc* hypothesis lacking the crucial condition of falsifiability" (Meserve 1988: 160). This criticism is absolutely invalid. Meserve himself attempts to empirically refute the hypothesis (Meserve 1988: 160)! Because an hypothesis that can be refuted by empirical evidence is falsifiable by definition, no further comment seems necessary (Popper 1968, Bunge 1983). On the other hand, I clearly indicated in my original paper the type of evidence needed to test empirically the hypothesis (Simonetti 1988: 24). The effect of disturbance on guild structure can be properly tested through a two-step procedure.

First, the causal relationship between disturbance and the abundance of degus should be demonstrated: "If the abundance of *O. degus* results from human alteration of the shrublands, this species should become progressively more common in the zooarchaeological record [read: time] and should become dominant when the shrub cover of a dense and undisturbed shrubland patch is experimentally reduced" (Simonetti 1988: 24). Clearly, this statement

[1] SIMONETTI JA (1988) Human disturbance and community patterns in central Chile. Symposium "Impact of past human disturbance in shaping present-day communities". 73rd Annual Meeting, Ecological Society of America, Davis, California. Bulletin of the Ecological Society of America (Supplement) 69 (2): 296 (abstract).

may be empirically falsified. If demonstrated false, no relationship could then be established between disturbance and the prey supply (at least, regarding *O. degus*) of local predators. Archaeozoological work now in progress supports the contention that degus have become increasingly more abundant through time in comparison to congeneric species. While in the past *O. bridgesi,* an inhabitant of dense woodlands dominated among *Octodon* species, the relative abundance of *O. degus* increased through time to a point where it has become to dominate the fauna, and *O. bridgesi* has all but disappeared (Simonetti 1988[2]). Although the relationship between changing abundances of *O. degus* and human disturbance (assessed as increasing land clearing) is yet to be established, the evidence gathered points to the right direction (Simonetti 1988[2]).

Second, the relationship between changing prey supply and predator diets, and consequently guild membership should be established: "if human modification of the shrubland increases their profitability to predators by increasing the abundance of suitable prey items, those predators should either concentrate hunting in those profitable patches and/or exhibit a reduction in their trophic niche breadth as they concentrate hunting effort on a few (or a single) abundant prey items" (Simonetti 1988: 24). This statement can also be empirically falsified, and research on this topic is currently underway (FM Jaksić, personal communitation April 1989).

In closing, my hypothesis is empirically falsifiable in all aspects regarding the relationship between human disturbance, prey supply, predator diets and, by extension, guild structure. Meserve (1988) himself agrees with this tacitly, by attempting to offer empirical evidence refuting my hypothesis. The evidence he presented is discussed next.

Empirical evidence

According to Meserve (1988), two studies falsify my hypothesis that human disturbance affects guild membership in predatory assemblages of central Chile. These two studies deal with the diet of just one guild member, the fox *D. culpaeus* (Meserve *et al.* 1987, Iriarte *et al.* 1989). In two localities, Parque Nacional Fray Jorge in north-central Chile, and San Carlos de Apoquindo in central Chile, *D. culpaeus* was shown to prey primarily upon *O. degus,* despite its not being the most abundant potential prey. Unfortunately, one of the studies mentioned has some methodological shortcomings that cast doubts about the authors' conclusions. For instance, Meserve *et al.* (1987) analyzed the diet of *D. culpaeus* based on feces aged up to 11 months old and compared this averaged consumption with a prey availability assessment, based on a three-night sampling of small mammals in June 1985. Despite known fluctuations in rodent populations (Meserve & Le Boulengé 1987), Meserve *et al.* (1987) admitted: "While it is recognized that prey remains contained in pellets/scats [they also studied *Athene*'s diet] up to 11 months old may represent varying degrees of predator selectivity perhaps influenced by fluctuating small mammal abundances over time, we assume that summing them together gives an overall view of predator diet that is useful in comparison with similar time scales of trapping data" (Meserve *et al.* 1987: 95).

Therefore, the mismatch between availability and consumption does not necessarily represent prey selection but may be a consequence of inadequate sampling. Even assuming that these problems are negligible or nonexistent as in Iriarte *et al.* (1989), the evidence offered by Meserve (1988) is necessary but insufficient to falsify my hypothesis. The data made available by the studies mentioned involves just one of the four guild members referred to in my paper. The crucial point is to demonstrate that guild structure is invariant regardless of a reduction in the abundance of *O. degus* and/or an increase in alternate potential prey. That is, all guild members have to be considered. As long as such evidence is lacking, my hypothesis is not falsified.

A point well made by Meserve (1988) is that which regards the difference between rank and absolute abundance of small mammal prey. While my analysis was based on the rank abundance of prey, predators may respond to absolute, not relative, abundance. Absolute prey abundance may be the variable that predators target on, but

[2] SIMONETTI JA (1988) Análisis histórico de la abundancia de *Octodon* en Chile central. XXXI Reunión Anual, Sociedad de Biología de Chile, La Serena. Archivos de Medicina y Biología Experimentales 21 (2): R333 (resumen).

there is no clear-cut relationship between abundance and prey availability (read: vulnerability). For instance, although the abundance of two hawks, *Buteo jamaicencis* and *Buteo lagopus* is higher in habitats that support greater densities of their major prey, the meadow vole (*Microtus pennsylvanicus*), not all patches of high prey density support high abundance of hawks. Factors such as shrub cover influence prey availability, reducing patch profitability (Baker & Brooks 1981). In fact, absolute abundance cannot be equated to prey availability until the encounter rate is determined (Stephens & Krebs 1986).

In central Chile, degus dominate the small mammal fauna of sparsely covered shrubland patches. Here, although they may be less numerous in absolute terms than in open and undisturbed patches (Simonetti 1986a, for review), they may be more vulnerable to predators due to the reduced interference posed by decreased cover.

Final comments

Do guilds emerge as an indirect effect of human disturbance? A definitive answer will not arise if we follow the advocacy method (Wilson 1975). I have attempted to demostrate that my hypothesis is logical and falsifiable, rebutting Meserve's (1988) criticisms. However, we have gathered no new evidence. In my opinion, predator/prey studies have progressed considerably over the last decade, allowing the detection of patterns and the proposition of refutable hypotheses, such as that of Jaksić *et al.* (1981) concerning opportunism versus competition, that of Simonetti (1988) relating disturbance to guild membership, and that of Bozinovic & Medel (1988) regarding predator energetics and prey selection (see Jaksić & Simonetti 1987 for review). However, much more natural history data are needed on prey vulnerability with reference to population abundance and shrub cover, on prey availability as related to predators' hunting mode, and on the spatio-temporal relationship between human disturbance and small mammal assemblages. Well designed observations and experiments are needed to test these factors that impinge on the dynamics of predator/prey relationships and on the emergent features that stem from them.

ACKNOWLEDGEMENTS

Francisco Bozinovic, Fabián Jaksić, and Peter Meserve (who may disagree) commented on the manuscript. This research was supported by grants from the Universidad de Chile DTI 2596-8824 and from FONDECYT 89-0871.

LITERATURE CITED

BAKER JA & RJ BROOKS (1981) Distribution patterns of raptors in relation to density of meadow voles. Condor 83: 42-47.

BOZINOVIC F & RG MEDEL (1988) Body size, energetic and foraging mode of raptors in central Chile. Oecologia (Berlin) 75: 456-458.

BUNGE M (1983) La investigación científica: su estrategia y su filosofía. 2a edición, Ediciones Ariel, Barcelona.

CARNAP R (1958) Introduction to symbolic logic and its application. Dover Publications, New York, New York.

GODOY C & CA MORENO (1989) Indirect effects of human exclusion form the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. Oikos 54: 101-106.

IRIARTE JA, JE JIMENEZ, LC CONTRERAS & FM JAKSIC (1989) Small mammal availability and consumption by the fox, *Dusicyon culpaeus*, in central Chilean shrublands. Journal of Mammalogy 70: 79-87.

JAKSIC FM & HE BRAKER (1983) Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. Canadian Journal of Zoology 61: 2230-2241.

JAKSIC FM & M DELIBES (1987) A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: causes, correlations, and consequences. Oecologia (Berlin) 71: 461-472.

JAKSIC FM & JA SIMONETTI (1987) Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. Revista Chilena de Historia Natural 60: 221-244.

JAKSIC FM, HW GREENE & JL YAÑEZ (1981) The guild structure of a community of predatory vertebrates in central Chile. Oecologia (Berlin) 49: 21-28.

MAYR E (1961) Cause and effect in biology. Science 134: 1501-1506.

MESERVE PL (1988) Are predator diets a consequence of human disturbance in central Chile? – a reply to Simonetti. Revista Chilena de Historia Natural 61: 159-161.

MESERVE PL & E LE BOULENGE (1987) Population dynamics and ecology of small mammals in the northern Chilean semiarid region. Fieldiana, Zoology, New Series 39: 413-431.

MESERVE PL, EJ SHADRICK & DA KELT (1987) Diets and selectivity of two Chilean predators in the northern semi-arid zone. Revista Chilena de Historia Natural 80: 93-99;

MILLER TE & WC KERFOOT (1987) Redefining indirect effects. In Kerfoot WC & A Sih (eds) Predation: direct and indirect impacts on aquatic communities: 33-37. University Press of New England, Hannover.

ORIANS GH (1962) Natural selection and ecological theory. American Naturalist 96:257-263.

POPPER KR (1968) The logic of scientific discovery. Harper & Row, New York, New York.

SIMONETTI JA (1986a) Microhabitat use by small mammals in central Chile. Doctoral Dissertation, University of Washington, Seattle, Washington.

SIMONETTI JA (1986b) Human-induced dietary shift in *Dusicyon culpaeus*. Mammalia 50: 406-408.

SIMONETTI JA (1988) The carnivorous predatory guild of central Chile: a human-induced community trait? Revista Chilena de Historia Natural 61: 23-25.

STEPHENS DW & JR KREBS (1986) Foraging theory. Princeton University Press, Princeton, New Jersey.

WILSON EO (1975) Sociobiology: the new synthesis. Belknap Press, Cambridge, Massachusetts.

WILSON DS (1986) Adaptive indirect effects. In Diamond J & TJ Case (eds) Community ecology: 437-444. Harper & Row, New York, New York.