

On the Relationship between Productivity and Food Chain Length at Different Ecological Levels

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Submitted September 2, 2005; Accepted June 23, 2006;
Electronically published December 4, 2006

Online enhancements: appendix tables and figures.

ABSTRACT: The effects of energy on food web structure have been debated for at least 80 years. Nevertheless, the empirical evidence is meager, especially from terrestrial ecosystems. We analyzed long-term temporal variation in food chain length in a semiarid continental ecosystem, where productivity shows large interannual variations. Incidence of nonherbivorous prey in predator diet was used as a proxy of trophic position, allowing us to analyze the effect of productivity on food chain length within the assemblage of top predators (which comprises the most abundant and persistent top predators in the system) and to compare observed patterns at the species and assemblage levels. At the species level, the relationship between trophic position and productivity took different forms, varying in magnitude and shape. This pattern contrasts with the consistent increase in food chain length, with productivity observed at the assemblage level. Our results indicate that productivity can be a main determinant of food chain length, but not necessarily because of energy limitation. Further, the increase in food chain length with available energy probably represents an aggregate attribute, driven to a large extent by predators with higher consumption rates, rather than being the result of compensatory responses among predators.

Keywords: food web, food chain length, productivity, scale, raptors.

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The processes that account for variation in food chain length have been debated on empirical and theoretical grounds for almost 80 years (Post 2002). Energy limitation for food chain length was proposed early as an intuitively appealing hypothesis, based on the expectation of reduced viability of populations at the top of food webs as a consequence of the low efficiency at which energy passes through trophic connections (Elton 1927; Lindeman 1942; Hutchinson 1959). Early theoretical models predicted an increase in food chain length with available energy (Fretwell 1977; Oksanen et al. 1981; Oksanen and Oksanen 2000), but other models yielded the opposite, that is, a reduction in food chain length as productivity increases (Rosenzweig 1971; Abrams and Roth 1994). The analysis of population models suggests an alternative determinant of food chain length: the dynamic stability of trophic configuration (Pimm and Lawton 1977; Pimm 1982). Nevertheless, the stability of short food chains in this latter case originates from the number of self-regulated populations and not by the effect of trophic configuration (Sterner et al. 1997). When self-regulation is considered, longer food chains are in fact more stable (Sterner et al. 1997).

Energetic and dynamic interpretations have been at the core of the debate on food chain length, but other explanations have also been proposed. Attention has been called to the role of ecosystem size (Cohen and Newman 1991; Spencer and Warren 1996; Post et al. 2000; Holt 2002; Post 2002), environmental dimensions (Briand and Cohen 1987), differences between predator and prey body sizes (Pimm 1982; Cohen et al. 1993, 2003; Jennings and Warr 2003), biophysical limitations to top predator existence (Pimm 1982) or to prey consumption (Hairston and Hairston 1993), and disturbance (Marks et al. 2000). Studies that combine the effect of energy and trophic configuration dynamics indicate that the length of food chains can also be affected by energy because of the stability of intraguild predatory interactions. Intraguild predation occurs when a predator and a prey species share a resource (Polis et al. 1989). At low productivity, the intraguild prey excludes the intraguild predator; at intermediate productivity, both

species coexist, thus increasing food chain length; and at high productivity, the intraguild predator excludes the intraguild prey by the combined effect of predation and competition (Holt and Polis 1997). Therefore, in a gradient of available energy, the length of food chains should show a humped pattern as a consequence of the dynamics of the intraguild predatory system. Predictions from such models have been supported by theoretical approaches and empirical studies (Morin and Lawler 1996; Morin 1999; Amarasekare 2000; Diehl and Feiel 2000, 2001; Mylius et al. 2001; Borer et al. 2003). Further, intraguild predation is more widespread than previously suspected (Arim and Marquet 2004) and thus has the potential to be a determinant of food chain length in nature.

One problem for studying the effect of energy on community structure is that potential determinants of available energy in natural ecosystems are diverse, involving productivity, productive space (area times productivity), detritus, and external inputs (Schoener 1989; Moore et al. 1993, 2004; Polis et al. 1997; Pace et al. 2004). Empirical studies have reported associations between food chain length and energy for comparisons among communities, for populations in different communities, and in microcosms. At the community level, positive (Schoener 1989; Jenkins et al. 1992; Persson et al. 1992; Townsend et al. 1998; Oksanen and Oksanen 2000; Thompson and Townsend 2005), negative (Pimm and Kitching 1987; Jepsen and Winemiller 2002; but see Jenkins et al. 1992), and lack of associations between community chain length and productivity have been reported (Briand and Cohen 1987; Post et al. 2000; but see Holt 1993; Yodzis 1993). At the population level, positive responses to productive space (Vander Zanden et al. 1999) and to space alone (Post et al. 2000) have been detected. Microcosm studies show a positive response to productivity in a food chain system (Jenkins et al. 1992; Kaunzinger and Morin 1998) and a humped association in systems with omnivory (e.g., Morin 1999; Diehl and Feiel 2000).

Considering its 80 years of history, the empirical evidence relating energy and food chain length is remarkably scarce. Terrestrial continental ecosystems are particularly underrepresented in food web studies, which is reflected in the lack of reports on the association between food chain length and available energy. Since 1987, a long-term ecological research project has been conducted in a central Chilean semiarid environment. The system is characterized by large variations in primary productivity driven by the El Nio phenomenon (Jaksic 2001; Meserve et al. 2003). The diets of top predators have been monitored for more than 16 years, allowing the analysis of variation in food web structure in relation to changes in primary productivity over time (Arim and Jaksic 2005). Following a simple but novel methodological approach, we here report the

association between primary productivity and food chain length, the first such report for a terrestrial continental community. Our objective is to analyze the effect of primary productivity on predator species trophic position and on predator ensemble food chain length. These two approaches enable a contrast between the observed patterns at different ecological levels within the same community over time.

Methods

This study is based on information collected at Las Chinchillas National Reserve near Auc, Chile (31°30'S, 71°06'W; elevations ranging 400–1,700 m). Characteristics of the reserve have been detailed elsewhere (Jaksic et al. 1993). During 16 years (1987–2002), the diets of the strigiforms *Speotyto cunicularia* (burrowing owl), *Bubo magellanicus* (Magellan horned owl), *Glaucidium nanum* (austral pygmy owl), and *Tyto alba* (barn owl), the falconiform *Falco sparverius* (American kestrel), and the canid *Pseudalopex culpaeus* (culpeo fox) were monitored. These species are the most abundant and persistent top predators at the site. A total of 90,446 prey were determined from 19,838 regurgitated raptor pellets and 6,568 fox feces.

Productivity

Throughout this article, precipitation is used as a proxy of productivity. This is justified because in arid and semi-arid environments, productivity is closely related to precipitation (Rosenzweig and Abramsky 1993). Driven by El Nio, large changes in rainfall take place in the study area, increasing aboveground cover of herbs (200%–400%), seed bank density (400%–1,000%), and herb species richness (60%–190%), thus strongly affecting primary productivity (Jaksic 2001; Meserve et al. 2003). Depending on the life-form involved, the response may be immediate for ephemeral herbs or lagged by 1 year for perennial herbs (Jaksic 2001). Further discussion on the use of precipitation as a proxy of productivity in the study system was presented by Arim and Jaksic (2005).

Food Chain Length

The approach used here to estimate food chain length differs from previous ones. We focused on the incidence of herbivorous versus nonherbivorous individual prey among top predator diets as an index of trophic position. A predator with a diet of only herbivorous prey has the lowest possible trophic position. To the contrary, a diet composed entirely of nonherbivorous prey will represent the topmost trophic position that our index can yield.

Nonherbivorous prey incidence is positively associated with chain length and thus yields a direct index of chain length. It should be highlighted that the use of this index brings a conservative estimate of variation in trophic position of predators because nonherbivorous prey may involve different trophic levels (e.g., primary or secondary carnivorous species). In addition, the effect of energy on food chain length should be stronger in the shortest food chains than in the longest ones (Yodzis 1993), and variations in the shortest chains are those that our index is more prone to detect. Further, precipitation and the incidence of nonherbivorous prey are monotonically related with the variables they represent (rainfall and trophic position, respectively) and thus convey a robust estimation of the functional association between the original variables (Arim and Jaksic 2005). The large difference in body size between invertebrate and vertebrate prey implies differences in their energetic value to predators. The analysis based on individual prey without considering these differences may overestimate the effect of small invertebrate prey. To minimize this potential bias, we analyzed the incidence of nonherbivorous prey for the complete set of prey and independently for vertebrate and invertebrate prey.

Based on relevant publications (Peña 1986; Cuezco 1998; Jaksic 1998; Jaksic and Lazo 1999; Brescovit et al. 2002; Kury and Pinto-da-Rocha 2002; Lourenço 2002; Silva 2005), 76,048 of the 90,446 individual prey identified were classified as either herbivorous or nonherbivorous (table A1, available in the online edition of the *American Naturalist*). The incidence of nonherbivorous prey in the diets was analyzed as the proportion of nonherbivore individuals in relation to the total number of individual prey consumed during a given year. Proportions of nonherbivorous individual prey were assessed independently for each predator species, providing estimates of trophic positions, and for the combined diets of all predators, providing an estimate of the food chain length for the entire predator ensemble. The six top predators studied comprise the most abundant and persistent top predators in the system, thus adequately representing the top predator assemblage in the community. Plants were a significant food item only in the *P. culpaeus* diet. For this fox species, the incidence of nonherbivorous items among animal prey was analyzed as in the other predators, but in addition, the incidence of feces with nonplant remains was also analyzed. The fox scat (rather than the individual prey, as in previous analyses) was used as the unit of analysis in this case because animal and plant remains (mostly seeds) are not comparable, rendering it difficult to relate number of seeds with number of plant individuals consumed.

Incidence of Nonherbivorous Prey

Variations in the incidence of nonherbivorous prey among predator diets were studied by logistic regression analyses (Hosmer and Lemeshow 1989; Neter et al. 1996). Incidences or proportions are typically calculated from individual observations classified in categories (Cox and Snell 1989), as in our case, where individual prey items are classified as herbivorous or nonherbivorous. The probability that a single observation comes from one of these categories in relation to the state of other variables (e.g., precipitation) can be analyzed by logistic regression (Cox and Snell 1989; Hosmer and Lemeshow 1989; Neter et al. 1996), which allows estimation of variation in the proportion of nonherbivorous prey from individual prey observations. Further, logistic regression enables an optimal use of available information for estimating variations in proportions through the incidence of nonherbivorous prey from the total number of individual prey observed for each predator (38,743 for *S. cunicularia*, 6,948 for *B. magellanicus*, 1,703 for *G. nanum*, 7,864 for *T. alba*, 956 for *F. sparverius*, and 19,834 for *P. culpaeus*).

Long-term trends in the incidence of nonherbivorous prey in predator diets over the 16 years of study were observed among most predators, indicating the need for inclusion of covariables in order to remove this trend and attain a proper interpretation of food web patterns (Bengtsson 1994; Arim and Jaksic 2005). The inclusion of the variables year and its quadratic value as potential explanatory variables in regression models allows control for long-term trends, attaining a better estimate of the association between productivity and food chain length (Hosmer and Lemeshow 1989; Neter et al. 1996; Freckleton 2002). This procedure was done by using multiple logistic regressions and coding years from 1 to 16 throughout the study period (1987–2002).

Eight explanatory variables were considered. Six variables are related to productivity. We included precipitation during the current year, precipitation during the previous year, precipitation during the previous two years, and the quadratic value of these three variables. In addition, two variables were included to control for long-term trends in data: the year of study and its quadratic value. The incorporation of quadratic terms allows detection of U-shaped, humped, or monotonic associations (Neter et al. 1996). Predictor variables were centered on the mean to control for correlation between quadratic and linear variables (Sokal and Rohlf 1995). Parameters of the logistic regression estimate the increase in the probability of observing a nonherbivorous prey in a predator's diet with an increase by one unit of precipitation. If precipitation is expressed in millimeters, model parameters indicate the change in probability of observing a nonherbivorous prey

in a top predator diet when precipitation increases by 1 mm. We chose to work with precipitation expressed as millimeters \times 100; thus, model parameters estimate change in probability when precipitation increases by 100 mm because this better captures the scale of variability in productivity and improves model fit (see Hosmer and Lemeshow 1989).

Models were constructed from best-subset analysis based on Akaike Information Criterion (AIC) ranks (Hosmer and Lemeshow 1989; Hilborn and Mangel 1997). The best model based on AIC data is that with the lowest AIC value (Hilborn and Mangel 1997). Differences in AIC values between models greater than two units are statistically significant (Richards 2005). When models with differences smaller than 2 were detected, we retained the most informative model, that is, the one with the larger number of independent variables, with significant parameter estimations.

The effect of variables related to precipitation was evaluated by estimating their partial deviance (Neter et al. 1996). Deviance values represent a measure of model fit, and partial deviance can be used to contrast the relative importance of independent variables in order to explain the dependent variable state (Neter et al. 1996). In addition, the difference between deviance values in nested models follows a χ^2 distribution with degrees of freedom equal to the number of parameters set to 0 in the nested model. Thus, in each analysis, the significance of independent variables was determined with partial deviance, with the effects of the variable and its quadratic term combined whenever both variables were considered in the final model.

Results: Incidence of Individual Prey

No consistent pattern of response was observed among the six predators (fig. 1; table A2, available in the online edition of the *American Naturalist*). All predators showed an association between productivity and food chain length (fig. 1), but this association varied in functional form. It should be noted, however, that the patterns reported for vertebrate and invertebrate prey are consistent with those observed when all prey were analyzed together (figs. A1, A2, available in the online edition of the *American Naturalist*). For all the logistic regressions, the final model and all their parameters were significant ($P < .05$). Models recommended by best-subset procedure, the final model retained, and the retained model's AIC differences are presented in table A2.

The model with the lowest AIC value for *Glaucidium nanum* included all the independent variables. However, estimated parameters showed disparate confidence intervals for year and its square value (0–0.00228 and 45–

328,889,600, respectively). Disparate confidence intervals indicate a wrong model (Hosmer and Lemeshow 1989). The same problem was observed in the second-best model. Consequently, we retained the third model in AIC rank, in which all variables related to precipitation were significant and parameter estimation displayed narrower confidence intervals. The same problem was detected for the models that considered only invertebrate or vertebrate prey (table A2). Therefore, these models should be considered tentative. In most cases, the largest partial deviance was observed for precipitation with a 1-year lag (fig. 1). The exception was *Bubo magellanicus*, whose larger partial deviances were related to precipitation without lag.

The best-subset logistic regression for the top predator ensemble (i.e., for the combined diets of all predators) selected a model with the eight dependent variables. Nevertheless, the parameter related to precipitation with 2-year lag was not significant. A model that did not include this variable showed less than 2 units of difference in AIC value from the previous model (table A2), and thus it was selected as the best model, given that it was the second model in AIC rank and that all its parameters were significant (fig. 2; table A2). For the top predator ensemble, vertebrate and invertebrate prey showed a congruent pattern (fig. 3). However, two issues should be highlighted: first, the range of variation in the nonherbivorous category is smaller among invertebrate than among vertebrate prey; second, for invertebrate prey, the response with 2-year lag and without lag dominates, while for vertebrate prey, the response with 1-year lag dominates.

With regard to the incidence of feces without plant remains in *Pseudalopex culpaeus*, the AIC data selected a significant model indicating a positive association between nonherbivorous prey and precipitation without lag and precipitation with 2-year lag and a humped association with precipitation with 1-year lag (fig. 4; table A2). The logistic approach makes optimum use of available information, with a large statistical power to detect the effect of variables included in the model, even if the biological pattern is not strong. Consequently, because all models were significant in our case, attention should focus on the magnitude of the effect, which can be assessed by considering the partial deviance. Under this criterion, *Speotyto cunicularia* and *Tyto alba* are characterized by a U-shaped response to productivity with a 1-year lag, while *B. magellanicus* and *Falco sparverius* show a humped pattern in response to precipitation and precipitation with 1-year lag, respectively. In the case of *P. culpaeus*, the dominant effect is a positive trend with increasing precipitation with 1-year lag, while for *G. nanum*, the effect of all variables is weak, suggesting only

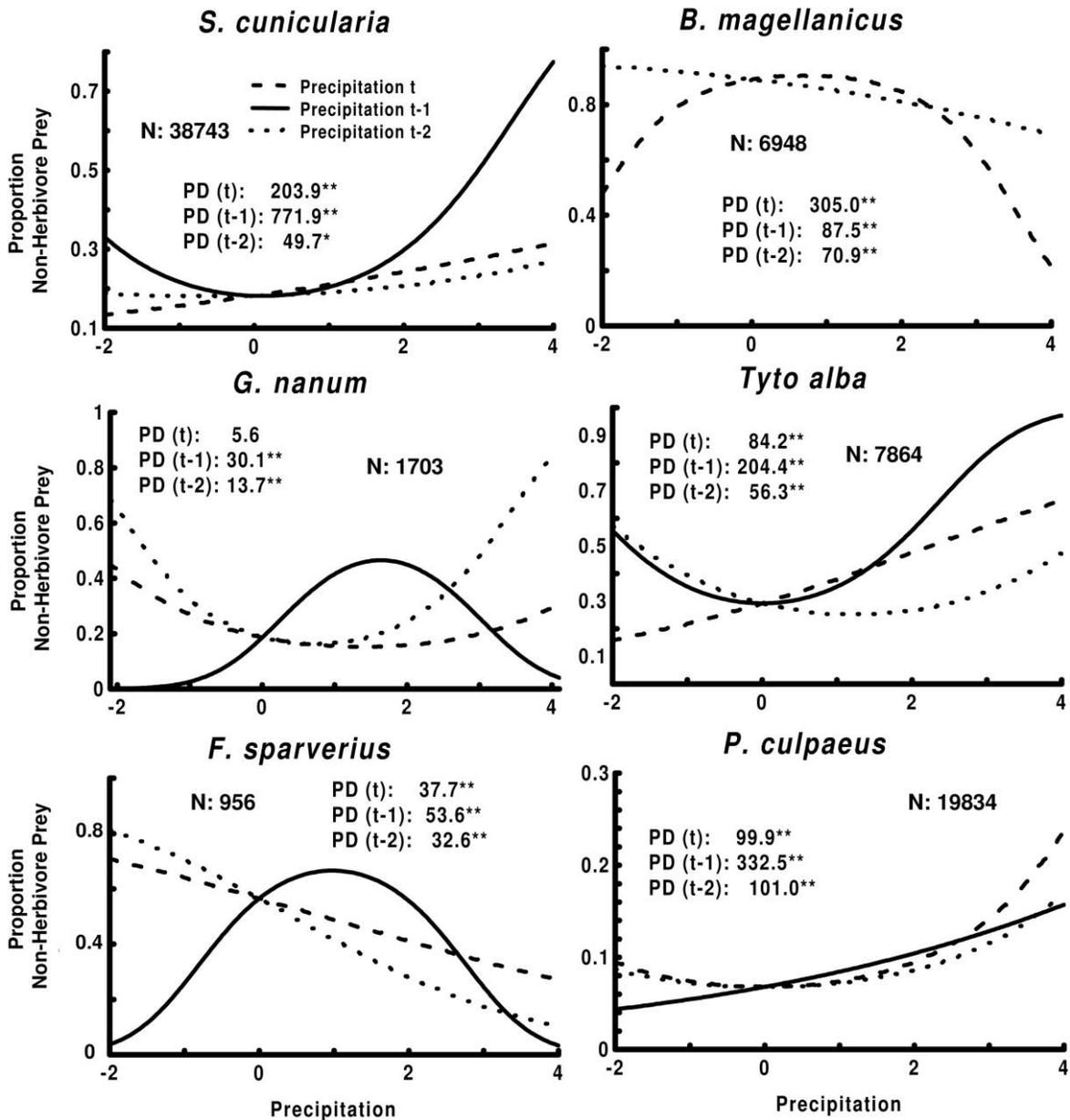


Figure 1: Estimated incidence of nonherbivorous prey—representing food chain length—as a function of precipitation, a proxy of productivity. Dashed, solid, and dotted lines represent the estimated association between precipitation without time lag, with 1-year lag, and with 2-year lag, respectively. PD = partial deviance, difference in deviance when the variable and its quadratic form are excluded from the model. Note that partial deviance for $t - 1$ is usually larger than deviance from other time lags.

a slight effect of productivity on nonherbivorous incidence in its diet.

Discussion

Our study differs from previous ones in two important ways: first, changes in food chain length that are related

to productivity emerge over long multiyear time series; second, these changes occur in a terrestrial continental system, wherein food chains have not received enough attention. Both the analysis of terrestrial systems and that of temporal variation in food web structure represent topics where more studies are needed (Warren 1989; Schoenly and Cohen 1991; Closs and Lake 1994; Tavares-Cromar

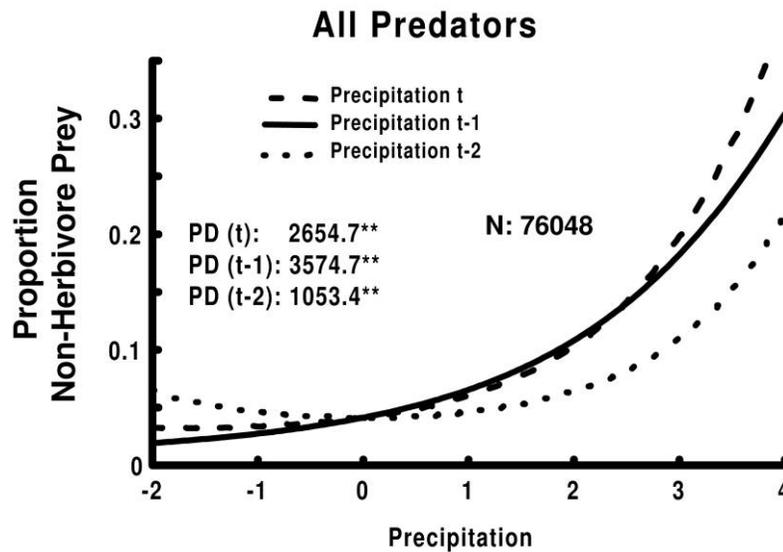


Figure 2: Incidence of nonherbivorous prey in the combined diets of six predators as a function of precipitation (productivity). Curves estimated from multiple logistic regression. PD = partial deviance; lines are as in figure 1.

and Williams 1996; Hall and Raffaelli 1997; de Ruiter et al. 2005). In general, our results show contrasting patterns when changes in food chain length are analyzed at the species or ensemble level, suggesting that this distinction will improve the understanding of this phenomenon, as was the case for species and community trophic cascades (Polis et al. 2000).

Our results point out the existence of an association between productivity and food chain length. Nevertheless, it is one thing to demonstrate an association between a given variable and food chain length and quite another to show that observed lengths are the result of changes in that variable (Kitching 2001). Positive associations, as shown by most predator species at some time lag in our study (fig. 1), could be interpreted within the framework of classical energy limitation. The fact that not a single predator presented a consistent positive response in trophic position at all lags from the productivity pulse (figs. 1, 4), such as those observed for the entire community (fig. 2), poses a challenge. While it seems likely that productivity is the main determinant of food chain length in our system, one has to consider that productivity changes drive huge variations in community richness, abundance, composition, and food web structure (Jaksic et al. 1993, 1996, 1997; Jaksic and Lazo 1999; Jaksic 2001; Lima et al. 2002; Arim and Jaksic 2005).

The connecting mechanism may not be energy limitation, the process most often invoked to link productivity with food chain length (Elton 1927; Lindeman 1942; Hutchinson 1959; Fretwell 1977; Oksanen et al. 1981;

Schoener 1989; Vander Zanden et al. 1999). Other processes that connect productivity with food chain length, such as intraguild predatory dynamics, predict a humped pattern and the turnover of top predator species (Holt and Polis 1997; Diehl and Feiel 2000, 2001; Mylius et al. 2001). Nevertheless, the humped patterns that we detected among top predator diets occurred without predator turnover. This suggests that an unstable trophic configuration, as predicted by models, leads to a change in trophic structure faster than to species exclusion, but this point remains to be explored (Arim and Marquet 2004). Some models predict a negative association between food chain length and productivity (Rosenzweig 1971; Abrams 1993; Abrams and Roth 1994), but robustness of this prediction to variations in food web configuration, such as inclusion of omnivory (Mylius et al. 2001), existence of vulnerable and invulnerable prey (Chase 2003), and alternative modeling approaches (e.g., Arditi and Ginzburg 1989; Abrams 1996; Jensen and Ginzburg 2005) need to be considered as well.

The most surprising pattern at the species level was the U-shaped association observed for the owls *Speotyto cunicularia*, *Tyto alba*, and *Glaucidium nanum* (fig. 1). This could originate from the combined effect of two or more processes dominating at different levels of available energy or be the result of a single mechanism yet to be understood. To our knowledge, no theory has predicted a U-shaped pattern. In addition, the detection of a significant association between productivity and food chain length, with and without time lags, suggests that both functional and numerical responses of predators could be involved.

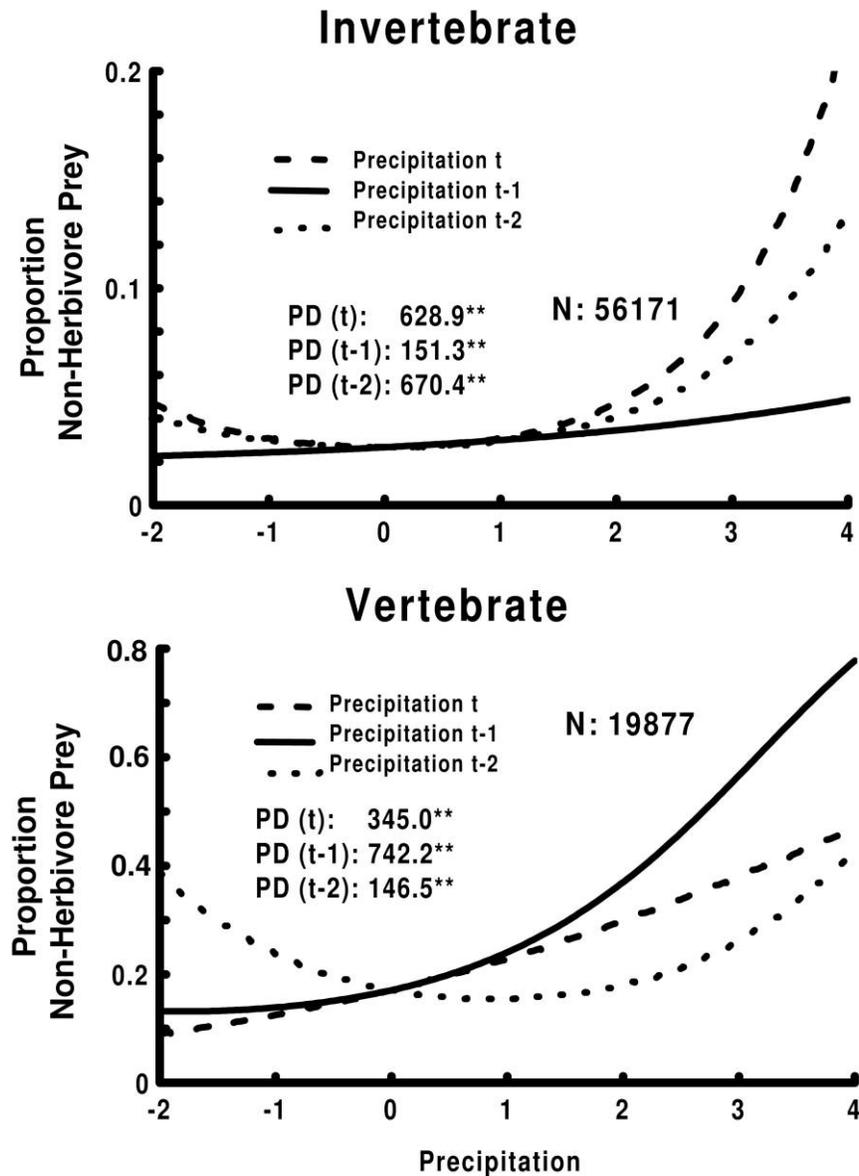


Figure 3: Incidence of nonherbivorous prey in the combined diets of six predators as a function of precipitation (productivity), discriminating between vertebrate and invertebrate prey. Note that general patterns are congruent with the observed associations in figure 2. The most remarkable difference is the association between nonherbivorous vertebrate incidence and precipitation with a 2-year lag. However, the partial deviance for this variable is lower than those observed in other variables considered.

The community response to productivity is usually more complex than a parallel increase in abundance in all predator populations because many factors change with variations in available energy (Kitching 2001). Community composition, food web structure, species abundance, and population sizes are affected by available energy. In addition, pulses of energy may introduce changes in competitive abilities (Tilman 1982) and in the relative importance of competition and predation (Bohannan and

Lenski. 2000). Also, abundance can be positively or negatively affected by productivity (e.g., Abrams 1993; Morin 1999; Diehl and Feiel 2001; Mylius et al. 2001). Similarly, the diets of predator species change with variations in productivity that affect prey richness and abundance (Arim and Jaksic 2005), and so do the patterns of diet overlap among predators (Jaksic et al. 1993, 1996, 1997), which in turn modify the effects of predators on prey populations (Lima et al. 2002). Specifically, variations in predator

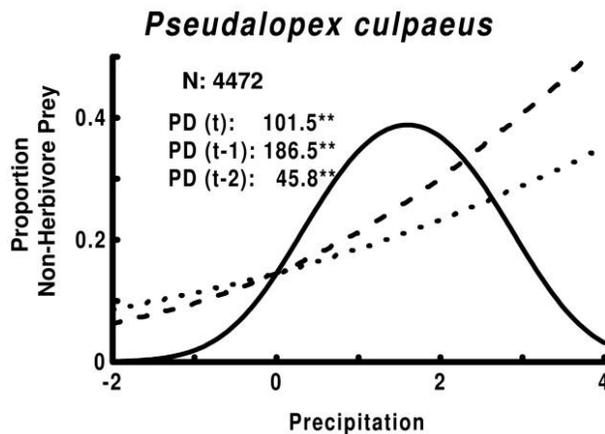


Figure 4: Estimated incidence of *Pseudalopex culpaeus* feces without plant remains—a proxy of food chain length—in a gradient of precipitation (productivity). PD = partial deviance; lines are as in figure 1.

abundance in our study system result from the combined effect of environmental variables, intraspecific competition, and predator-prey interactions (see Lima et al. 2002). In addition, different mechanisms may preclude transmission of energy to populations in upper positions of the food web (Abrams 1993). In this context, the increase in total energy entering the system may be experienced differently by different predators. The availability of different prey at higher trophic levels, and their relative benefits, may increase for some predators but decrease for others, a scenario that also depends on the time since the productivity pulse. The idiosyncratic behavior observed at the predator population level is expected, while the congruent and time-invariant relationship observed at the predator ensemble level is remarkable.

The question here is whether the observed invariant pattern at the ensemble level originates because of compensatory responses among predators or whether it can be explained by the dominant effect of some predators with a disproportionate contribution to the pattern. The second explanation is more plausible in our system. The ecological effects of changes in available energy, as discussed above, suggest that heterogeneous responses to productivity among predator species in a community are likely to be more common than parallel ones. To the contrary, at the predator ensemble level, the net effect of productivity pulses is an overall increase in resource availability at higher trophic levels. Excess consumption by some species of the ensemble could lead to an increase in food chain length, as long as they keep high consumption rates. This is apparently true in our study, where the ensemble-level pattern is driven by the two predator species with positive responses (i.e., *S. cunicularia* and *Pseudalopex cul-*

paeus), which account for 61% of the total number of prey consumed. In fact, the aggregate response of these two species is consistent with the pattern observed for the complete ensemble (fig. A3, available in the online edition of the *American Naturalist*). There is a simple statistical explanation for the ensemble response to productivity: the ensemble pattern is determined by the two species with highest consumption rate, rather than being the result of compensatory interactions among predators.

Our results suggest that the species and higher-level patterns of response to productivity are not necessarily congruent. A similar situation may be observed regarding the effect on food chain length of other variables, including total area, productivity space, and environmental dimensions, with idiosyncratic responses occurring at the species level but nevertheless leading to an overall increase in community chain length. A key point that remains to be explored in other systems refers to the mechanisms that connect patterns observed at different ecological levels. In our study, the species with the highest consumption rates accounted for the ensemble pattern, pointing out a statistical explanation for the observed association. However, in other communities, and for other food web metrics even in the same system (Arim and Jaksic 2005), the pattern observed at higher ecological levels could originate from interactions among component species.

Our focus on the incidence of nonherbivorous prey as an index of trophic position and the use of logistic regression analysis represent a novel methodological approach to food chain length. This method requires only detailed information about predator diets and the ability to classify prey as herbivorous or nonherbivorous. The required information is currently available for many predators in different systems and within the same system over time. Thus, the proposed approach could increase the availability of empirical data relating food chain length to environmental variables. Future work might be oriented to exploring the sensibility of the patterns reported with regard to the method used, be that isotopic signatures (e.g., Vander Zanden et al. 1999), whole food web description (e.g., Briand and Cohen 1987), or nonherbivorous incidence, among others.

Nevertheless, as with any other approach, ours has limitations. Probably the most important one is that of considering all prey items as contributing equally to the dietary requirements of a given predator. This may not be a problem if the interest is in food web topology, but it may lead to biased results from the point of view of energetics. The congruence observed between the patterns for vertebrate and invertebrate prey (figs. 3, A1, A2) in relation to all prey combined (figs. 1, 2) is noteworthy. The results were consistent at both the predator species and the ensemble levels of analysis, indicating that no considerable effect

was introduced by jointly analyzing prey of such different sizes as vertebrates and invertebrates and that a common mechanism determining food chain length could be operating between both types of prey.

Theory aims at making predictions consistent with natural patterns, thus improving our understanding of the possible mechanisms involved. This article is about patterns, discussing whether results are congruent with theoretical predictions, and reporting the existence of patterns that are not predicted by current theory. The wide range of associations between species trophic positions and available energy represents a new challenge to ecologists. It is necessary to explore the attributes of other species, communities, and environments that produce the patterns described here and in particular, the connections between productivity and other determinants of food web structure. Indeed, it is still poorly understood which mechanisms connect patterns in food web structure observed at the species and higher levels. Our article is a first step in this direction.

Acknowledgments

This article was improved by comments made by R. L. Kitching and one anonymous reviewer. M.A. thanks S. Abades, A. Farias, F. Labra, P. Neill, and M. Rivadeneira for discussion. M.A. also acknowledges a fellowship from Dirección de Investigación de la Pontificia Universidad Católica and support from Proyecto Clemente Estable 05-076. This study was funded by Fondo de Areas Prioritarias-Fondo Nacional de Investigación Científica y Tecnológica grant 1501-0001 to Centro de Estudios Avanzados en Ecología y Biodiversidad Programs 2 and 4, to F.M.J. and P.A.M., respectively. P.A.M. also acknowledges support from project Iniciativa Científica Milenio ICM P05-002.

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