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Trophic exploitation in grassland food chains: simple models and a field experiment

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Abstract. This study provides insight into the importance of top carnivores (top-down control) and nutrient inputs (bottom-up control) in structuring food chains in a terrestrial grassland system. Qualitative predictions about food chain structure are generated using 4 simple models, each differing in assumptions about some key component in the population dynamics of the herbivore trophic level. The four model systems can be classified broadly into two groups (1) those that assume plant resource intake by herbivores is limited by search rate and handling time as described by classic Lotka-Volterra models; and (2) those that assume plant resource intake by herbivores is limited externally by the supply rate of resources as described by alternatives to Lotka-Volterra formulations. The first class of models tends to ascribe greater importance to top-down control of food chain structure whereas the second class places greater weight on bottom-up control. I evaluated the model predictions using experimentally assembled grassland food chains in which I manipulated nutrient inputs and carnivore (wolf spider) abundance to determine the degree of top-down and bottom-up control of grassland plants and herbivores (grasshoppers). The experimental results were most consistent with predictions of the second class of models implying a predominance of bottom-up control of food chain structure.

Key words: Food chain structure – Bottom-up control – Top-down control – Population dynamics – Grasshoppers

Studies of trophic exploitation seek to understand the processes that limit the abundance and dynamics of species within interacting trophic levels of food chains (McQueen et al. 1986; Leibold 1989; L. Oksanen 1990). A central issue is whether the abundances and dynamics of species in component trophic levels (food chain structure) are limited by consumers in the top trophic level (top-down control) or by nutrient inputs to the lowest trophic level (bottom-up control) (McQueen et al. 1986). These ideas have been expressed in two principal hypotheses which attempt to explain the structure of food chains composed of three interacting trophic levels: plants, herbivores and carnivores.

Hairston et al. (1960, hereafter called HSS) proposed that in terrestrial systems plant and carnivore populations are limited by their respective food resources and are therefore regulated by competition. Herbivores, being limited by their predators, seldom reach sufficient densities to be food limited and, therefore, are not likely to compete for plant resources. This hypothesis derives from the simple premise that the world would not be green if herbivores limited the abundance of plants (Hairston et al. 1960). In this case, the abundance and dynamics of populations or species in all, lower trophic levels are thought to be limited directly or indirectly from above by carnivores. A similar idea (the "cascading trophic effects" hypothesis) is championed by Carpenter et al. (1985) for aquatic systems.

The alternative hypothesis argues that populations or species in all trophic levels are limited by the abundance of food and by competition for food resources (Sinclair 1975; White 1978; Belovsky 1986). The reason the world is green is that all plants are not edible because they are either nutritionally unacceptable or protected by plant antiherbivore defenses (Murdoch 1966; Sinclair 1975; Price et al. 1980; Belovsky 1986; Weis and Berenbaum 1989). In this case, food chain structure is limited from below by the supply of nutrients.

More recently, Fretwell (1977) and Oksanen et al. (1981) blended the previous two concepts to develop the "Exploitation hypothesis" (Oksanen 1983; Jager and Gardner 1988; T. Oksanen 1990). They pointed out that resources and predators limit species within a trophic level simultaneously, but the importance of one or the other limiting factor varies with nutrient supply (environmental productivity). This was an important step because

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it not only provided a mathematical basis for the HSS and bottom-up hypotheses but it also showed how population biological models could be used to make explicit predictions about interactions at the level of entire food chains.

The Exploitation hypothesis is based on a specific set of assumptions about the dynamics of populations within and between trophic levels. More recent studies (e.g., McCauley et al. 1988; Schmitz 1992) have shown that different, but equally plausible, sets of assumptions may give rise to alternative sets of predictions about trophic exploitation. Unfortunately, there are too few explicit examinations of dynamics in natural food chains to judge the general predictive success of any of the theories. Here I generate sets of predictions about trophic exploitation using simple models that incorporate different assumptions about the dynamics of populations. The model predictions are compared with the results of an experimental study on trophic dynamics in a grassland food chain composed of plants, herbivores (grasshoppers) and carnivores (wolf spiders). The study gives some insight into the type of trophic interactions we might observe in natural grassland environments and the importance of top down (predator limitation) and bottom up (nutrient limitation) control of food chain structure in such grasslands.

The food chain models

The approach adopted here follows that of McCauley et al. (1988) in that I try to find the simplest mathematical representation to describe the key features of the interaction between plants and herbivores and how this interaction might be affected by changes in the supply rate of nutrients and carnivore numbers. Predictions about trophic exploitation in the study system are generated using sets of coupled differential equations which describe the population dynamics of plants (V) and herbivores (H). Nutrients and carnivores will not be treated as explicit trophic levels in the models because in the field experiment I controlled nutrient inputs and spider abundances. Nutrient levels and carnivore abundances can then be considered as components of the "environment" of the plant-herbivore interaction (McCauley et al. 1988) and, as such, are treated as fixed constants in the equations for plant and herbivore dynamics.

I will consider four model systems, each differing in basic assumptions about the population processes in the herbivore trophic level. I only focus on the herbivore trophic level because if we compare theories of food chain dynamics (Oksanen et al. 1981; Schmitz 1992) we find that qualitative predictions about trophic interactions hinge on the dynamics of herbivores. The qualitative predictions are unaffected by assumptions about plant population dynamics (i.e. Logistic growth [Oksanen et al. 1981], Monod growth [Schmitz 1992]), at least when all plant species are treated as a single functional group. The four model systems can be grouped into two broad classes: (1) those that assume plant resource intake by herbivores is limited by search rate and handling time as described by classic Lotka-Volterra models (e.g., Oksanen et al. 1981; T. Oksanen 1990); and (2) those that assume plant resource intake by herbivores is limited externally by the supply rate of resources as described by alternatives to Lotka-Volterra formulations (e.g. Schoener 1973, 1978; Schmitz 1992). Although both classes of model assume that top-down and bottom-up controlling factors operate simultaneously, the first class of models (Models I and II) tends to ascribe greater importance to top-down control of food chain structure (Schmitz 1992) whereas the second class (Models III and IV) places greater weight on bottom-up control (Schmitz 1992).

Model I

The first model describes the dynamics of the classical Exploitation hypothesis which is discussed in detail by Fretwell (1977) and Oksanen et al. (1981). This model assumes that: (1) plants exhibit logistic population growth; (2) herbivore population growth is density independent; (3) per capita consumption rate of plants by herbivores is limited by food search rate and handling time, as implied by a Type II functional response, and that competition for those resources is implicitly via exploitation; and (4) per capita consumption rate of herbivores by carnivores also follows a Type II functional response. This last assumption seems to be supported empirically for wolf spiders (Hardman and Turnbull 1974; Nakamura 1974, 1977). These assumptions give rise to the following set of equations:

$$dV/dt = rV\,[1-(V/K)] - \alpha VH/(1+\beta V) \qquad (I.1)$$

$$dH/dt = \varepsilon\alpha VH/(1+\beta V) - cH - \alpha' HP/(1+\beta' H) \qquad (I.2)$$

where r and K are respectively the intrinsic rate of increase and carrying capacity of the plant population, ε is the energy content per unit plant biomass, c is a natural loss rate due to metabolic costs, senescence, etc and P is carnivore density. These equations incorporate Abrams' (1987) form of the Type II functional response ($\alpha VH/[1+\beta V]$) where α or α' is the search rate for resources and β or β' is the product of search rate and handling time. The plant-herbivore interaction described by these equations is called Laissez-faire (Caughley and Lawton 1981) because herbivores do not interfere with each other's search for food, i.e. there is no negative feedback due to density dependence.

The equilibrium solution to these equations are obtained by setting $d/dt = 0$ and solving for the plant and herbivore isoclines. In the absence of herbivory (i.e., a single trophic level chain) $H = 0$ and the equilibrium plant biomass simply will be $V' = K$. In a two trophic level chain, $H > 0$, $P = 0$ and the plant and herbivore population isoclines are respectively

$$H'_V = (r/\alpha)\,[1-(V/K)]\,[1+\beta V] \qquad (I.1')$$

$$V'_H = c/(\varepsilon\alpha - c\beta) \qquad (I.2')$$

These isoclines are plotted in a phase plane in Fig. 1A. In the absence of a herbivore trophic level, the

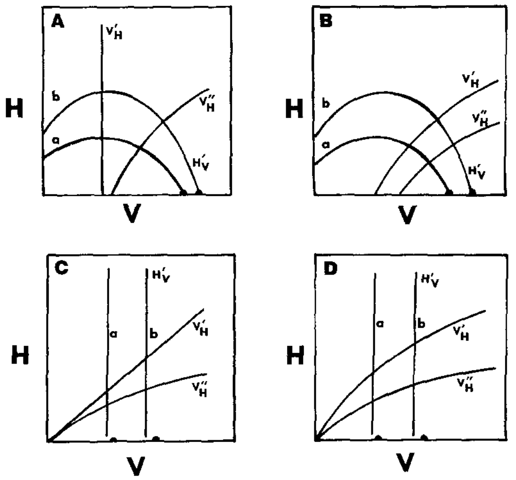

Fig. 1A–D. Graphical analysis of the zero population growth isoclines for 4 different food chain models. The plant isocline is denoted by H'_V, the herbivore isoclines in the absence of carnivores is V'_H and when carnivores are present it becomes V''_H. The effect of increasing nutrient supply rate on the plant isocline is indicated by the change from plant isocline a to isocline b. The dots on the V-axis represent equilibrium plant biomass in the absence of herbivores at the respective nutrient supply rates. **A** and **B** correspond to Models I and II which assume a dominance of top-down control. **C** and **D** correspond to Models III and IV which assume a dominance of bottom-up control

equilibrium plant biomass is represented as a point on the plant axis. The addition of a herbivore trophic level produces the classical hump-shaped plant isocline (Fig. 1A). If we assume that nutrient supply rate determines environmental productivity (Tilman 1988) and that r and K are linear functions of environmental productivity (Oksanen et al. 1981), then the effect of increasing the supply rate of nutrients to a system can be described by a second hump-shaped isocline that extends above and beyond the original one (Fig. 1A). The hypothetical example in Fig. 1A presents plant isoclines for a nutrient poor and a nutrient enriched environment. The herbivore isocline in a 2 trophic level chain will be linear, rising vertically from the plant axis (Fig. 1A).

To faithfully model the dynamics in the experimental study system involving three trophic levels (i.e., plants, grasshoppers and spiders), I assume P will be a fixed constant greater than 0. In this case, the plant isocline (Eq I.1′) remains unchanged but the herbivore isocline becomes

$$V''_H = \frac{H\beta'c + c + \alpha'P}{H\beta'[\varepsilon\alpha - c\beta] + \varepsilon\alpha - c\beta - \alpha'\beta P} \qquad (I.2'')$$

The addition of the carnivore trophic level will cause the herbivore isocline to become nonlinear, extending away from the origin (Fig. 1A).

Model II

In Model II, I change assumption (2) of Model I by incorporating a negative feedback term to account for direct density dependent herbivore population growth. Many herbivore populations are either known to or suspected to exhibit density dependent population growth (Sinclair 1989). Recent experiments have also demonstrated that some grasshopper populations exhibit density dependent dynamics (Ritchie and Tilman 1992; Belovsky and Slade).

Subtracting the term δH^2 to account for the loss rate due to herbivore density gives the following plant-herbivore system (Rosenzweig 1973; T. Oksanen 1990):

$$dV/dt = rV[1-(V/K)] - \alpha VH/(1+\beta V) \qquad (II.1)$$

$$dH/dt = \varepsilon\alpha VH/(1+\beta V) - cH - \delta H^2 - \alpha'HP/(1+\beta'H) \qquad (II.2)$$

Note, Eq II.1 is identical to Eq I.1 so the plant isoclines in nutrient poor and nutrient enriched environments will not differ from those in Model I (Fig. 1B).

In a 2 trophic level food chain (i.e., P = 0), the herbivore isocline is given by

$$V'_H = (c+\delta H)/(\varepsilon\alpha - c\beta - \delta H) \qquad (II.2')$$

Unlike its counterpart in Model I (Eq I.2′), this isocline will be nonlinear extending away from the origin (Fig. 1B). The addition of a constant number of carnivores to the system (i.e., P is a fixed constant greater than 0) produces the following herbivore isocline:

$$V''_H = \frac{H(\beta'c + \beta'\delta H + \delta) + c + \alpha'P}{H[\beta'(\varepsilon\alpha - c\beta - \beta\delta H) - \beta\delta] + \varepsilon\alpha - c\beta - \alpha'\beta P} \qquad (II.2'')$$

This isocline is again nonlinear but herbivore density increases at a lower rate with plant biomass than in a 2 trophic level chain (Fig. 1B).

Model III

In Model III, I change assumption (3) of Model I by specifying a different function to describe the rate of resource intake by consumers. Models I and II describe growth of herbivore populations whose resource (energy) intake is determined by the ability of population members to feed. That ability is assumed to be limited by the time associated with searching for and ingesting resources, as described by a Type II functional response. Schoener (1973) suggested that an alternative might be a system in which the total resource input to a population is limited externally and the members of the population are not restricted in their ability to harvest that fixed input. In this case, it is assumed that resources are supplied to the consumer population at a fixed rate and consumers compete exploitatively for their share of resources (Schoener 1973). The population level and trophic level dynamics associated with this assumption have also been explored in detail by Lomnicki (1988) and Schmitz (1992).

In Model III, the per capita consumption rate of resources by consumers is given by the term pV/H where p is the proportion of total plant biomass that is useable by the herbivore population per unit time (Schmitz 1992). The total consumption rate by the herbivore population will be pV (= [pV/H]H) (Schmitz 1992). This is similar in form to Arditi and Ginzburg's (1989) ratio dependent function, although they invoke a different biological mechanism to obtain this functional form. The assumption of a fixed energy supply rate seems to be supported by recent studies on the dynamics of some grasshopper populations (G.E. Belovsky and J.B. Slade unpublished work). This assumption gives rise to the following set of Eqs:

$$dV/dt = rV[1-(V/K)]-pV \qquad \text{(III.1)}$$

$$dH/dt = \varepsilon pV - cH - \alpha' HP/(1+\beta' H) \qquad \text{(III.2)}$$

Equation III.2 is only appropriate when herbivore densities are comparatively high or at equilibrium because of its inherent unrealistic behavior at low H (i.e. $dH/dt > 0$ when $H = 0$). Schoener (1978) provided a modification to increase the equation's realism at low population density. However, numerical analyses using data for the study system indicate that the qualitative dynamics of the two equations quickly converge at moderate population density (e.g., $H = 3$–5 grasshoppers m^{-2}). Moreover, I only examine model solutions at equilibrium so I assumed that Eq III.2 was a reasonable first approximation.

The plant isocline is determined by setting $dV/dt = 0$. This gives a disjoint function (Schmitz 1992):

$$V' = K \qquad \text{if } H = 0$$

$$\text{and} \qquad \text{(III.1')}$$

$$V' = K[1-(P/r)] \qquad \text{if } H > 0$$

Maximum plant biomass in the absence of herbivores ($V' = K$) is represented as a point on the plant axis. In food chains with two or more trophic levels, the plant isocline will be linear and independent of herbivore density (Fig. 1C). Plant isoclines for nutrient encriched systems will be further from the origin than isoclines for nutrient poor systems (Fig. 1C).

The herbivore isocline in a 2 trophic level chain becomes

$$V'_H = cH/\varepsilon p \qquad \text{(III.2')}$$

The herbivore isocline will start at the origin and rise linearly with increasing plant biomass (Fig. 1C). The addition of carnivores to the system gives the following equation

$$V''_H = (H/\varepsilon p)[c + \alpha' P/(1+\beta H)] \qquad \text{(III.2'')}$$

which describes a nonlinear herbivore isocline (Fig. 1C). Herbivore density will increase less rapidly with plant biomass in a 3 trophic level chain than in a 2 trophic level chains.

Model IV

Model IV differs from Model III by incorporating a term to describe the loss rate due to direct density dependent interactions within the herbivore population (δH^2). It is a simple exercise to show that the isoclines in Model IV differ qualitatively from Model III in only 1 respect: the herbivore isocline for a 2 trophic level food chain will be nonlinear rather than linear (Fig. 1D).

Model predictions

The intersections of the plant and herbivore isoclines determine the equilibrium plant biomass and herbivore densities. These equilibria can be used to make qualitative predictions about expected trends in plant biomass and herbivore density in food chains in both nutrient poor and nutrient enriched environments. The models make the following predictions for plant biomass in 1-, 2- and 3-trophic level food chains.

Model I

1) In single trophic level food chains, equilibrium plant biomass should increase with nutrient addition (Fig. 2A).
2) Equilibrium plant biomass in 2-trophic level food chains should be lower than in single level chains. Equilibrium biomass in 2-level chains should not change with nutrient enrichment (Fig. 2A).
2) Equilibrium plant biomass in 3-trophic level chains should be lower than in single trophic level chains. Equilibrium plant biomass in 3-level chains should be higher in nutrient enriched environments than in nutrient poor environments (Fig. 2A).
3) Equilibrium plant biomass in both nutrient poor and enriched environments should be greatest in single trophic

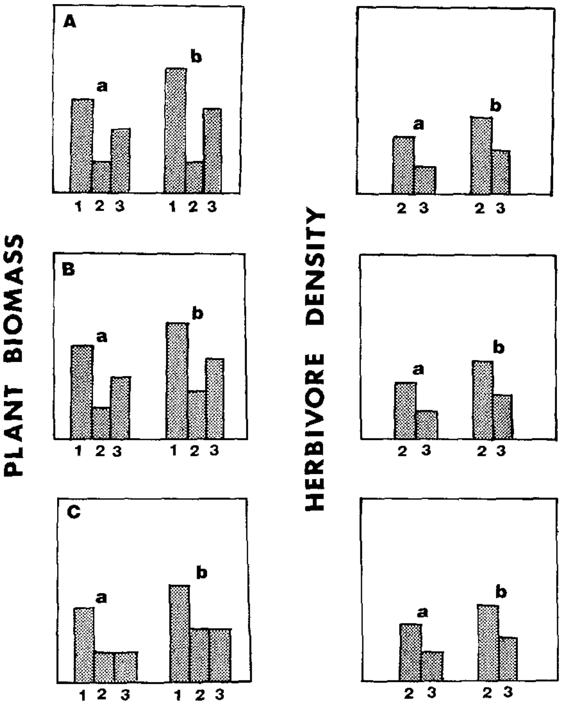

Fig. 2A–C. Qualitative predictions, generated from the intersections of the plant and herbivore isoclines in Fig. 1 for plant biomass and herbivore density in 1-trophic level (1), 2-trophic level (2) and 3-trophic level (3) food chains. **A** gives predictions of Model I, **B** gives predictions of Model II and 2C gives predictions of Models III and IV. With respect to the plant trophic level, Models I and II (**A** and **B**) produce the classic cascading trophic effect. Models III and IV (**C**) do not produce this effect. Carnivores should control herbivores in all systems level chains, intermediate in 3 trophic level chains and lowest in 2 trophic level chains, i.e., we should see a trophic cascade (Fig. 2A).

Model II

1) Same as Model I (Fig. 2B).
2) Equilibrium plant biomass in 2-trophic level food chains, should be lower than in single level chains. Equilibrium plant biomass in 2-level chains should be higher in nutrient enriched than in nutrient poor environments. (Fig. 2B).
3) Same as Model I (Fig. 2B).
4) Same as Model I (Fig. 2B).

Model III and IV

1) Same as Model I (Fig. 2C)
2) Same as Model II (Fig. 2C)
3) Same as model I (Fig. 2C).
4) In both nutrient poor and enriched environments, equilibrium plant biomass should be greater in single trophic level chains than in 2 and 3 trophic level chains. Equilibrium plant biomass in 2 and 3 level chains should be identical, i.e., a trophic cascade is not expected.

Finally, herbivore density, in all food chains, should increase with nutrient enrichment. Carnivores should reduce herbivore abundance in both nutrient poor and enriched environments (Fig. 2).

Methods

I evaluated the model predictions empirically by examining the effect of manipulating nutrient inputs and carnivores on plant and herbivore abundance using a field experiment. The study was conducted in a Palouse prairie in western Montana. Dominant grasses and forbs at the site were *Poa pratensis, Achillea millefolium, Taraxacum* sp. and *Penstemon* sp. Experiments involved nymphs of a single Melanopline grasshopper species *(Melanoplus sanguinipes)* and adults of a single species of Lycosid (wolf) spider *(Tarentula kochi)*. A more detailed description of the study area is presented by Belovsky et al. (1990). Because grasshopper population dynamics are stage dependent (G.E. Belovsky and J.B. Slade unpublished work), the experiment was only conducted within one temporal "window" representing the entire juvenile phase of the grasshopper life-cycle. This was appropriate for the present purposes because I was primarily interested in disvovering which mechanisms of population interaction best described the food chain dynamics in a simple field system that would likely satisfy underlying model assumptions. My intent was not to give a detailed account of the dynamics between all grasshopper life-cycle stages, their plant resources and their predators.

Assembling experimental food chains

The experiment was conducted using enclosure cages constructed with aluminum screening and fastened at the base to aluminum garden edging. Cages were secured by sinking the garden edging beneath the soil surface and by fastening the sides of the cages to wooden stakes. Cages had a basal area of 0.1 m^2 and height of 1 m. Cages were placed randomly in the environment with the proviso that the entire cage bottom be filled with vegetation. This was done to ensure that all the grasshoppers would not starve immediately so that the degree of density dependent mortality could be measured. A complete description of the protocol for establishing and maintaining caged populations is presented by (Belovsky and Slade unpublished work). The biophysical and biotic conditions within the cages are similar to natural environments (Belovsky and Slade unpublished work).

Nutrients were supplied at 2 levels: (1) no water (control) and (2) 350 ml of water + 0.025% nitrogen, by volume, from fish fertilizer (Chevron IN, USA) every 2 days. Treatments were randomly assigned to cages. The water-nitrogen solution was applied by slowly flood irrigating the cage bottom using a water bottle. Each treatment was applied to 24 cages (total of 48 cages). Nutrient application began 4 days before the cages were stocked with the experimental food chains.

I assembled three kinds of food chains in the experimental cages: (1) plants only; (2) plants and grasshoppers; and (3) plants, grasshoppers and spiders. All animals were caught in the field and were transferred to the cages as quickly as possible (always within 24 h after capture). If animals were not immediately stocked they were housed under shade in terraria with ample food supplies. Belovsky and Slade (unpublished work) have shown that this protocol minimizes losses of individuals due to handling stress. I stocked either 15 early instar grasshopper nymphs or 15 early instar grasshoppers and 1 adult spider to the cages. These levels are slightly above field densities measured at the time of stocking (9 grasshoppers/0.1 m^2 and 0.75 hunting spiders/0.1 m^2 of vegetated surface respectively, O.J. Schmitz unpublished data). I intentionally stocked the cages at these levels to produce a pulse perturbation. Estimates of natural field densities matched those from studies on the same species in similar environments (Hagstrum, 1970; Belovsky and Slade unpublished work). Eight cages of each food chain were randomly assigned to each nutrient treatment.

Testing model assumptions

The food chain model is based on 3 important assumptions. (1) All populations will return to a steady state following a small pulse perturbation. (2) The proportion of plant biomass (p) that can be used by herbivores remains constant at different productivity levels. This assumption is a feature of the model in its current form. But, p could be made a function of nutrient supply rate if it was shown to vary with nutrient supply rate. However, model predictions would have to be modified accordingly. (3) The spider *T. kochi* is capable of killing and eating *M. sanguiripes* nymphs.

To test the first assumption, I measured changes in plant biomass and herbivore densities over time. To examine changes in plant biomass in the absence of herbivory, I applied the 2 nutrient treatments to an additional 24, 0.1 m^2 plots which excluded herbivores. All green plant biomass was clipped from 8 plots (4 per nutrient treatment) every 8 days. Plant samples were dried at 60° C for 48 h and weighed to estimate available dry biomass. I counted grasshoppers in all the stocked-cages every two days. Plant biomass (Fig. 3) and grasshopper density in absence and presence of spiders (Fig. 4) declined toward a steady state, at both treatment levels during the lifetime of the juvenile stage of the grasshopper population.

To test the second assumption, I analyzed all dried plant samples used to test the first assumption for solubility in acid/pepsin (Terry and Tilley 1964). The solubility estimate is an index of the fraction of available plant biomass that is nutritionally suitable for consumption by grasshoppers (Belovsky 1986; Belovsky Slade unpublished work). In each sampling period, digestibility values (Table 1) were not significantly different between treatments (all *t*-tests, $P > 0.05$).

To test the third assumption I estimated the maximum size of grasshopper nymph the spiders willingly killed and consumed. I captured 6 adult *T. kochi,* measured their body mass and placed them in plastic terraria. I presented each spider with a single *M. sanguinipes* nymph every 24 h (grasshoppers were usually captured by spiders within 10 h after presentation). Each grasshopper nymph was freshly caught from the field before being presented to the

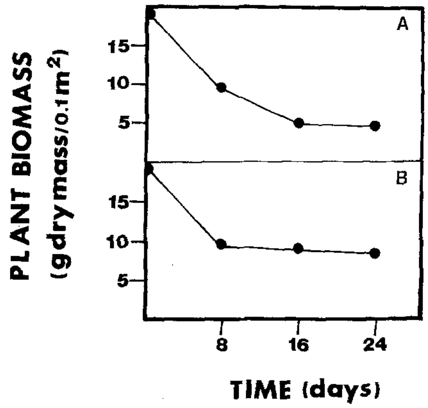

Fig. 3A, B. Changes in mean dried green plant biomass clipped at 8 day intervals during the course of the study. Mean values are estimated from $n=4$ plots in each sampling period in control (**A**) and nutrient enriched (**B**) plots

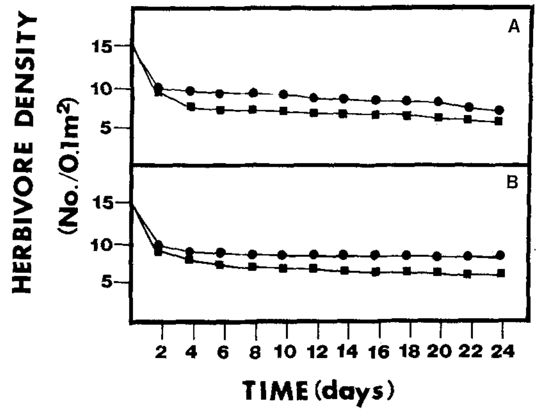

Fig. 4A, B. Changes in mean grasshopper abundance over the course of the study in control (**A**) and nutrient enriched (**B**) cages. Circles represent cages containing grasshoppers only and squares represent cages containing grasshoppers and spiders. In each case, mean values are based on $n=8$ cages

Table 1. Mean and standard error in percent solubility of plant biomass in acid and pepsin as a function of nutrient supply rate to plants

Sample[a]	*n*	Nutrient treatment	
		Control	H_2O+N
1	4	37.5±4.6	39.1±4.3
2	4	40.4±1.9	41.8±2.2
3	4	40.4±1.6	41.5±1.5

[a] Samples were taken from 0.1 m^2 plots at 8-day intervals

spiders. In most cases, the predation event was observed; if not, I examined dead grasshoppers under a microscope for puncture marks to confirm that the mortality was due to spider predation. Spiders were presented with progressively larger-sized nymphs, in each feeding trial. If the grasshopper was not killed within 72 hrs after capture, I assumed that the spider could no longer subdue the prey item. The relationship between spider body mass and maximum prey mass subdued is presented in Fig. 5. In the laboratory trials, the spiders readily killed and consumed grasshopper nymphs equal to or smaller than their own body mass (Fig. 5).

Testing model predictions

The experiment was terminated after 24 days. During this time period *M. sanguinipes* nymphs passed from the early (2nd) instar stage to the late (5th) instar stage. Plants and grasshoppers maintained a steady state biomass or density for 10–20 days during this time (Figs. 3 and 4). The experiment was terminated because the grasshopper nymphs were molting into adults which would have resulted in a population decline to a new steady state (Belovsky and Slade unpublished work). Moreover, spiders are not a significant source of adult *M. sanguinipes* mortality (Belovsky et al. 1990) so the carnivore trophic level would no longer have an affect on trophic dynamics if the experiment was continued.

All grasshoppers and spiders were censused on the termination date. However, I only terminated 24 cages to estimate available plant biomass. (The other 24 cages were continued as part of another experiment.) I randomly selected the cages that were terminated in each food chain-treatment level combination. Cages were removed from the plot sites and all remaining green plant biomass was clipped, dried at 60° C for 48 h and weighed.

Results

The means and standard errors in steady state plant biomass and grasshopper numbers for the different experimental food chains at the two treatment levels are presented in Fig. 6. In the overall experiment, the effects of nutrient level and food chain length on food chain structure were significant (ANOVA, $P<0.05$).

Evaluating model predictions

1) Plant biomass in cages with single trophic level chains (Fig. 6) was significantly higher in nutrient enriched than in nutrient poor environments (*t*-test, $P<0.05$) (Consistent with all models)

2) Plant biomass in 2 level food chains (Fig. 6) was significantly lower than in single level chains (*t*-test, $P<0.05$). Plant biomass in 2-level chains increased significantly (*t*-test, $P<0.05$) with nutrient enrichment (Consistent with Model II, III and IV).

3) Plant biomass in 3 level food chains (Fig. 6) was significantly lower than in single level chains (*t*-test, $P<0.05$). Plant biomass in 3-level chains was significantly higher (*t*-test, $P<0.05$) in nutrient enriched than nutrient poor environments (Consistent with all models).

4) ANOVA followed by a Tukey test revealed that plant biomass was greater in single level food chains than in 2 and 3 level chains (Fig. 6). Plant biomass was not different in 2 and 3 level chains in both nutrient poor and enriched environments ($P>0.05$), i.e. no trophic cascade (Consistent with Model III and IV).

Finally, herbivore density in 2- and 3-level chains increased with nutrient supply (Fig. 6), consistent with predictions of all models. Spiders significantly lowered grasshopper densities in nutrient enriched cages (*t*-test, $P<0.05$) but had no significant effect on grasshopper numbers in the nutrient poor treatment. This occurred even though spiders were observed to capture and subdue grasshoppers in these cages.

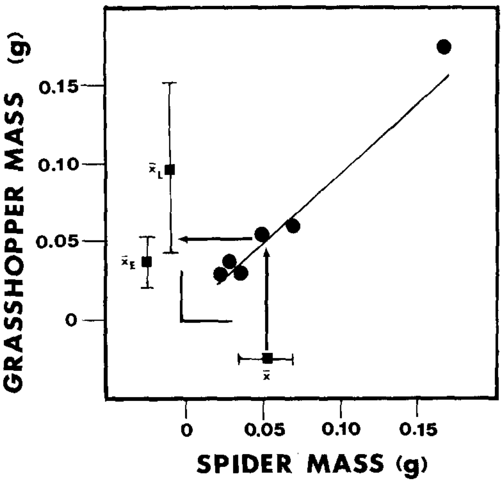

Fig. 5. Relationship between spider body mass and maximum grasshopper mass captured in laboratory feeding trials. The relationship is linear ($Y = 0.0057 + 0.84$, $R^2 = 0.81$, $n = 6$, $P < 0.05$). Eliminating the largest value still produces a significant relationship ($R^2 = 0.77$, $P < 0.05$). The squares and error bars represent means and 2 SE's associated with spiders ($\bar{x}$), early instar nymphs ($\bar{x}_E$) and late instar nymphs ($\bar{x}_L$) used in the field experiments. The *arrows* indicate that an average spider in the experiment was capable of consuming all available early instar nymphs and a small fraction of late instar nymphs

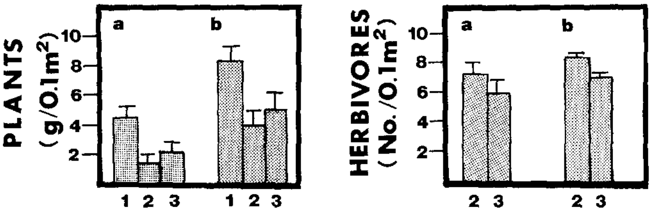

Fig. 6. Plant biomass in 1, 2 and 3 trophic level food chains and herbivore density in 2 and 3 level food chains in control (*a*) and nutrient enriched (*b*) cages. Values are means and standard errors ($n = 4$ and 8 cages per food chain and nutrient level for plants and herbivores respectively)

In the plant trophic level, nutrients and grasshoppers together explained 68% of the variation in plant biomass. Nutrient addition alone accounted for 35% of the variation and grasshoppers accounted for 33% of the variation and both effects were significant ($P < 0.05$). In the herbivore trophic level, the combined effects of nutrients and spiders explained 64% of the variation in grasshopper density. Spiders and nutrients alone each accounted for 32% of the variation. The effects of nutrients and spiders were both significant ($P < 0.05$).

Discussion

This study gives some insight into the importance of top-down and bottom-up control of food chain structure. Qualitative predictions about food chain structure are generated using 4 simple models, each differing in assumptions about some key component in the dynamics of the herbivore population. The models can be divided into 2 main classes depending upon assumptions about plant resource exploitation by herbivores. The first class (Models I and II) assumes plant resource intake by herbivores is limited by feeding time, typical of many Lotka-Volterra food chain models (Oksanen et al. 1981; McCauley et al. 1988). In such models, we expect to see cascading trophic effects (*sensu* Carpenter et al. 1985) and hence a predominance of top-down control by carnivores. The second class (Models III and IV) assumes that harvesting rate by herbivores is limited by the supply rate of plant resources and that herbivores are not restricted in their ability to consume this fixed supply (Schmitz 1992). This class of model does not give rise to cascading trophic effects implying that bottom-up control is most dominant. The model predictions are compared with the dynamics of an experimental food chain composed of grassland plants, grasshopper nymphs and wolf spiders. Neither class of model is intended to be a precise description of the trophic dynamics in the natural food chain. Rather, the intention is to obtain some qualitative insight into the type of control that is most likely operating.

Although certain predictions of all models were supported by the field experiment, only predictions of the class of models which assume that resource consumption rate by herbivores is energy-limited rather than time-limited (i.e., Models III and IV) were supported in all cases. In this class of system, we expect that at a given rate of nutrient supply, the equilibrium plant biomass in 2-trophic level food chains should be lower than in single trophic level chains because of the limiting effect of herbivores. Adding carnivores to the food chain should not reduce the degree herbivores limit plant populations even though herbivores should be limited by carnivores (Fig. 2), i.e. there is no trophic cascade. Despite this evidence for bottom-up control in the experimental food chain, the data in Fig. 6 show a weak trophic cascade even though the trend is not significant statistically. This could be interpreted as limited support for the top-down view (HSS and the Exploitation hypothesis) but that low sample size precluded detecting any statistical difference in biomass between 2- and 3-level chains. To ascertain the likelihood of this, I conducted a power analysis. This revealed that the probability of failing to detect a trophic cascade when there really is one (i.e. a Type II error) was 0.9% in the nutrient poor treatment and 7.0% in the nutrient enriched treatment. It appears that statistical support for Models III and IV is robust despite the small sample sizes for each treatment. Thus, neither HSS nor the Exploitation hypothesis are likely to describe food chain structure in the study system.

This is not to say that HSS and the Exploitation hypothesis will not adequately explain food chain structure in all grasshopper-plant systems. In another food chain experiment Kajak et al. (1968) examined the effects of web spiders on grasshopper-plant dynamics using a perturbation experiment. In the experiment, plant abundance in the 3-trophic level chains was twice as high as in the 2-trophic level chains (Kajak et al. 1968). In this system, spiders had a dramatic impact on the ability of grasshoppers to limit plant populations as predicted by HSS and the Exploitation hypothesis. These results should be interpreted cautiously, however, as both grasshopper and spider densities were unnaturally high in the experiment (Kajak et al. 1968). Hence, grasshopper abundances tended toward outbreak proportions which may violate a fundamental assumption of HSS (Hairston et al. 1960).

Congruence of the field data with the bottom-up view implies that when considering all trophic levels in the food chain, carnivores (spiders) will not have an important effect on the plant trophic level but nutrient inputs to the plant trophic level determine the degree spiders impact grasshopper populations. This is consistent with the overall pattern in the study system. When considering the dynamics between adjacent trophic levels (i.e. plant-herbivore or herbivore-carnivore), however, a different picture emerges. At these levels of resolution, the effects of nutrient supply rate and consumers (herbivores or carnivores) accounted for an equal share of the variation resource (plants or herbivores) biomass and density. The assembled plant and herbivore trophic levels individually appear to be structured equally by "bottom-up" and "top-down" controlling factors.

The results of this study apply specifically to the juvenile-stage of *M. sanguinipes*. This represents a temporal "window" in the entire grasshopper life-cycle. In this stage, both grasshopper and plant populations tend to be in a steady state for about 90% of the time so the system satisfied an important assumption of all food the chain models described in this study. It is not yet clear how top-down and bottom-up control influences food chain structure beyond the juvenile stage. This would involve an entirely different set of experiments because adult grasshopper populations reach a different steady state with their plant resources than do juveniles (Belovsky and Slade unpublished work). Moreover, adult grasshoppers are susceptible to an entirely different suite of predators than are juvenile grasshoppers (Belovsky et al. 1990).

More generally, there is mixed support for the top-down view (HSS) among a wide range of ecosystems (Schoener 1983; Lawton 1989). Lawton (1989) suggested that bottom-up control appears to be most likely for many food chains that involve plants and herbivorous insects. This study provides further support for this view. In contrast, Schoener (1983, 1989) showed that most of the support HSS was in terrestrial systems, the exception being systems with large herbivores. Some larger herbivore populations appear to exhibit Model III or IV type dynamics also (Belovsky 1986) which might explain why HSS does not predict the dynamics in the large herbivore systems.

This study shows that terrestrial food chains may not be simply structured predominantly from above by consumers in the top trophic level, as predicted by HSS and the Exploitation hypothesis, or from below by nutrient inputs as predicted by HSS's major alternative (White 1978). These hypotheses are probably better viewed as points along a continuum (Lawton 1989; Schmitz 1992). Instead, it is probably more important to examine how different kinds of dynamics within and between trophic levels determine the degree to which top-down and bottom-up control should affect overall food chain structure. Only then can we begin to fully appreciate how top carnivores and nutrient inputs control the abundance and dynamics of populations among intermediate trophic levels.

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