FOOD WEBS FROM THE SMALL TO THE LARGE

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by

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INTRODUCTION

In 1960, Hairston, Smith, and Slobodkin published their revolutionary paper in which a relatively reductionist approach, interaction ecology, was joined to a relatively holistic one, trophic-web ecology. The paper had a stormy reception, both before publication (rejected from ECOLOGY, F. Smith, *personal communication*) and after (Murdoch 1966, Ehrlich and Birch 1967). The latter, carefully reasoned critiques, provoked a long clarification (Slobodkin et al. 1967). A brief version of Hairston et al. (1960; hereafter referred to as HSS) is that the importance of competition vs. predation alternates in a terrestrial food web, such that carnivores (which have no predators) compete, herbivores (held down by carnivores) are controlled main-

ly by their predators, and producers (whose predators are held down by carnivores) again compete. Herbivores are taken to mean folivores, not frugivores, granivores, or nectarivores.

Despite an early piece on food webs (MacArthur 1955), MacArthur's major efforts were devoted to development of competition and niche theory, and HSS was temporarily forgotten during his heyday. It was revived in two independent places: an obscurely published, potentially very important paper by Fretwell (1977), and an increasingly influential paper by Menge and Sutherland (1976; hereafter referred to as MS), which provided HSS with its major challenge. The latter (MS) argued that in marine systems, the lower a population in its food web, the more likely it is to be controlled by predation as opposed to competition. MS hinges on the existence of a significant effect of omnivory, in particular that, in contrast to HSS, predators eat prey at levels lower than just the adjacent one (see also Menge et al. 1986, Menge and Sutherland 1987).

[1] Unfortunately, Dr. Schoener was unable to present the lecture in person because of illness.

[2] Photograph by Ethan Temeles.

In MS, that level most controlled by competition, the top one, varies in its species composition as a function of the degree of physical disturbance; barnacles and mussels, for example, may be at the top in an environment with much wave action but not in a less disturbed one where carnivores such as *Thais* can move around and feed.

The most recent revivals of HSS are with respect to reviews of the frequency of detectable interactions in field experiments. In a survey of interspecific competition experiments, Schoener (1983, 1985) found substantial support for HSS in terrestrial but not marine systems (freshwater ones were ambiguous). Oksanen (1988) did a reanalysis of the plant experiments and found that most exceptions to HSS were in areas of low productivity, supporting the idea of Oksanen et al. (1981) that herbivores should be regulated by resources, not predators, when productivity is low. In a survey of predation experiments, Sih et al. (1985) found only mixed support for HSS, but consistent support for MS, even in terrestrial systems. In ongoing studies of vole cycles, Henttonen et al. (1987) found no support for the principal alternative to HSS (Murdoch 1966, White 1978), that plants are underpredated because much of their biomass is inedible, due to defenses and/or poor nutrient content.

The Schoener tabulations suggest a major difference between terrestrial and marine systems. This perhaps results from the ambiguity of filter feeders, a major space competitor in marine intertidal systems. Or it may result from differences in degree of omnivory, as terrestrial foliage seems to require rather specialized adaptations for consumption (but see section, Similarities and Differences in Food-web Properties Between Kinds of Species, below). The discrepancy between the reviews of competition and predation experiments seems to present a more explicit contradiction, especially as it exists for terrestrial systems: herbivores compete least yet are less affected by predation than producers. While both results are statistically significant, terrestrial differences between trophic levels are substantially greater in competition experiments: 36.8 of producers as compared to 46.7% of herbivores are unaffected by predation; the same figures are 50.0 vs. 18.7% (all experiments) or 62.5 vs. 21.5% (experiments without enclosures) unaffected by competition. Even the marine predation experiments show little difference: respective figures are 32.7 vs. 42.2% (intertidal), or 41.0 vs. 59.3% (other marine).

Part of the difficulty with "survey" evaluations of hypotheses such as HSS is that species having a particular trophic habit may occur in webs with variable numbers of levels, so that, for example, it may be top in one web but not another. A more exact if limited way to test such hypotheses is to analyze one system where various combinations of levels exist. Islands in the Bahamas provide such an opportunity, and we have been doing research on these subtropical, terrestrial webs for over a decade. This research has shed some light on the controlling interactions for various trophic types, as I now discuss.

THE BAHAMIAN ISLAND SUBTROPICAL SYSTEM: A PARTICULAR TERRESTRIAL WEB

The "typical" web in the Bahamian system has four central trophic elements:[2] medium (-sized) carnivores, small carnivores, small herbivores, and producers. The largest islands have large carnivores (for specifications see section below, Terrestrial Food Webs in General), and the smallest islands lack medium carnivores and sometimes even small carnivores.

On most islands having medium carnivores (in this case primarily lizards), both HSS and MS predict that this trophic element should be dominated by competition. A great deal of research in the Bahamas and on other Caribbean islands has demonstrated the importance of competition for lizards, both as an ecological (or instantaneous) and as an evolutionary force. The evidence is briefly summarized as follows:

1) Small-to-medium islands show a remarkable niche separation of lizard species, primarily either by body or head size (correlated with food size) or by structural habitat (perch height and perch diameter). Size differences are most extreme in the Lesser Antilles, and most null models pronounce them nonrandom (Schoener and Gorman 1968, Schoener 1969a, Williams 1972, Schoener 1988a). On most other small-to-medium islands, size differences are less, but virtually no structural habitat is represented by more than one lizard species (Schoener 1969a, Williams 1972); this can be shown to be unexpected by the most sensible null models (Schoener 1988a).

2) On the largest islands, *Anolis* lizards separate nonrandomly in climatic and structural habitats, taken jointly (Schoener 1970 and included references). On such islands, particular *Anolis* show patterns of character displacement in head and body size consistent with expectations from competition for food (models in Schoener 1969b; data in Schoener 1970; see also F. Hopf et al., *unpublished manuscript* for a supportive reanalysis of certain of these data).

3) Lizards shift (on an evolutionary scale) structural habitats nonrandomly, mainly in the presence of other lizards of the same or larger size and of the same climatic habitat (Schoener 1974a, 1975). *Anolis* lizards also show behaviorally induced habitat shifts (Jenssen 1973). Whether this pattern results from assortative

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[2] "Element" is used here as a more inclusive category than "species" or "trophic species" (see below for definition). It is best thought of as a kind of trophic species, distinguished according to body size and position on a plant-eating to animal-eating continuum: a variety of trophic species may compose an element, and certain elements, e.g., small carnivores, may have a number of levels, i.e., linked species. Finally, food webs composed entirely of trophic elements are not meant to be full webs, in the sense that those analyzed below are full webs.

A. HSS SCHEME   **DOMINANT INTERACTION**   **B. 4-LEVEL SCHEME**

MEDIUM CARNIVORES

CARNIVORES   **COMPETITION**

⇧

SMALL CARNIVORES

HERBIVORES   **PREDATION**

⇧

SMALL HERBIVORES

PRODUCERS   **COMPETITION**
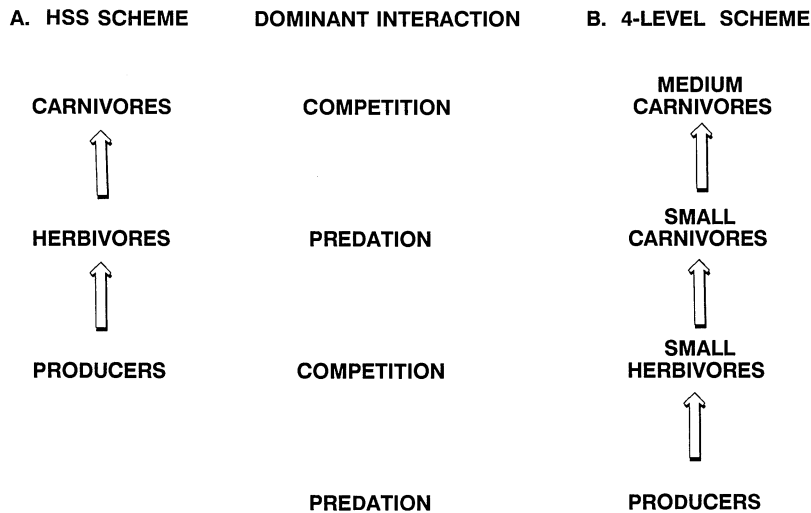
⇧

PREDATION   **PRODUCERS**

FIG. 1. Alternating control by predation and competition. A) Hairston, Smith, and Slobodkin 1960 (HSS) hypothesis. B) Four-level alternate to HSS.

invasion and competitive extinction (Roughgarden et al. 1983) or also character displacement in situ (J. Losos, *unpublished manuscript*) is currently debated.

4) *Anolis* lizards show extraordinarily high densities in certain of the Bahamas, up to 1 individual/m², higher than nearly any other lizard population and orders of magnitude higher than most continental populations (Andrews 1976, Schoener and Schoener 1980). These densities can be reached very quickly: a propagule of 10 lizards released on a lizardless island had increased to >100 in 1 yr, and the island was filled in ≈3 yr, as determined by subsequent censuses (T. W. Schoener, *unpublished manuscript*). However, many *Anolis* species are moderately to extremely territorial (Rand 1967, Jenssen 1970, Philibosian 1975, Schoener and Schoener 1980, 1982*a*), so that despite such high densities one might suspect sufficiently great self-regulation via territoriality to avert strong interspecific competition for food. Two facts argue against this, however. First, males tend to be more territorial than females, in some cases (e.g., *A. sagrei* [Schoener and Schoener 1982*a*]) strikingly so, and male territoriality seems to be directed mainly toward mating success (Stamps 1983). Second, even where females are territorial, territory sizes vary greatly in apparent response to factors such as food availability (Schoener and Schoener 1982*a*), rather than act as an "inelastic disc" (perverting Huxley 1934) that would hold populations below values predicted by resource levels and thereby avert food competition.

5) Two similarly sized *Anolis* lizard species on the Lesser Antilles have been experimentally shown to compete; two dissimilarly sized species, which differ more in their resource use, do not compete (Pacala and Roughgarden 1982, 1985). Our introduction experiments with Bahamian lizards also detect competition, but this may not be severe enough to lead to extinction;

these experiments are not yet completed, however, so cannot be further discussed here.

Given a top carnivore level whose members strongly compete for food, one must predict a great predatory effect on the next lowest level. But also, given the four important elements listed above, it is not obvious that an HSS-type scheme will work for the typical Bahamian web. Suppose one arranges the four elements linearly. Then the HSS predictions (Fig. 1A) are reversed for herbivores and producers (Fig. 1B). Fretwell (1977) discussed this sort of possibility, making different predictions about the validity of HSS depending upon whether four- or three-level webs occurred. Indeed, the prevailing paradigmic web for sufficiently large lakes, for which there is some experimental evidence, is like the four-level system of Fig. 1B: piscivorous fishes, planktivorous fishes, herbivorous zooplankton, and phytoplankton (Carpenter and Kitchell 1988). Recently Jager and Gardner (1988) simulated linearly arranged food webs having various numbers of levels. They found that Fretwell's alternating control scheme was supported with respect to total biomass at the separate levels; it alternated between high and low. In contrast, they also found that, the farther down the web was a population, the more likely were extinctions to be caused by predator overexploitation as opposed to food shortage. The latter result, which is nonintuitive and not understood analytically, is not quite so relevant to Fretwell (1977) or HSS.

One way in which HSS can work with four elements is if the two carnivore levels were decoupled, so that their effects were additive (Fig. 2). Fortunately, this scheme is instantly subject to test in the Bahamian system, as substantial work has been done with a principal small carnivore, web spiders (mainly Araneidae). In fact, the effect of lizards on spiders is profound. The evidence is summarized as follows:
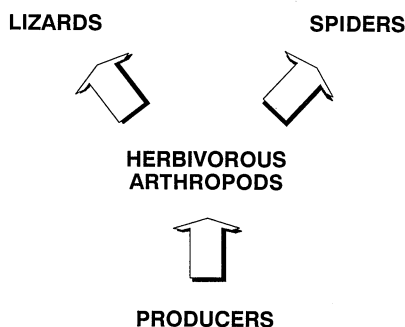
LIZARDS   SPIDERS

HERBIVOROUS
ARTHROPODS

PRODUCERS

FIG. 2. Hypothesis that carnivores are additive in their effects in the basic Bahamian food web.

1) Islands without lizards average ≈10 times the density and ≈2 times the number of species of spiders as those with lizards (Schoener and Toft 1983, Toft and Schoener 1983).

2) Introductions of spider propagules (using 5 or 15 individuals in separate experiments) onto lizard and no-lizard islands show an immediate (within 4 d) and severe effect of lizards; such propagules never survive on lizard islands (0 of 5 islands for both experiments) but often do on other islands, including those smaller and apparently poorer in resources than lizard islands (3 [first experiment] or 6 [second experiment] of 10 islands; T. W. Schoener 1986a and *unpublished manuscript*).

3) Lizard-removal experiments using very large enclosures (large enough to hold 8–10 lizards at natural densities and with normal home ranges), show a major effect of lizards on spiders (Schoener and Spiller 1987, Spiller and Schoener 1988). In lizard plots, number of spider individuals is smaller by a factor of ≈3, and number of species by a factor of 1.3. Both spider survival and the fraction of spiders consuming prey are significantly lower in lizard plots, suggesting, respectively, predation and consumptive competition (sensu Schoener 1983) as mechanisms. We cautioned, however, that reduced consumption of food by spiders could have been caused by interference (spiders avoid times or places of high lizard activity) or differential predation by lizards on spiders in food-rich places. More recently (D. A. Spiller and T. W. Schoener, *unpublished manuscript*) we have found strong evidence of consumptive competition: (a) lizards' and spiders' diets overlapped considerably; in general, both preferred large arthropods over small; (b) lizards reduced the number of large prey consumed by spiders, but not the number of small prey; total biomass consumed was reduced by lizards; (c) lizards reduced the number of large insects caught in sticky traps, but not the number of small insects; (d) lizards reduced spider adult body size and fecundity; and (e) food supplementation increased spider fecundity. Thus both consumptive competition with and predation by lizards affect spiders.

Having ruled out that predation by carnivores is

additive because they are decoupled (Fig. 2), we are left with two possible food webs given that only herbivores eat producers, true for the phytophagous element of the web at least (see also this section, below). These are shown in Fig. 3: the left scheme supports and the right scheme does not support HSS with respect to herbivores and producers. In these diagrams I have distinguished two thicknesses of arrows, to be interpreted as follows. An arrow from B to A gives the effect of A on B in the absence of effects on A from other elements of the food web that connect to A, i.e., predators on A or alternative prey of A. In particular, the population size of A *as directly affected by other elements of the web* is not reflected in arrow thickness. A thin arrow can have at least three interpretations: (1) a density-independent per-capita effect of A on B is low (where "per-capita" is "per-prey-individual-per-predator-individual"); (2) A strongly self-regulates by interference-type mechanisms such as territoriality, so that its population is relatively low; and (3) A's population is low because it is reduced by physical factors.

We are currently testing the two hypotheses and in particular plan a 2 × 2 spider/lizard removal with enclosures to measure compensatory predation. Presently we have four other types of evidence, all of which favor the HSS version (Fig. 3, left).

1) A conspicuous physical defense against herbivorous arthropods of the ubiquitous buttonwood mangrove (*Conocarpus erectus*) is the presence of tiny leaf-surface "hairs" called trichomes. Buttonwood has two extreme morphs, pubescent and glabrous (with some intermediates), and the percent coverage of the former is greater on no-lizard than lizard islands (Schoener 1987a).

2) Also in buttonwood, percent leaf damage is greater on islands without than with lizards (Schoener 1988b). The factor of increase in damage is 1.5, the same as

LIZARDS   LIZARDS

SPIDERS   SPIDERS

HERBIVOROUS   HERBIVOROUS
ARTHROPODS   ARTHROPODS

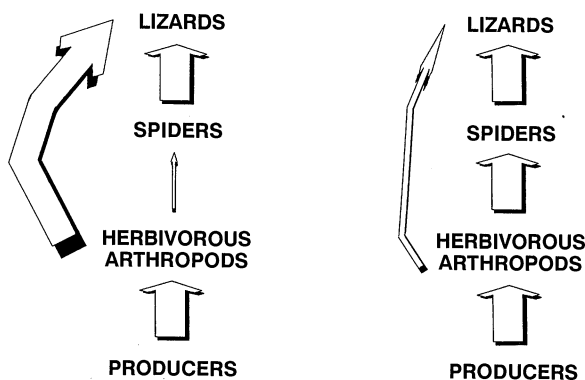PRODUCERS   PRODUCERS

FIG. 3. Alternative hypotheses for the basic Bahamian food web (this is a partial web only). Left: scheme supporting HSS for herbivorous arthropods and producers. Right: scheme not supporting HSS for same elements. See the text section, The Bahamian Island Subtropical System: A Particular Terrestrial Web, for explanation of arrow thicknesses.

the factor for pubescent vs. glabrous forms, but much less than factors for the effect of lizards on spiders. The effect of lizards on spiders is direct, whereas the effect of lizards on plants is indirect (being separated by another level), perhaps accounting for the difference in magnitude. We also attempted to relate spider density to buttonwood damage. For all islands combined, the relation was rarely significant, but when it was, the effect was positive! This is the opposite expected were spiders to reduce arthropod herbivores. Two possible explanations are (1) spider density varies inversely with lizard density (the latter could not be precisely measured on most islands), and (2) spider density indicates general suitability of an island for arthropods. Were the first explanation correct, the relation between spider density and leaf damage should be more positive on lizard islands; if the second were correct, the relation should be more positive on no-lizard islands, as the latter are smaller, and thus more likely to be battered by storms into unfavorableness. In fact, the second explanation is supported. Moreover, one analysis on lizard islands (glabrous leaves) even gives a marginally significantly negative effect of spiders on plants, weakly suggesting that an increased population of spiders partly compensates in predatory effect for lizard removal.

3) The sea grape (*Coccoloba uvifera*) has greater leaf damage on islands without than with lizards; the factor of difference is ≈5 (D. A. Spiller and T. W. Schoener, *unpublished manuscript*).

4) Sea grape tends to be more damaged in lizard-removal plots than plots with lizards, but this was statistically significant in only one year (T. W. Schoener and D. A. Spiller, *unpublished manuscript*).

Thus plants are often adversely affected by lizard absence, supporting HSS. Additionally, the existence of consumptive competition as a mechanism of the lizard effect on spiders also supports the HSS version in Fig. 3: lizards strongly affect the prey of spiders (not necessarily just the herbivore prey, as in the figure, but perhaps other prey as well). Thus spiders seem a "dead end" element in the Bahamian food web, affected strongly by lizards but affecting nothing very strongly themselves. Probably the reason is the action of occasionally quite severe physical factors, e.g., major storms, which reduce spiders even in the absence of lizards (Spiller and Schoener 1988).

In conclusion, work on Bahamian island subtropical webs up to now supports HSS for all elements but small carnivores; this group behaves more as MS might predict, but the simple (1976) version of MS is not supported by producers, nor is the degree of omnivory in this web probably anything like that needed to make MS work. Aside from HSS, the greater importance of predation than competition for small as compared to medium-sized carnivores is in line with the arguments that smaller individuals should be more vulnerable to predators and larger ones more likely to compete (Schoener 1974b, Connell 1975).

Terrestrial Food Webs in General

When performing intensive, detailed, and lengthy research on a particular system, one occasionally looks up to ask how typical the system is and to what degree conclusions from that research can be generalized. Pursuing this question is potentially disheartening, given the great diversity of the ecological world. Nevertheless, somewhat optimistically, I will be evaluating this kind of issue for the remainder of this paper. In this section I ask to what degree the Bahamian island subtropical system is representative of terrestrial systems as a whole, and if differences in web structure that might exist are likely to alter hypotheses such as HSS for prevalence of the various interactions.

To begin with the more particular, the roles of lizards and spiders have been investigated in a number of other terrestrial ecosystems. Pacala and Roughgarden (1984) show an effect of lizards on spiders at least as profound as the one we have demonstrated; they find a lizard effect on other arthropod groups as well, but not on vegetation. The evidence is mixed concerning the degree to which spiders can affect substantially lower levels of the food webs (Nyffeler and Benz 1987). Those replicated field experiments that show an effect (and a number do not) were done in agroecosystems (e.g., Mansour et al. 1980, S. E. Riechert and L. Bishop, *unpublished manuscript*). Such systems may differ from the Bahamian ones in at least three ways: (1) spider densities, especially if manipulated, may be unnaturally high (indeed, "natural" in a man-made habitat loses some meaning); (2) vertebrate predators may be scarce or absent; and (3) physical disturbances (e.g., major storms) may be fewer; in addition, contrary to our experiments, some of these studies considered cursorial spiders, at least in part.

More generally, and in an Eltonian revival (Elton 1927), I would like to distinguish seven major kinds of trophic elements in terrestrial webs. The elements are discriminated on the basis of body size and position along a vegetarian–carnivore diet:

1. *Producers.* — This is a necessary element of nearly all terrestrial webs.

2. *Small phytophagous herbivores.* — These are the very abundant, very diverse folivorous arthropods (Lawton and Strong 1981, Strong et al. 1984).

3. *Large phytophagous herbivores.* — These are mostly mammals, ranging in size from very large (buffalo, giraffe) to medium-large (rabbits, voles). This category is very distinct in size from the previous one. It might be more accurately labelled "large–medium," but most of the smaller mammalian herbivores appear to be larger than most medium carnivores (see number 5).

4. *Small carnivores.* — These are mainly arthropods, such as spiders and predatory insects. Parasitoids are also included here.

5. *Medium carnivores.* — These are typically birds, reptiles, or amphibians, with some mammals, that feed

primarily upon small carnivores and herbivores. Examples are many passerines (e.g., warblers), most lizards, frogs and toads, and shrews.

6. *Large carnivores.* — These are typically birds, mammals, or reptiles that feed primarily upon medium carnivores and large herbivores; they also feed on other large carnivores in a few cases. Examples are hawks, felids, and snakes. A less discrete size gap appears to exist between medium and large carnivores than between medium and small carnivores.

7. *Medium omnivores.* — Many medium-sized animals, particularly birds and mammals, consume both plant and animal matter. The plant matter is mainly fruit or seeds; the former seems to require somewhat less specialization than the latter. Omnivores can be broken down according to which category of plant food is prevalent, but I do not do this here.

John Lawton (*personal communication*) has suggested that an eighth element should be considered major: small omnivores, as represented by certain ant genera (e.g., *Formica, Myrmica,* and *Camponotus*), as well as certain Coleoptera and Dermaptera. In fact, no such trophic category occurred in the 17 terrestrial webs culled from Briand and Cohen's (1987) list (see section below, Food-chain Lengths, for methods), although these data must be viewed sceptically. Ants were explicitly listed in three webs, but their trophic classifications were small predator, small herbivore, and small predator/scavenger. Moreover, ants are sometimes much protected against predation, so might be weakly connected from above; indeed in the Bahamian island subtropical system, unlike for spiders, lizard occurrence did not affect total ant species statistically in an observational survey (S. Rissing et al., *unpublished manuscript*). For these reasons, I have chosen not to include small omnivores as major here, although the situation could certainly change with better data.

Other kinds of trophic elements exist in terrestrial systems. Both small and medium nectar/pollen feeders occur, e.g., bees and hummingbirds. All sizes of frugivores exist in the tropics, e.g., fruit bats, manakins, and fig wasps. Small granivores (e.g., *Pogonomyrmex* ants) are important in desert food webs (Brown et al. 1986), while medium omnivores can often facultatively become granivores at certain times, e.g., certain finches. Root eaters are sometimes important in terrestrial webs, e.g., in grasslands, as are bark eaters in forests. In addition, parasites and decomposers (with mixtures of this category and others) occur in all systems, terrestrial included (see this section, below). Still other categories exist. The seven I have singled out, however, tend to dominate published food webs: for the 17 terrestrial webs, the seven categories compose from 43 to 92% of the total "trophic species," with a median of 78%. "Trophic species" are determined by lumping those investigator-distinguished species having the same investigator-distinguished prey species

and predator species (see also editing method number 3 in the next section, Food-chain Lengths).

The typical or basic Bahamian island subtropical web (Fig. 3) has four of the seven major elements: producers, small phytophagous herbivores, small carnivores, and medium carnivores. These elements are nearly ubiquitous: of the 17 terrestrial webs, 15 have small phytophagous herbivores, 16 have small carnivores, 16 have medium carnivores, and all have producers. The true figures are probably even closer to ubiquity: while two very northerly webs (tundra, reindeer pasture) have no recorded small folivores (Summerhayes and Elton 1928, Brown 1971), and a Himalayan mountaintop has no medium carnivores (Swan 1961), small carnivores, not recorded for a rain forest web (Harrison 1962), are almost certainly important there.

The elements missing from the basic Bahamian web are not quite so ubiquitous but are still common: 15 of 17 have large carnivores, 15 of 17 have large herbivores, and 10 of 17 have medium omnivores. Nine webs have all three missing categories. How would the presence of these elements affect arguments about HSS based on the basic Bahamian web? I discuss each element in turn, assuming arrow thicknesses of the basic web are as in Fig. 3 (left).

1) Large carnivores are linked to the basic web via medium carnivores as in Fig. 4A. The effect of a strong such link (where "strong" is interpreted as is a thick arrow in Fig. 3) is to lower the density of medium carnivores, in turn reversing all predictions of Fig. 3 (left) made with the simpler web (see also Caughley and Lawton 1982). To the degree that large carnivores eat arthropods (some do commonly, e.g., certain small hawks of the genus *Falco* [Craighead and Craighead 1956], but most do not), the reversal is mitigated and the two uppermost carnivore levels (large and medium) act in an additive fashion. In the 17 terrestrial webs, only 3 of 43 large carnivores eat small carnivores or small herbivores (numbers using trophic species). Bahamian islands larger than used in our experimental research have breeding populations of large carnivores, in particular large birds such as lizard cuckoos. In a study comparing two relatively large islands, South Bimini (1300 ha) and Andros (4.1×10^5 ha), survival in sex classes of three species of *Anolis* was nearly always greater on the smaller island (Schoener and Schoener 1978). Care was taken in this study to use habitats of comparable vegetation structure and diurnal lizard species composition; sites with the highest apparent densities islandwide were used. The smaller island had many fewer bird species than did the larger; in particular, large carnivores were differentially low. While consumptive competition may also be involved, predation by large carnivorous birds seems likely the chief perpetrator of the survival differential. Curiously, population densities in comparable study sites were
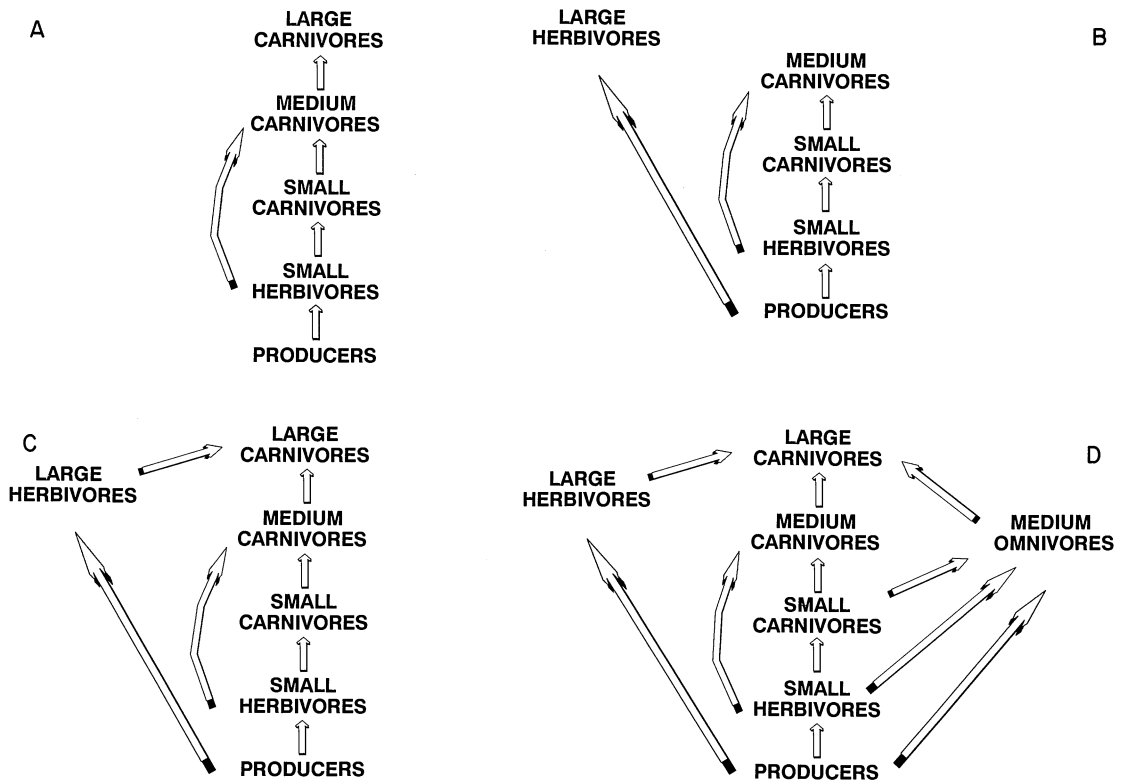
FIG. 4. Terrestrial webs more complicated than the "basic" Bahamian web (Fig. 1B). A) Large carnivores added. B) Large herbivores added. C) Large carnivores and large herbivores added. D) Large carnivores, large herbivores, and medium carnivores added.

not very different between the two islands; we speculated that resource-rich habitats acted as sinks for the often highly vagile *Anolis* individuals (Schoener and Schoener 1982*b*), resulting in poorer habitats being relatively bereft of lizards. Failure to affect density in the better habitats suggests that large carnivores may have less effect on predictions from the basic web than one might initially imagine; this of course remains to be determined experimentally, should such a thing be possible.

2) Large herbivores, when added by themselves (Fig. 4B), give an additional drain on producers, and one that is not potentially controllable by any other element of the seven (although parasites and pathogens may do so). The result of a strong link here is that producers should be relatively depredated, thereby being mainly under the control of predation, contrary to HSS. Manipulations of medium carnivores should affect producers less than in the basic web. In fact, however, only 2 of the 15 webs having large herbivores lack large carnivores; both are located in depauperate regions of Spitsbergen (Summerhayes and Elton 1928). Adding large carnivores (Fig. 4C) now places a control on large herbivores, but if their effect on medium carnivores is sufficiently strong, HSS is still reversed for small herbivores and producers, for reasons given in the pre-

vious paragraph. However, possibly large carnivores prefer large herbivores where both that element and medium carnivores are present, thereby allowing HSS for producers. In fact, of the 14 terrestrial webs having all three categories, i.e., large carnivores, medium carnivores, and large herbivores, large carnivores concentrate more on large herbivores in six webs, more on medium carnivores in three webs, and distribute their diets evenly in five webs. (This was determined by examining diets of each trophic species that consists [partly or entirely] of large carnivores and tallying for each web the number of cases in which more trophic species of large herbivores vs. medium carnivores are eaten. Because "concentration" is affected by prey abundance as well as by "preference," and because trophic species do not necessarily contribute equally to tropic elements, such tallies are not exact measures of arrow thicknesses.) Decisive trends do not exist, but HSS should work much of the time in terrestrial systems, according to these data.

3) Medium omnivores, when added to the basic web, complicate the picture beyond prediction: this group can eat small carnivores, small herbivores, and producers. However, in the 17 terrestrial webs medium omnivores never occur without at least one of large carnivores and large herbivores, and in 7 of the 10

cases where medium omnivores occur, both latter groups occur as well. So a more applicable picture (Fig. 4D) has all three elements added to the basic web. Here again, the effect of medium omnivores can be mitigated if large carnivores prefer them sufficiently more than the other appropriate prey elements. This appears only true, however, in one of nine possible comparisons from real food webs (procedure and reservations as in number 2). Moreover, if medium omnivores are added to medium carnivores, and the question asked whether that combined group or large herbivores are more prevalent in the diet of large carnivores, figures shift (from the comparison under number 2) toward the medium animals; of 14 webs, 2 have large herbivores more prevalent, 6 have medium animals more prevalent, and 6 are even. This can disrupt HSS or not, depending on the various arrow thicknesses. Finally, however, and unambiguously on the side of HSS, the omnivores in the terrestrial systems considered may have little direct effect on the producers. They will do little harm (and some help) as frugivores, as dispersal is facilitated. They will do more harm as granivores but perhaps will have little effect in many webs, given clonal methods of propagation and the huge number of seeds relative to available space. North American deserts, however, do not support this last argument: both small and medium granivores affect both density and composition of producers greatly (Reichman 1979, Inouye et al. 1980; summary in Brown et al. 1986). Moreover, of the 10 terrestrial webs having omnivores, only 2 have strictly frugivorous omnivores, while 7 have omnivores with some degree of granivory. So omnivores may not be so easily dismissed, and if they do have a major effect via seeds, bring the terrestrial systems closer to MS (as indeed Menge et al. [1986] and Menge and Sutherland [1987] suggest).

In addition to the seven major elements of terrestrial webs just discussed, parasites (including pathogens) and decomposers must be ubiquitous in terrestrial systems.

Only 4 of the 17 terrestrial webs include parasites, probably, as has been noted many times (e.g., Price et al. 1986), because parasites are unstudied in most systems. Were parasites and pathogens important, they would add at least one extra level onto any web, reversing effects or not as their impact on various elements is high or low. Parasites and pathogens may have major effects, e.g., *Myxoma* virus on rabbits in Britain (Fenner and Ratcliffe 1965). Parasites may not always complicate things, however, but may reinforce other interactions. Starvation effects or susceptibility to predators can increase with parasite load. Parasites may thereby sometimes act as amplifiers rather than new circuits in food webs.

Decomposers are recognized more frequently in published terrestrial webs: 15 of 17 have some sort of decomposer. (My usage of decomposer is in the broadest sense of any organism that feeds substantially on nonliving organic matter.) In contrast to aquatic webs, terrestrial webs do not seem to be replete with decomposers. The median fraction of decomposer trophic species is 0.10, lower than that for any other kind of system except marine pelagic (see section below, Similarities and Differences in Food-web Properties Between Kinds of Systems). Moreover, in terrestrial webs decomposers seem less connected to the bulk of the web than other species. To measure this, define for a trophic species its "loose-knitness" as the mean of the distribution of minimal distances (in units of links) necessary to reach each of the other species in the web. (Paths can be upward or downward; when webs are broken up into isolated units, only reachable species are counted in the average; solitary isolated species are dropped.) The smaller the loose-knitness, the less isolated a species is. We can then compare decomposer species with some other group of roughly the same body size and taxonomic affiliation. The comparison of small decomposers vs. small carnivores (not including parasitoids) is the one involving the most webs. Here, decomposers have higher values of mean loose-knitness in 8 of 13 possible webs (excluding ties), while carnivores have higher means in three webs (binomial $P = .113$). Figures for medians are 8 of 10 ($P = .055$). If webs that have isolated units of more than one species are deleted, probabilities are better ($P = .090$ and .035, respectively). Related to this tendency, small decomposers are closer to the bottom of food webs. To measure this, define for a trophic species its "upward reach" as the total number of different trophic species encountered along all possible strictly upward paths to all possible top species (top species are eaten by no species). Small decomposers have higher web averages for upward reach in 11 of 13 webs; small predators only have higher values in one web ($P = .003$). These figures are subject to the major caveat, of course, that terrestrial ecologists often have not studied decomposers very carefully, at least until recently; a greatly increased species-richness of decomposers could change conclusions.

The same sort of comparison can be made for other "ignored" groups. Parasites and large carnivores show virtually no difference in either loose-knitness or upward reach for the four webs for which comparisons can be made. Parasitoids, another group neglected in our Bahamian studies but included in the basic web under "small carnivores," show no difference from typical small carnivores in either loose-knitness or upward reach for the three webs for which comparisons can be made. Both comparisons are suspect, as sample size is small and two webs in each case have isolated units of more than one species. Indeed, parasitoids, virtually absent from published terrestrial webs (again, one feels as an artifact of ignorance) may be the most important kind of organism determining chain length in medium-to-large terrestrial webs (see next section, Food-chain Lengths).

In summary, omission of decomposers from our

studies on Bahamian webs is not likely to affect conclusions about web interactions because of their apparent relative isolation in terrestrial webs. Omission of parasitoids and parasites may alter conclusions to an unknown degree, although we can explain a number of major direct and indirect effects without them. Large carnivores, large herbivores, and medium omnivores do not occur in the basic Bahamian web, but they do occur commonly in other terrestrial webs, so that our conclusions concerning HSS cannot be expected to be extremely general. HSS is most likely to hold when (1) large carnivores have prey in common with medium carnivores; (2) medium carnivores immigrate from elsewhere, reducing effects of large carnivores on their density; (3) large herbivores are preyed upon by large carnivores preferentially over medium carnivores; and (4) medium omnivores prey upon small herbivores more than upon producers. Only the first of these conditions is unlikely; however, the absence of all four is also not unlikely; we have a long, difficult set of research projects to accomplish before understanding the various ways terrestrial food webs can work.

FOOD-CHAIN LENGTHS

Quite apart from the issue of whether our Bahamian web is typical with respect to major trophic elements and interactions, we can ask what contribution our research might make to a theory of food-chain length, a topic of much current interest (Cohen 1978, Pimm 1982, Briand and Cohen 1987, Lawton 1989).

In this literature, maximum chain length, hereafter referred to as "Cohen's maximum chain length," is defined as follows. Calculate all possible chains between a given "basal" (having no trophic species as prey [Pimm 1980a, Briand and Cohen 1984]) and a given "top" (having no trophic species eating it [Briand and Cohen 1984]) trophic species; do this for all possible combinations having one basal and one top species. Measure chain length as the number of links in the chain. Then the maximum of the distribution of these chain lengths is Cohen's maximum chain length.

In the Bahamian archipelago, which consists of very small to relatively large islands, Cohen's maximum seems to be easily explainable on the basis of island size, when the major elements alone are used as trophic species. The largest islands have large carnivores, medium carnivores, small carnivores, small herbivores and producers, so the maximum chain length is four (or three, if the small-carnivore-to-small-herbivore association is so weak as to be dropped). Smaller islands lack large carnivores, and the maximum drops to three (or two). Still smaller islands have no medium carnivores, and the maximum is two. The tiniest islands have no orb spiders, although they sometimes have ants and cursorial spiders (Schoener and Toft 1983, Toft and Schoener 1983, S. Rissing et al., *unpublished manuscript,* T. Schoener, *personal observation*). For

some of those islands conceivably the number of links is sometimes one (that between small herbivores and producers) or even zero, when producers alone occur. This progression seems to result from the fact that larger animals, and particularly larger carnivores, are less likely to occur on smaller islands. Larger animals (especially carnivores) require larger home ranges to satisfy energy requirements per individual (McNab 1963, Schoener 1968, Turner et al. 1969) and/or larger areas to maintain persistent populations intrinsically, i.e., without immigration from surrounding areas (see also this section, below).

Having a reasonably satisfactory explanation for maximum chain length in the Bahamian island subtropical system, I was surprised upon reviewing the literature (Pimm 1982, Lawton 1989) to find no hypothesis directly corresponding to it that had been tested for food webs in general. Pimm (1982) summarized four hypotheses for chain length: (1) a *productivity* hypothesis, in which not enough energy makes it to the top of food webs to support a top level or top levels; (2) a *design constraint* hypothesis, which seems to focus on the feasibility of top predators being able to feed on organisms of the next lowest level; (3) an *optimal foraging* hypothesis, which has over evolutionary time more specialists attracted to the more abundant prey of lower levels; and (4) a *dynamical stability* hypothesis (originally developed in Pimm and Lawton 1977), in which longer food webs are (a) less likely to have "feasible" equilibria (which can be related to energy availability, so is an explicit version of number 1 [Pimm 1982]), or (b) more characterized by extinction or population-size variability (slow return times to equilibrium).

Of these hypotheses, (1) and (2) seem closest to the island-size explanation given for Bahamian webs. Examining Pimm's (1982) justification for (1) more closely, we find two kinds of arguments mixed in, one dealing with the units "trophic levels," and the other dealing with the units "populations" and "individuals." Citing Hutchinson (1959), the trophic-level argument calculates the diminishing amount of energy reaching higher and higher levels of the food web: ". . . this amount of energy may not be sufficient to support another trophic level" (Pimm 1982:106). The second kind of argument is represented as follows: "Alternatively, a species at the putative fifth trophic level might have to feed over a much larger area in order to obtain sufficient food" (Pimm 1982:106). In philosophical terminology, the first type of explanation might be termed holistic and the second type reductionistic or (more ecologically) mechanistic (e.g., Schoener 1986b). It is quite possible that, rather than being alternatives, the two "explanations" are essentially identical, the second providing the mechanism for the holistically phrased phenomenology of the first. Ecological efficiencies, which are used to make predictions about energy availability at various levels, can then be viewed as having their causes

and consequences being explained by the same individual-level-energetics and minimal-population-size arguments used to explain food-chain lengths. Whatever the epistemological issues, clearly the individual/population version meshes much more closely with our explanation for Bahamian island webs than a simple "productivity" hypothesis. For a food-limited situation, the amount of area (or volume) needed to support a single individual of a particular species depends on that area's productivity; roughly area (or volume) = food requirements ÷ productivity. If this condition is not met, even an immigrant individual cannot persist for long. The area (or volume) needed by a population of individuals must usually be an increasing function (perhaps a simple multiple, as when territoriality occurs) of the area (or volume) needed by an individual. The population argument is completed by noting that smaller populations are less likely to persist (as shown experimentally for *Anolis* lizards in the Bahamian system [Schoener and Schoener 1983]).

These considerations lead to a hypothesis related to the productivity hypothesis but with a rather different emphasis. I call this hypothesis the *productive space* hypothesis, where productive space equals space (area or volume) times productivity. It states that maximum food-chain lengths are determined by the amount of productive space required to allow critical component species populations to persist with some high probability. Because of increasing trends in individual energy requirements and decreasing trends in amounts of energy per area (or volume) available from prey, this argument will usually be applied at top levels of the food web.

The productive space hypothesis not only includes the major element of Pimm's productivity hypothesis, but it also overlaps rather substantially with his "design-constraint" hypothesis, in that most of the important data bearing on the latter, e.g., the relation of energy requirements to body size, are used in calculations of productive space requirements.

The productive space hypothesis can also be viewed as consistent with the general machinery of the dynamical stability hypothesis, not only because of Pimm's (1982) relation between energy availability and feasibility, but also because stochastic perturbation, simulating environmental variability, is argued to diminish population persistence in the dynamical models. In particular, it is consistent with the productive space hypothesis that populations become extinct more frequently in variable environments, thereby shortening food chains on average.

The productive space hypothesis implies tht maximum food-chain lengths should be greater, the greater the quantity: area (or volume) occupied by the food web times the productivity of that web. This shift of emphasis from productivity alone and the partial assimilation of the design-constraint hypothesis is not trivial: attention is now focussed at first evaluation as

much on area or volume occupied by the web as on average productivity, the latter of course being measured per unit area or volume. It may well be that the degree of variation in the areas (or volumes) occupied by food webs exceeds that in productivity. In the Bahamas, islands with food webs range over seven orders of magnitude in area; while we have no measures of productivity, it is unlikely the range is nearly this great. Indeed, productivity ranges in vegetation or aquatic–environment types over the world are not nearly this great. Lieth (1975) gives annual net primary productivity for various terrestrial vegetation types: except for dry desert and ice desert (not considered in food-web studies), these range from 10–$250 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for desert scrub to 1000–$3500 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for tropical rain forest, at most something over two orders of magnitude. Marine planktonic systems show ≈ 1.5 orders of magnitude variation in primary productivity, ranging from means of $70 \text{ mg} \cdot \text{m}^2 \cdot \text{d}^{-1}$ in certain oligotrophic waters to $1000 \text{ g} \cdot \text{m}^2 \cdot \text{d}^{-1}$ in neritic waters (Koblentz-Mishke et al. 1970). Marine benthic habitats appear more variable, ranging from 0.01 to $0.03 \text{ g} \cdot \text{m}^2 \cdot \text{d}^{-1}$ for benthic microflora (Scottish sediments) to ≈ 10–$20 \text{ g} \cdot \text{m}^2 \cdot \text{d}^{-1}$ for various seaweeds and coral reefs (Bunt 1975), something over three orders of magnitude. Freshwater systems are about as variable as marine benthic systems: values of net primary productivity (as C) range from 1 to $35 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in antarctic lakes to 100–$7600 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in tropical lakes (Likens 1975). In summary, most systems whose food webs have been studied probably vary at most over about three orders of magnitude in productivity (Whittaker and Likens 1973 and above).

For purposes of testing the productive space hypothesis beyond the Bahamian system, we are very fortunate to have available a data set consisting of 113 food webs, compiled by Briand and Cohen (1987). These authors calculated Cohen's maximum chain length for each of their webs and tested three explanatory hypotheses, two of which are Pimm's (1982): the productivity hypothesis and the dynamical stability hypothesis. The third, dimensionality hypothesis, which is inductive, says that chains are longer in three-dimensional environments than in two-dimensional environments; specifically, chains are longer in forest than grasslands and longer in open ocean than shallow reefs or benthic areas. In their analysis, support was found mostly for the third hypothesis; no support whatever existed for the productivity hypothesis, and most of the success of the dynamical stability hypothesis was due to associations between environmental variability and dimensionality.

To examine the productive space hypothesis as well as some other food-web properties (see next section, Food-web Properties in Relation to Food-web Size), I reanalyzed the webs of Briand and Cohen (1987; hereafter referred to as BC). I collected all of their original sources I could find (only four, two of which are un-

published, were not located). I then both added to and subtracted from their lists, as follows. Some webs in a particular source paper were not included in BC's compilation, e.g., the Birkeland shallow subtidal web in Paine's (1980) discussion. Other webs included in BC were not found acceptable; the main basis for discard was that major levels of the web were absent, e.g., stream or oceanic communities without fish (e.g., webs 34 or 42 of BC). Other reasons for excluding webs were lack of precision in description (e.g., web 1 in BC) or habitat too disturbed by man (e.g., web 18 in BC). The Appendix lists which of BC's 113 webs were included as well as the additional ones. In total, 98 webs were considered in this analysis.

Because food-web properties are likely to vary by general type of system, I divided the 98 webs into eight categories: terrestrial, marine benthic, marine pelagic, marine estuarine, intermediate estuarine (either having a major freshwater [webs 2, 4, 14, 57 in BC] or terrestrial [webs 3, 5, 8 in BC] component), lentic, lotic, and mixed. Although some overlap between system categories exists (e.g., marine estuarine and marine benthic), most placements were unambiguous. The system category for each web is given in the Appendix.

Food webs were edited (or as Paine [1988] puts it, "sanitized"), sometimes considerably, as follows:

1) Only living organisms were allowed as web elements or "trophic species"; all nonliving elements, e.g., detritus, dissolved organic matter (DOM), humus, and feces, were excluded as trophic species. As a result, detritivores as well as producers were "basal," that is, species not feeding on living organisms. Predators on bacteria, when specifically noted as such, were not considered basal but rather intermediate or top, as appropriate. The procedure of not counting nonliving food-web entries as trophic species is contrary to Briand and Cohen's procedure (F. Briand, *personal communication*); in their webs, basal species are mostly producers or detritus-type groupings.

2) Obvious trophic impossibilities were edited out in various ways. "Dangling" nonproducers and non-detritivores, that is species of an obviously nonbasal nature represented as having no prey, were eliminated, either by (a) determining what their prey were (sometimes by consulting the author of the web) and including those prey in the web, or (b) deleting that portion of the web having such species. Sometimes a web had "immigrant" species from other systems (e.g., web 22 of BC, Bear Island, with respect to marine organisms); these species were deleted unless they were apparently a major part of the productive base of the web. Wherever phytoplankton and zooplankton were lumped into a single category, I distinguished them, as Moore et al. (1989) criticized BC for not doing. However, I did not surmise the presence of top predators not actually drawn in the web unless said to be there in the text or in conversations with authors (webs without such predators are at least trophically possible). I agree with

Briand and Cohen (1989; reply to Moore et al. [1989]) that it is more conservative not to include predators acquiring a large fraction of their food outside the space occupied by the web, especially in view of the sometimes major disagreement as to the significance of such predators (Edwards et al. 1982 vs. Menge 1982). Finally, published aquatic webs are variable with respect to the microbial portion; Fenchel (1988) argues that full representation of this portion will increase estimated food-chain lengths.

3) Investigator-distinguished "species" or elements were combined into "trophic species" as did Briand and Cohen (1984). Solitary isolated species (having neither predators nor prey) belonging to different trophic elements (here always a producer and decomposer) were not combined. Some webs (e.g., Wilbur's [1972] wonderfully clear temporary pond web) already come that way, but many do not. Additionally, when the same stage of an investigator-distinguished species occurred in several elements or "boxes," the latter had to be broken up and redistributed.

4) Loops, either involving one or a group of trophic species, were dealt with in two ways. First, some loops imply that particular investigator-distinguished species are actually several trophic species, e.g., large fish eating small fish of the same taxonomic species. When the source indicates this is likely, investigator-distinguished species were fractioned appropriately. Second, other loops actually represent mutual predation (in the mechanistic, not population sense; see Abrams 1987). For example, in the Prudhoe tundra, mosquitoes and warble flies parasitize birds, and birds eat mosquitoes and warble flies (Brown 1975). In this kind of situation, loops were averted with respect to calculation of chain length, upward reach, etc., by breaking them up in favor of the more obligatory interaction. For this example, ectoparasites will not exist without their hosts, whereas birds eat many prey other than their ectoparasites, so that the arrow "ectoparasites eat birds" is left in. I found very few loops, whether a single or more than one species was involved. Were nonliving organisms included as trophic species, I think more cycles should occur, at least if all the proper arrows were drawn in and detritus was not mainly allochthonous. Cohen and Briand (1984, Briand 1983) also found few cycles, despite their including detritus categories as trophic species; this may reflect their procedure (F. Briand, *personal communication*) of deleting arrows from living organisms to detritus categories.

5) Humans, who tend to "close" webs at the top, were deleted as trophic species, because many webs may not be stably adjusted to human activities.

Cohen's maximum chain length, as well as Cohen's mean chain length (take the mean of the same distribution giving the maximum; see above), were calculated for the 98 webs included here. The two are very closely correlated: Pearson r's ranged from 0.891 to 0.973 in the separate kinds of systems, and the overall

TABLE 1. Maximum web length: lentic.

Maximum number links	Web	Source*
1	Temporary rockpool (4 L)	101
2	Permanent rockpool (2.5 × 1.5 × 0.3 m)	82a
3	Permanent rockpool (3 × 1 × 0.4 m)	82
3	Sandy shore, Lake Nyasa	39
3	Rocky shore, Lake Nyasa	38
4	Lock Leven	68
4	High mountain lake (Vorderer Finstertaler)	75
4	Temporary pond (Michigan)	84
4	Crocodile Creek, Lake Nyasa	33
4	Neusiedler Lake	76
4	Lake Abaya	77
4	Hafnersee	73
4	Lake Ikroavik	94a
4	Lake Pääjärvi (littoral)	80
5	Lake George	78
5	Moosehead Lake	19
6	Lake Pääjärvi (pelagic and profundal)	79

* Numbers without letters refer to webs in Briand and Cohen (1987). Numbers with letters refer to webs not considered by Briand and Cohen (1987) but in papers having one or more webs used by Briand and Cohen. For example, for web 82a see the paper having web 82 in Briand and Cohen (1987).

r is 0.939. Therefore, only Cohen's maximum will be discussed further.

The productive space hypothesis is difficult to evaluate directly for most webs, as even fewer studies provide figures on the area or volume occupied by the web as on productivity. We can gain insight into whether the "space" portion of the hypothesis has merit in two ways.

First, the two freshwater systems, lentic and lotic, range over such great differences in food-web space that a revealing qualitative inspection can be made of their maximum chain lengths. Tables 1 and 2 give lentic and lotic webs, respectively, listed in order of increasing maximum chain length (parasites are excluded from these tables and Table 3). The smallest maximum chains (those of one or two links) clearly come from the smallest bodies of water (e.g., Cone Spring [Tilly 1968], Linesville Creek [Cummins et al. 1966]). Such small food chains are also typically found in the lentic phytotelmata not included in BC: Cohen's maximum (excluding nonliving matter [detritus] as we do here) is one (six webs), two (three webs) or three-or-four (one web) (Pimm and Kitching 1987). At 3–4 links, things get murkier for lentic webs, although a fair portion of the largest lakes have 4–6 links. Among the lotic webs, the largest maxima, five or six links, are found in the Mississippi River and Volga River, respectively. In this listing, only the Thames River and Morgan's Creek, with three and four links, respectively, seem obviously out of order.

Other types of systems are less clearly ranked by area or volume; the listing for terrestrial webs is given in Table 3.

Some of the terrestrial webs with small maxima obviously have little area. The smallest maximum, two links, is for a salt meadow in New Zealand, which is described as a belt 20 m wide between large areas of *Salicornia* on the one side and grass and herbs on the other (Paviour-Smith 1956).

Webs with three-link maxima include the again spatially intermediate but sometimes widespread willow community of an Aspen parkland (Bird 1930), three tundra or similar communities, an alpine community in the high Himalayas, and (perversely!) a tropical rain forest. The tundra regions are of low productivity, but are not necessarily restricted in area, although the Spitsbergen region seems to be. Of the Spitsbergen Reindeer pasture, Summerhayes and Elton (1928:218) write: "[the Arctic Fox is] extremely scarce, only two foxes having been seen by us in two summers, and it seems probable that there is not enough in the way of food or land to support it on the Peninsula, and that it only spends a small fraction of its hunting days actually on it. . . . In other words, there are not enough invertebrates to support a bird population large enough to maintain even one or two foxes, on an area of something like 80 to 100 square miles." (Foxes were stricken from the Reindeer pasture web as a result of this passage.) This is a nice particularization of the productive space hypothesis. Of the Spitsbergen barren regions, Summerhayes and Elton (1928:210) simply write ". . . there is not a sufficiently dense bunting and sandpiper population to support even the ghost of an Arctic Fox. . . ." The high Himalayas are probably restricted in both area and productivity. This leaves the tropical rain forest (Harrison 1962). I was tempted to scrap this web at the outset, because it is obviously incomplete; recall that this was the only terrestrial web without small carnivores, an improbable absence that when corrected must add an extra link to the maximum.

Thus in terrestrial webs, those with small maximum chains, i.e., those of 2–3 links, are probably of low area, low productivity, or both. Areas are impossible to sur-

TABLE 2. Maximum web length: lotic.

Maximum number links	Web	Source*
1	Cone Spring	45
2	Linesville Creek	64
2	Uppermost station, Yoshino River	65
3	Thames River	66
4	Morgan's Creek	35
5	Mississippi River	67
6	Rybinsk Reservoir, Volga River	71

* Numbers refer to webs in Briand and Cohen (1987).

mise for most of the other webs except to say that they mostly cannot be small. Productivity per se clearly plays little role in sorting out the longer webs, e.g., the maximum Cohen's maximum is six, found in the Namib desert! The latter web, incidentally, is very rich in small and medium predators, perhaps as much a predilection of the investigators (Holm and Scholtz 1980) as anything else—this is a very fine study! A defect in previous productivity analyses, as well as the one here, however, may be that annual productivity is used rather than productivity during the time the web is observed; this does not, however, change conclusions from Table 3 in any obvious way.

The second way to evaluate the productive space hypothesis compares distributions of Cohen's maximum chain length between systems (Fig. 5). Rather major differences occur in the extremes: the median for marine pelagic webs is 5 links and the median for marine estuarine and lotic webs is 3 links. The other systems all have medians of 4 links. Means follow a similar order, and for some idea of statistical separation, (a) a one-way ANOVA on all systems gives a probability of no heterogeneity of .0002; and (b) six pairwise comparisons are significant at $\alpha = .05$ using the Tukey family test (for a posteriori comparisons). System differences in maximum chain length seem to support the productive space hypothesis, at least with respect to space. Excluding the two freshwater systems, which have huge variations in space, those systems with the spatially most restricted webs are the estuarine ones (marine and intermediate estuaries have different medians but nearly identical means, 3.58 and 3.57 links, respectively), whereas that system with the spatially least restricted webs is probably the marine pelagic, which has the longest maximum chains (mean = 5.90 links). Although having similar chain lengths, marine benthic webs might seem on average more restricted spatially than terrestrial ones; rocky intertidal habitats, in particular, are often quite spatially restricted, being separated by areas of sand or mud; subtidal habitats are probably less so. That marine benthic systems have maximum chain lengths comparable to terrestrial systems may result in part from their high productivity (I am indebted to B. Menge for these last two remarks). System comparisons also support Briand and Cohen's dimensionality hypothesis to some extent: marine pelagic webs are three-dimensional. While the two-dimensional benthic webs have larger maxima than the intermediate-dimensional marine estuarine webs, the comparison is not significant (Tukey test). Note that the productive space and dimensionality hypotheses are necessarily related, in that the total energy available to a food web will be greater, the greater the volume it occupies.

In passing, we can also use our idiosyncratic revision of the food-web data to reevaluate one aspect of the dynamical stability hypothesis. A corollary of the hy-

TABLE 3. Maximum web length: terrestrial.

Maximum number links	Web	Source*
2	Salt meadow (New Zealand)	28
3	Willow communities (Aspen parkland)	24
3	Barren regions (Spitsbergen)	61
3	Reindeer pasture (Spitsbergen)	62
3	Rain forest (Malaysia)	40
3	High Himalayas	92
3	Tundra (Prudhoe)	95
4	Salt marsh (terrestrial portion)	4
4	Prairie (Aspen parkland)	23
4	Aspen communities (Aspen parkland)	25
4	Wytham Wood	27
4	Trelease Woods (Illinois)	59
4	Wet tundra (Barrow)	94
4	Rajasthan desert	100
5	Kaibab Plateau (forest and adjacent grassland)	60
5	Coniferous forest (Japan)	91
6	Dunes, Namib desert	98

* Numbers refer to webs in Brian and Cohen (1987).

pothesis was tested by Briand and Cohen (1987): more variable webs have smaller maximum chain lengths. Using BC's designations of variability, I find this true also for all webs combined, although the trend is weak (means for fluctuating and constant webs are 4.10 and 3.88 links, respectively). But if analysis is done on a system-by-system basis, of the five systems having both kinds of webs, three do not come out in the hypothetical direction. Those systems having only one kind of web are the estuarine ones, and these are all classified by BC as fluctuating. So the result on variability can be viewed in part as a restatement of our result that estuarine webs have small maximum chain lengths (or vice versa). Moreover, the estuarine webs are all considered by BC to have small or mixed dimensionality, so the association of variability and dimensionality can also be viewed as partly embodied in the peculiarities of estuaries.

In conclusion, we have presented a fair amount of qualitative and a little quantitative evidence that supports the productive space hypothesis, especially for webs having relatively small maximum chain lengths. Yodzis's (1984) result that ectotherms, especially invertebrates, more often solely support a consumer than do endotherms, also is consistent. More precise testing will necessitate the difficult task of measuring areas or volumes that particular food webs occupy. Microbial components must also be more completely identified. Even were these things able to be accomplished, it may turn out that among webs having relatively high maximum chain lengths, the productive space hypothesis is mostly useless, as for those webs most existing kinds of top carnivores can be supported. Complexity at the
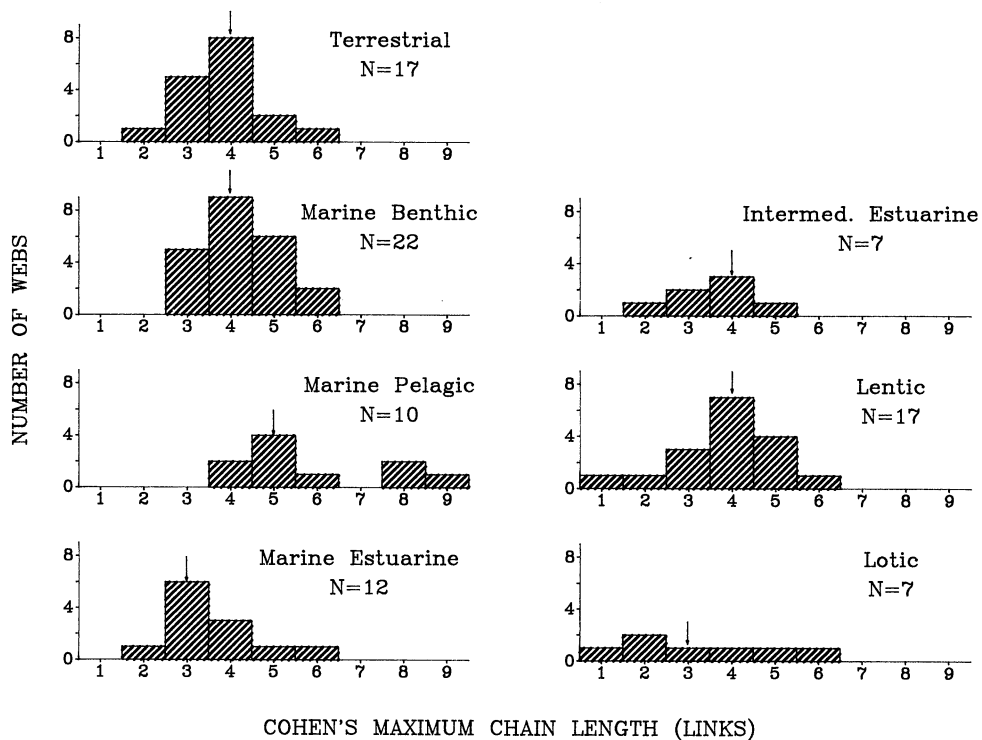
COHEN'S MAXIMUM CHAIN LENGTH (LINKS)

FIG. 5. Distribution of Cohen's maximum chain length by system. Vertical arrow denotes median category for number of links.

intermediate carnivore level may then determine maximum length. For terrestrial systems, as mentioned above, this may mainly involve the various levels of parasitoids. This group is relatively unknown, especially in tropical regions. Where parasitoids have been studied relatively intensely, they are quite diverse: Hawkins and Lawton (1987) find that phytophagous insects in Britain host an average of about five species of parasitoids (see also Owen and Owen 1974). If parasitoids and similarly ignored arthropod macropredators (see especially G. A. Polis, *unpublished manuscript*) determine maximum chain lengths in most terrestrial webs, we are far from even a description of the phenomenon, let alone being able to test explanations.

FOOD-WEB PROPERTIES
IN RELATION TO FOOD-WEB SIZE

The size of a food web can be defined as its number of trophic species, S. As such, the size of Bahamian subtropical island webs, especially given present levels of discrimination, is quite small. Were crucial food-web properties invariant with food-web size, Bahamian webs would still be quite representative with respect to food webs as a whole.

In a series of papers, Cohen and Briand (Cohen 1977, 1978, Briand and Cohen 1984, Cohen and Briand 1984) analyzed the relation of major food-web properties to food-web size. Their principal results are:

1. *The ratio of the number of prey* (defined as those

trophic species eaten by at least one other trophic species), *to the number of predators* (defined as those trophic species eating at least one other trophic species), *does not vary with food-web size*, S. The ratio is rather close to one (it is calculated as 0.8819, replacing Cohen's [1977] earlier figure of $\approx 3/4$).

2. *The fractions of trophic species in a web belonging to each of three classes, i.e., "top"* (species with no predators on them), *"intermediate"* (species with both predators and prey), *and "basal"* (species with no trophic species as prey), *do not vary with* S. Note that Result number 1 must follow from this result, given that predators = top + intermediate, and prey = basal + intermediate (Briand and Cohen 1984).

3. *The number of links* (direct interactions) *in a food web is directly proportional to* S; thus the number of links per species does not vary with S.

I would like to define two other food-web properties. Web "generalization" is the average number of prey eaten per predator in the web. Web "vulnerability" is the average number of predators per prey in the web. Notice that these numbers are not generally the same, because averages are taken with respect to only those trophic species having prey or having predators, respectively. I would now like to add to the above list two items that follow from the other three:

4. *Web vulnerability does not vary with food-web size,* S. If the number of links per web species is constant, and the fraction of prey species is constant, then web vulnerability must be constant; it equals the number

of links per species divided by the fraction of species that are prey. (Note that this kind of argument applies to constant quantities, not to expected values.)

5. *Web generalization does not vary with food-web size*, S. A similar argument gives this quantity as the number of links per species divided by the fraction of species that are predators.

Thus in the Cohen-Briand scheme, the prey–predator ratio, the fraction of top, intermediate, and basal species, the number of links per species, web vulnerability, and web generalization, all, inter alia, do not vary with S.

Pimm (1980b) gave the beginnings of an explanation of the first three properties in terms of the last two: were vulnerability and generalization independent of S, then the number of links in a food web would be proportional to S. Later Pimm (1982) justified the first of these propositions as following from constraints (behavioral, morphological) limiting the number of kinds of prey a particular individual predator can consume. This idea is quite sensible in the context of lower level theory: under expectations from functional morphology, microhabitat restriction, and so on, extensive generality is impossible. Pimm did not justify his other proposal, that the number of predators per prey should be constant. In fact, I would argue that the same genre of reasoning as for generalization does not lead to this proposition. Rather, the number of predators a prey *can defend against* should be constrained in the same way as the number of prey that can be eaten. In both cases we are dealing with a set of dimensions describing a property of the trophic environment, either the potential prey characteristics or predator characteristics. Individuals will be able to occupy points along each dimension with varying degrees of success, depending upon their phenotypic traits. If the number of predators a prey can defend against is fixed, then potential vulnerability, which is the number of predators a prey *cannot* defend against, should generally be an increasing function of S, assuming only that the number of predators increases with S. As an example from the rocky intertidal, Menge and Lubchenco (1981) noted the reduced effectiveness of particular antipredator defenses in tropical as compared to temperate localities, because of the greater diversity of types (and species) of predators in the former localities.

These considerations lead to a simple, two-line kernel for a theory of food-web structure:

$$\text{potential generalization} = C_G$$
$$\text{potential vulnerability} = f(S) - C_V, \qquad (1)$$

where C_G and C_V are constants representing the generalization and defense constraints, respectively, and $f(S)$ is an increasing function of S.

What would be the consequences of a potential vulnerability, or vulnerability constraint, that increased with S? One might imagine that actual vulnerability, the quantity measured directly from real webs, also would be an increasing function of S. For example, in the Bahamian system, herbivorous arthropods are eaten only by other arthropods on small islands, which have small numbers of species, but by arthropods and lizards on larger islands, which have larger numbers of species. However, this relation does not obviously always follow, given that actual vulnerability is constrained by the number of predators in the web and generalization. The following argument is an initial exploration of the consequences of a potentially limitless vulnerability, combined with a limited (i.e., constant with sufficiently large numbers of prey) generalization. It is phrased in both comparative and dynamical language, implying that the operant characteristics of the webs considered are assumed related to S (and dependent properties) only. Its major result is to predict certain food-web properties as dependent on S: vulnerability, prey–predator ratios, fraction basal and top species, and number of links per species.

We wish to compare food webs with $N + 1$ species to those with N species, to determine how the fraction of top (t), intermediate (i), and basal (b) species changes between the two webs. We consider the additional species to be, first, a consumer (top or intermediate), and second, a producer or decomposer (basal). We assume that if a web is sufficiently large, realized generalization will be C_G, the value of the generalization constraint. We refer to this state of being sufficiently large as a "generalization-saturated web." The assumption's justification is that species will be as generalized as possible, given the presence of sufficient species of high-quality prey in the web. The assumption is facilitated by our other assumption that potential vulnerability is only limited by the number of predators finding a prey suitable; in general, however, we imagine that webs will not become generalization saturated when the total number of prey equals C_G, but rather well above this point, as predators should show preferences, and these should vary among predators.

When a consumer is added to a generalization-saturated web, it can only be added as a top species, because no species already in the web can accept another prey. Whether this produces an increase or decrease in t, the fraction of top species, depends upon how many species that are top in the web of N species are converted into intermediate species by this addition. Assume that species are chosen as prey of the new species at random with respect to their identity as top, intermediate, or basal species; then each has a probability C_G/N of being such a prey. (We also assume that the web is large enough for the new species to find at least C_G favorable prey.) In particular, $C_G T/N$ top species will be converted into intermediate species, where T is the number of top species in the N-species web. The number of top species remaining at the top is $[1 - (C_G/N)]T$. The frequency of top species in the N-species web is T/N, and the frequency in the $(N + 1)$-species web is $\{[1 - (C_G/N)]T + 1\}/(N + 1)$. The frequency t

will be greater in the $(N + 1)$-species web than in the N-species web when the second of these quantities is greater than the first, a condition that reduces to

$$t_N < \frac{1}{1 + C_G}. \qquad (2)$$

Thus when t begins small enough (e.g., <0.33 for $C_G = 2$), it will increase, asymptotically, to a constant value determined by the generalization constraint. (If it begins larger than this value, it will of course fall to the same asymptote.) How quickly this increase occurs depends upon the value of N: it can be shown that the ratio t_{N+1}/t_N, where it exceeds 1, will change more slowly the larger is N. The likelihood of t beginning small enough depends upon how t is determined in webs smaller than generalization-saturated webs (see this section, below).

When a basal species (producer or detritivore) is added to a generalization-saturated web, it can only initially occur as an unconnected species. Whether and how it is counted is a matter of convention. In the analysis below, I counted a detached species as both top and basal. Under these circumstances, the web gains one of each kind of species, and both t and b will increase at the expense of i. If such species are not counted, then at least one predatory species is required to attach the producer or detritivore to the web. If one such species attaches it, then the fraction of basal species will decline upon attachment if $B/N > (B + 1)/(N + 2)$ or $b_N > 0.5$, where B is the number of basal species in the N-species web. In short, the addition of producers or decomposers to the generalization-saturated web can (1) result in an increase in t if they are counted while detached, or (2) result in a decrease in b when they are counted only if attached, if b is sufficiently high. Hence, while the frequency of basal species declines when a top species is added to an entirely connected web, always, the reverse is not necessarily the case, providing an asymmetry.

In webs below the generalization-saturated threshold, where new species can be added as prey of existing species, producers and decomposers can be added in one step without an intervening top predator, resulting in a clear increase in b no matter what the web structure. Consumers can be added as intermediate species, in addition to being added as top species; when a consumer is added as an intermediate species, i will increase at the expense of t and b, and t may decline even further because of top species converted into intermediate ones (although this last is unlikely because of size hierarchies and so on; see this section, below). The likelihood of a consumer being added as a prey will probably depend on the number of consumers and their likelihood of accepting a new prey. The latter should increase, the smaller is N, but the former will often decrease. Were the likelihood of accepting a prey a sufficiently sharply increasing function of the distance from C_G, the latter would be the dominant effect, and

consumers would be more likely added as intermediate than top species, the smaller the web. This will result in t decreasing and $(b + i)$ increasing with decreasing N. The fraction t, however, cannot decrease over very small values of N. When N is one, t equals one (when detached species are counted as both top and basal). When N is two and the species are connected, t equals 0.5. Only when N is three is there a possibility of t declining with decreasing N: it can equal 0.33 or 0.67.

Putting the above results together, we expect a tendency for the fraction of top species to increase with S, but asymptotically; moreover, if we have very small webs, this fraction may first decrease with S, e.g., Fig. 6. The fraction of basal plus intermediate species must be (approximately or exactly, depending on how detached species are counted) the mirror image of this curve, declining over most values of S. Whether b declines faster than i (including the possibility that it decreases so fast that i increases, or vice versa) depends upon the relative input of consumers vs. producers and decomposers, a quantity outside the logic of the above theoretical scheme. When a basal species is attached to a web, b may actually decrease or at least not increase much, weighing against an overall increase of b with S.

In addition to the indeterminate relative input of consumers vs. producers and detritivores, there are other reservations with the above scheme. First, consumers may not choose top vs. intermediate species randomly. Rather smaller species, more likely to be intermediate, may be differentially selected, resulting in the fraction of top species attaining higher values. Alternatively, top species able to eat large prey may only be attracted to sufficiently large webs, countering this trend and perhaps reversing it. This possibility is disfavored indirectly by the weak or absent relation of web height to number of species (see below): were top species differentially converted into intermediate species, webs would build strongly upwards as more consumers are added, giving a strong relation of web height to S. Second, the dimensions indexing food and predator characteristics are themselves finite in range. If this resulted in prey species being more finely packed, i.e., more similar, with S, especially likely at very high S, the generalization constraint C_G might again increase with S (a parallel argument can be made for C_V). If such an increase in C_G is even moderately large, the fraction top species may not increase over much of the range of S (Eq. 2), and the fraction intermediate species may increase substantially with S. Third, arguments about an ever increasing number of predators on particular prey species must be placed in the context of competitive exclusion; some dissimilarity in prey lists will result from ecological and evolutionary responses to competition, and this may limit vulnerability. On the other hand, "apparent competition" (Holt 1977) and competition for "enemy free space" (Jeffries and Lawton 1984), by eliminating prey that are too similar
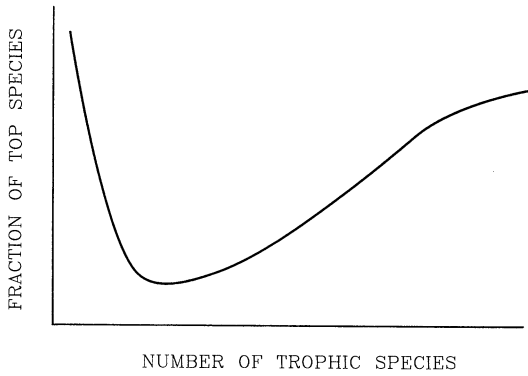
FIG. 6. Hypothetical relation of the fraction top species to the number of trophic species, S.

(Mithen and Lawton 1986) limit generality and provide an argument alternative to functional morphology for C_G to be constant. The second and third reservations, however, need to be considered bearing in mind that it is trophic species, not species, that are actually dealt with in the analyses; this consideration somewhat reduces their force.

Factors external to the above scheme may also favor the decrease of b with increasing S. Menge and Sutherland (1987) argue that as S increases, increasing predation pressure on basal species should cause some of them to go extinct. This is least likely to happen for top species, so t may increase as well.

Assuming that t increases with S and/or b decreases with S, other food-web properties are necessarily dependent on S. The prey/predator ratio can be written

$$(i + b)/(i + t) = (1 - t)/(1 - b). \qquad (3)$$

This will decrease with S, provided t increases or b decreases, or both, with S. For webs at or above the generalization-saturation threshold, the number of links per species can be related to generalization in the formula

$$C_G = \frac{(\text{number of links})/S}{1 - b} \qquad (4)$$
$$= \frac{(\text{number of links})/S}{i + t}.$$

Again, an increase in t or a decrease in b or both with S implies that (number of links)/S will increase. The formula for realized vulnerability, V, is

$$V = \frac{(\text{number of links})/S}{1 - t} \qquad (5)$$
$$= \frac{(\text{number of links})/S}{i + b}.$$

If (number of links)/S increases, t increases and/or b decreases with S, realized vulnerability will increase with S. These properties are now tested as predictions,

with the realization that given the theory they are all dependent, and some are dependent from the definitions alone.

1. *The fraction of basal species should decrease with increasing* S, *or the fraction of top species should (for webs sufficiently large) increase with increasing* S, *or both.*—Pearson r's for the fraction of basal species with S are negative in all cases but marine pelagic and are significantly so in three kinds of systems, terrestrial, marine estuarine, and lentic, as well as in all webs combined, where the value is -0.479 (Table 5).[3] A plot of this relationship for all webs combined is given in Fig. 7 (bottom). The relation seems obviously cur-

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[3] Here and elsewhere, I sometimes report significance values, contrary to recent treatments of Cohen and colleagues (e.g., Briand and Cohen 1987). While I acknowledge the point about observer bias in selection of webs for study, this is no different from many other areas of ecology (e.g., experiments on interactions), for which surveys have been treated statistically (e.g., Schoener 1983, Sih et al. 1985). The reader will have to decide whether the P values are useful or not, subject to the assumption that observer bias is not serious.
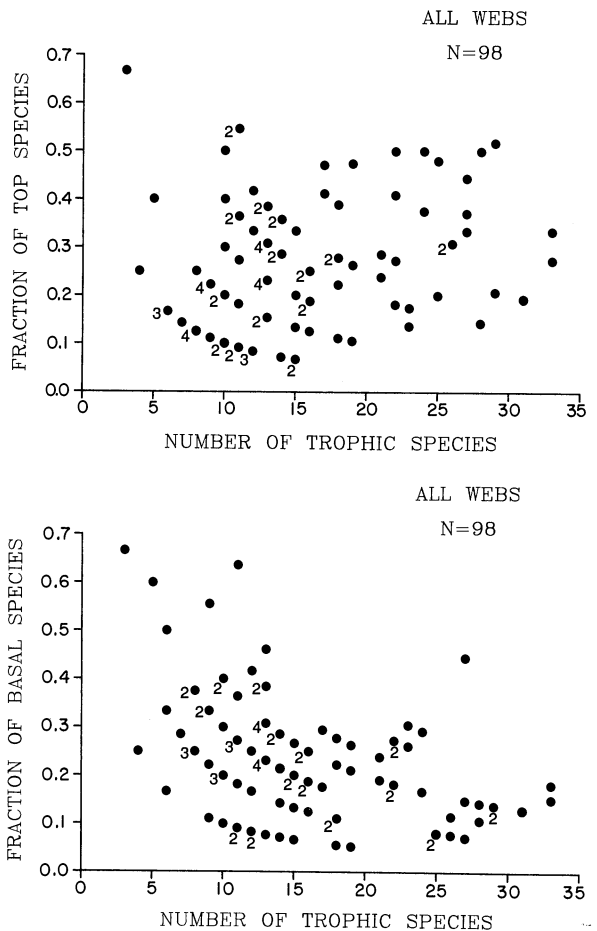

FIG. 7. Fraction top species (top) and fraction basal species (bottom) vs. the number of trophic species, S. Numbers give multiple observations for the same point.
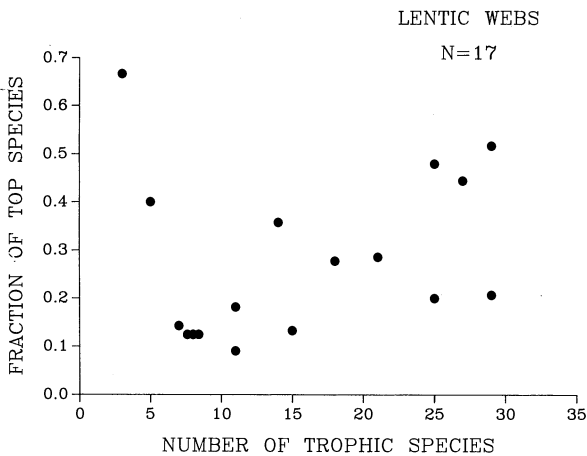
LENTIC WEBS

N=17

FIG. 8. Actual relation of the fraction top species to the number of trophic species, S for lentic webs.

vilinear, so evaluation of Pearson r is to some degree inappropriate, and a stronger measure of decrement could probably be obtained.

The prediction for fraction of top species is rather more difficult to test, as for webs sufficiently small a decreasing rather than increasing relation is expected (Fig. 6). For that system with a large number of webs and some very small ones (i.e., lentic webs) the relation is, by eye, rather close to that hypothesized (Fig. 8). Systems without small webs would be expected to show positive correlations of fraction top species to S, unless many webs were quite large. In fact, five of the seven kinds of systems (all but marine estuarine and lotic), as well as all webs combined (Fig. 7, top), do. However, only lentic webs with the two smallest webs deleted, marine benthic webs, and all webs combined, have significant r's (Table 5). But the two negative r's have the highest probabilities of a difference from zero being due to chance. That for all webs combined is 0.309 (three smallest webs deleted) or 0.206, not as large as the corresponding correlation for fraction of basal species. In short, these correlations for top species, while sometimes statistically significant, must be viewed as weak.

Rather than merely distinguishing top and basal species, it may be biologically interesting to distinguish kinds of such species. The most obvious candidate is basal, which can be broken up mainly into producers and decomposers. This procedure shows that the fraction of producers is the one more negatively correlated with S; all r's are negative, three significantly so, and the overall r is -0.465 ($P < 10^4$). The fraction of nonproducers (mainly decomposers, with a few immigrant species) is negatively correlated with S in only four systems (terrestrial, marine and intermediate estuarine, and lentic), and only significantly so in the last; r for all webs is -0.164 ($P = .108$). Moreover, two marine systems have significant or marginally significant positive r's (marine benthic, $r = 0.455$, $P = .033$;

marine pelagic, $r = 0.615$, $P = .058$). Distinguishing kinds of basal species seems to be very important in these data.

2. *The relation of the number of prey to the number of predators should not be linear but should bend downward with* S, *i.e., the second derivative should be negative.*—To test this prediction, quadratic regression was used to analyze plots of number of prey vs. number of predators. If the sign of the quadratic term is negative, a downward bend supporting the prediction is indicated. The linear term is not itself interesting, because the fact that the number of prey increase with the number of predators is itself expected as a statistical artifact (both variables include the quantity "number of intermediate species," usually the most abundant class of Briand and Cohen's [1984] three). Regression intercepts were forced through zero, because the plot should tend toward the origin as S declines.

Table 5 gives statistics for these regressions; note that significance levels here are of uncertain interpretation, as the variables are not independent. Regressions for five of the seven kinds of systems (all but marine estuarine and lotic), as well as all webs combined, have quadratic terms with negative signs, indicating a downward bend. Regression coefficients of the quadratic term are significantly negative in three of these systems and for all webs combined. The two positive coefficients have the largest probabilities of a difference from zero due to chance. Fig. 9, which has to be stared at rather hard, gives the actual plots for the three most numerous kinds of systems and all webs combined.

I have followed Briand and Cohen (1984) in using number of prey as the dependent variable in these regressions. However, choice of dependent variable is arbitrary, so I redid the regressions with x and y variables reversed. Now five of seven system regressions, as well as that for all webs combined, have positive quadratic terms, consistent with the prediction (almost but not the same five as above; Table 5). However, only one coefficient (a positive one) is significantly different from zero. Thus, results from reversal of the variables puts something of a damper on confirmation of prediction 2, although qualitatively things are mostly consistent.

Briand and Cohen (1984) noted the tendencies reported in this and the last section but described them as "slight." They do appear from the plots to be stronger in my version of the food-web data set, but I do not have comparative statistics. Recently, K. Schoenly et al. (*unpublished manuscript*) analyzed 61 "insect-dominated" food webs and found about the same r as here for fraction basal species vs. S (0.44), but a smaller r for fraction top species vs. S (0.06); as many of these webs (47) do not include vertebrate–invertebrate links (K. Schoenly, *personal communication*), comparability with the present results is obscure and somewhat suspect. Any claim about constancy or slope, of course,
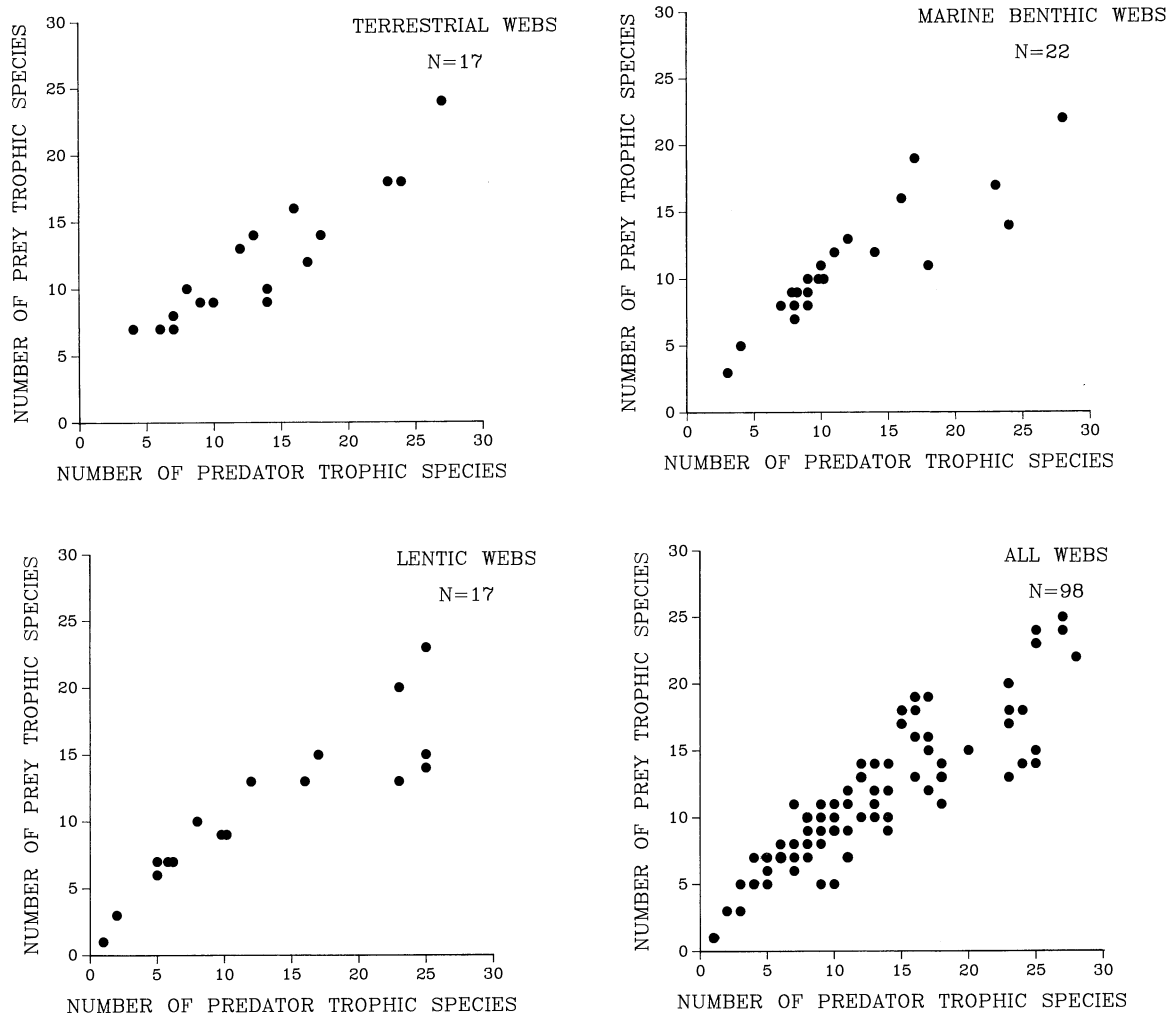
Fig. 9. Plots of number of prey vs. number of predators for terrestrial, marine benthic, lentic, and all webs combined.

must be viewed with the realization that all plots have considerable scatter.

3. *The total number of links in a web should increase more rapidly than* S, *rather than being directly proportional to the latter.* — To test this prediction, I first followed Cohen and Briand's (1984) method of plotting the number of links, L, and the number of links to the ¾ power, $L^{3/4}$, against S. Cohen and Briand found for their data that the former plot seemed tighter by eye. For the seven kinds of systems and all webs combined, I drew the opposite conclusion overall. Pearson r's are higher for the $L^{3/4}$ plot for all but intermediate estuaries (they are tied for lotic systems). Differences are very small (Table 5), but this is to be expected given the very strong correlation between L or $L^{3/4}$ and S to begin with. Another way to get at the issue is to determine by regression what power of L (or S) best fits each plot. This method is better done by nonlinear regression, but as there is no guarantee that a power function is the most appropriate for the data anyway, I took the

more casual approach of regressing $\log(L)$ against $\log(S)$ (the slope of this regression would provide a starting value for a nonlinear search). In all cases, the slope is substantially greater than one (Table 5), and for all webs combined it is 1.463. Using the same method, Cohen et al. (1986) calculate a somewhat smaller slope of 1.360 for their data. Our analysis indicates that the number of links in a food web increases roughly as the 1.5 power of S, or the links per species increase as the square root of S. Inversely, $L^{2/3}$ should be proportional to S, and indeed in five kinds of systems and all webs combined, r for this regression is as high (occurring once) or higher than for either L or $L^{3/4}$. Whether our square-root relationship is substantively different from linearity awaits evaluation of the biological implications, but it is certainly conceivably so: over the range of 4–36 species, for example, number of links per species varies threefold.

4. *Generalization should be unrelated to* S, *while vulnerability should be positively related to* S. — Generali-

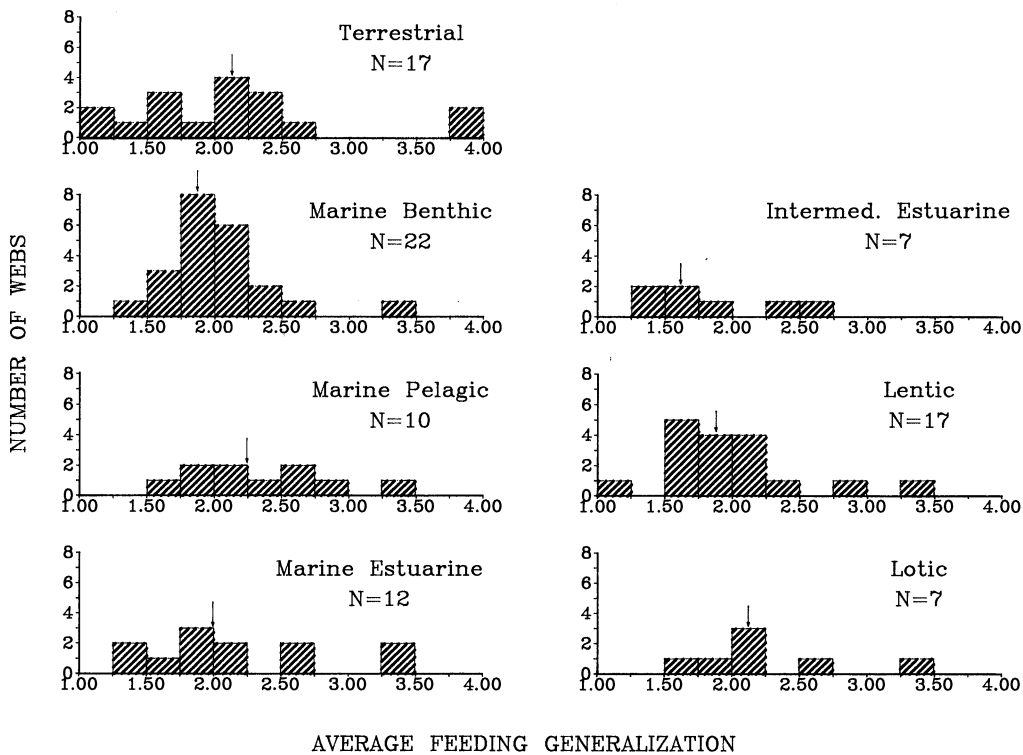AVERAGE FEEDING GENERALIZATION

FIG. 10. Distribution of web feeding generalization (mean no. prey per predator) by system. Vertical arrow denotes median generalization class.

zation and vulnerability were calculated separately for each of the 98 webs described above. Distributions of these quantities for the various kinds of systems show a fair amount of between-system similarity for generalization (Fig. 10), but a fair amount of between-system dissimilarity for vulnerability (Fig. 11).

Median generalization falls near 2 for all systems but intermediate estuarine and lentic, where values are between 1.5 and 1.75 (Table 4). A one-way ANOVA finds no significant overall heterogeneity ($P = .452$), and the extreme means (2.34 for marine pelagic vs. 1.75 for intermediate estuarine) are rather similar. Vulnerability has its highest system values for the marine pelagic and its lowest values for the intermediate estuarine; medians are 2.75–3.0 and 1.25–1.5, respectively. In contrast to generalization, the extreme means of vulnerability, 2.75 for marine pelagic and 1.57 for intermediate estuarine, are significantly different ($P < .05$) by a Tukey family test for a posteriori comparisons. Overall heterogeneity is marginally significant ($P = .0999$). In all systems, standard deviations for generalization distributions were lower than those for vulnerability distributions.

Because of some apparent system differences, the relation of generalization and vulnerability to S was tested separately for each system (Table 5). In five of seven systems (all but marine pelagic and lotic), and for all webs combined, web vulnerability was significantly positively correlated with S. In two of seven

systems and in all webs combined, web generalization was significantly positively correlated with S. In seven of eight cases (all but lotic), while Pearson r's were always positive, those for vulnerability exceeded those for generalization, often being about double. Hence the prediction is rather strongly supported, with the proviso that generalization may be weakly related to S, perhaps because of the lack of feeding constraints for sufficiently small webs (see above: note that this weak increase of generalization with S may account for the only weak support found for the prediction that fraction top species increases with S). Fig. 12 gives plots of generalization and vulnerability for terrestrial, marine benthic, and lentic webs, the three types of systems with the most webs.

Finally, if the fraction of top species is constrained to lie below an asymptote inversely related to C_G, we might expect the former to be inversely related to web generalization (other less deterministic arguments could also lead to this expectation). In fact, r's are negative for all system kinds, although only that for all webs combined (-0.330) is statistically significant ($P < .001$); values range from -0.064 to -0.659. Also from the constraint (Eq. 2), we would expect the fraction of top species seldom to exceed 0.5, as C_G should at a minimum equal one. In fact, individual values of this fraction exceed 0.5 in 4 of 98 cases (Fig. 7).

This ends treatment of the four predictions. Other predictions could be made with more specific assump-
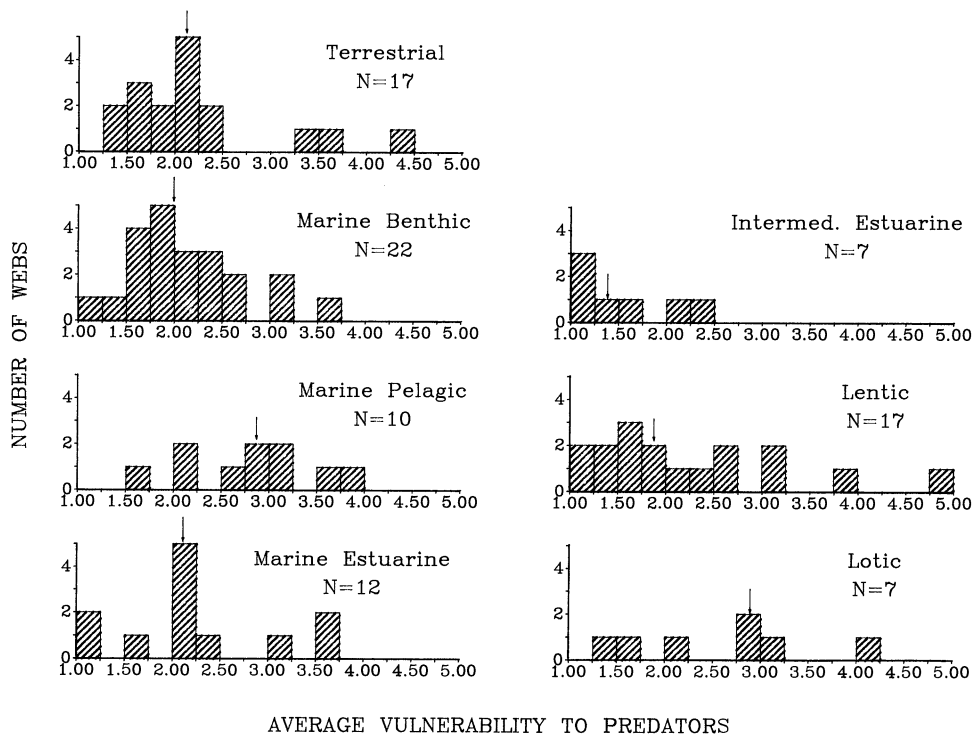
AVERAGE VULNERABILITY TO PREDATORS

FIG. 11. Distribution of web vulnerability to predators (mean no. predators per prey) by system. Vertical arrow denotes median vulnerability class.

tions, for example those dealing with maximum chain length. In an innovative, largely analytical set of papers, Cohen, Newman, and Briand used a "cascade" model to derive predictions about food-web properties such as maximum chain length (Cohen and Newman 1985, Cohen et al. 1985, Cohen et al. 1986, Newman and Cohen 1986). The cascade model assumes "upper triangularity," i.e., food-web species can be arranged

TABLE 4. Statistical properties of food webs, by kind of system.

		System							
		Terrestrial	Marine benthic	Marine pelagic	Marine estuarine	Intermediate estuarine	Lentic	Lotic	Total
1. Vulnerability vs. S	r^*	.678	.744	.366	.766	.817	.873	.337	.614
	P	.003	$<10^{-4}$	.30	.004	.025	$<10^{-4}$	.46	$<10^{-4}$
2. Generalization vs. S	r^*	.303	.364	.307	.633	.193	.625	.625	.391
	P	.24	.10	.39	.03	.68	.007	.13	$<10^{-4}$
3. Quadratic term of no. prey on no. predators	sign	−	−	−	+	−	−	+	−
	$P\dagger$	.11	$<10^{-2}$	.53	.95	.01	$<10^{-2}$	.68	$<10^{-2}$
4. Quadratic term of no. predators on no. prey	sign	+	+	−	+	+	+	−	+
	$P\dagger$	.44	.26	.33	.98	.07	.94	.14	.67
5. Fraction top spp. vs. S	r^*	.328	.632	.146	−.080	.479	.728[a]	−.278	.206[b]
	P	.20	.002	.63	.81	.28	.002	.57	.04
6. Fraction basal spp. vs. S	r^*	−.506	−.385	.036	−.755	−.691	−.753	−.161	−.479
	P	.04	.08	.92	.005	.086	$<10^{-3}$	.73	$<10^{-4}$
7. No. links vs. S	r^*	.835	.939	.846	.935	.910	.907	.821	.859
(no. links)$^{3/4}$ vs. S	r^*	.853	.944	.854	.941	.897	.935	.821	.878
(no. links)$^{2/3}$ vs. S	r^*	.858	.944	.855	.942	.893	.941	.820	.882
log-log slope		1.377	1.254	1.284	1.672	1.542	1.648	1.788	1.463
8. Cohen's maximum chain length vs. S	r^*	.134	.143	.196	.815	.168	.410	.318	.253
	P	.61	.53	.59	.001	.72	.10	.49	.01

* r = Pearson correlation coefficient; P values $<10^{-3}$ may be smaller.
[a] = two smallest webs excluded. Values for all lentic webs: $r = .210$, $P = .42$.
[b] = three smallest webs ($S \le 5$) included. Values for three smallest webs excluded: $r = .309$, $P = .002$.
† P is two-tailed; for one-tailed hypotheses, it should be halved.

TABLE 5. Summary of system differences (median category).

Category	System						
	Terrestrial	Marine benthic	Marine pelagic	Marine estuarine	Intermediate estuarine	Lentic	Lotic
No. trophic species, S	15–20	10–15	10–15	10–15	10–15	10–15	10–15
Cohen's maximum chain length (no. links)	4	4	5	3	4	4	3
Mean chain distance (no. links)	2.2–2.4	2.2	1.8	2.2–2.4	2.4–2.6	2–2.2	1.8–2
Generalization ($\bar{X}$ no. prey per predator)	2–2.25	1.75–2	2.25	2	1.5–1.75	1.5–1.75	2–2.25
Vulnerability ($\bar{X}$ no. predators per prey)	2–2.25	2.0	2.75–3.0	2–2.25	1.25–1.5	1.75–2	2.75–3.0
Fraction of top species	0.3–0.4	0.2–0.3	0.2	0.3–0.4	0.2–0.3	0.2–0.3	0.4–0.5

into a hierarchy such that any species can eat only species below it in the hierarchy (if any); all species do so with the same probability, that being derived from the mean number of links per species, the latter of which is "given" and calculated from actual data. This model gives S-independence, i.e., no relation of the fractions of basal or top species, or of the predator/prey ratio, to S; this is contrary to our predictions and data analysis above (but so is the assumption of a constant number of links per species). The cascade model also predicts that food-chain length will increase only weakly with S. In fact, it is an intriguing property of food webs that the various system kinds typically show rather weak correlations between Cohen's maximum chain length and S (Table 5): r's range from 0.134 to 0.410 for all system kinds but marine estuarine, where r is very high, 0.815. This is despite the fact that all systems are very similar in distributions of S (Fig. 13 and Table 4). Marine estuarine systems have unusually small maximum chain lengths (Fig. 5), as do lotic webs, where r is much smaller than 0.815 but still one of the larger values.

Speculating without mathematics, a model consistent with S-dependent food webs might produce at least as weak a relation of maximum chain length to S as the cascade model. A scheme assuming rather unlimited vulnerabilities, as the one we presented, would allow new top species to enter at any level; webs with more limited vulnerabilities should more often have species "pile up" on top of one another, as vulnerabilities for lower levels become saturated. Especially for the former case, the shorter the web, the more likely a new species will enter at the top (all other things being equal), giving a stronger relation of maximum chain length to S for shorter webs. It is perhaps interesting in this regard that the typically short marine estuarine webs have the only strong correlation between maximum chain length and S; along with lotic webs, marine estuarine webs fit predictions 1, 2, and 4 collectively least well, predictions derived for an S-dependent system.

A final complication is that while we have made arguments about web generalization and web vulnerability, we have not specified how these web means are related to generalizations and vulnerabilities of individual trophic species. One possibility is that there is little variation, or at least little systematic variation, in these individual quantities. However, when we consider that the higher a species is in a web the more prey it potentially can eat, and the lower it is the more predators it potentially has, such individual-species constancy would be unexpected from a purely statistical point of view.

A simple test of whether generalization increases as a species is higher in a web, and whether vulnerability increases as a species is lower, is as follows. For testing generalization, divide the predator species of a web into three groups: top species, species one link away from top species, and all others. Calculate average generalization for each of these three groups. Then note in what fraction of webs average generalization is greater, the higher the group. For testing vulnerability, divide prey species into the three groups: basal species, species one link away from basal species, and all others. Calculate average vulnerability for each of these three groups. Then note in what fraction of webs average vulnerability is greater, the lower the group. Note that this method is well defined and avoids having to designate the level of each species, a not-so-well-defined task.

If one considers only webs having representatives in each of the above-defined three groups, the majority of webs in four systems are consistent with the hypothesis for each of vulnerability and generalization; figures go as high as 15 of 17 webs consistent (generalization for marine benthic). (Since entries in the three web categories are complexly dependent, I did not evaluate such figures statistically.) Marine pelagic and marine estuarine webs are the most conspicuous exceptions; these webs are very tall (have long chains), or very short, respectively, giving many or few species in the third category, respectively. Results using only those two levels closest to the web edge are similar but less striking.
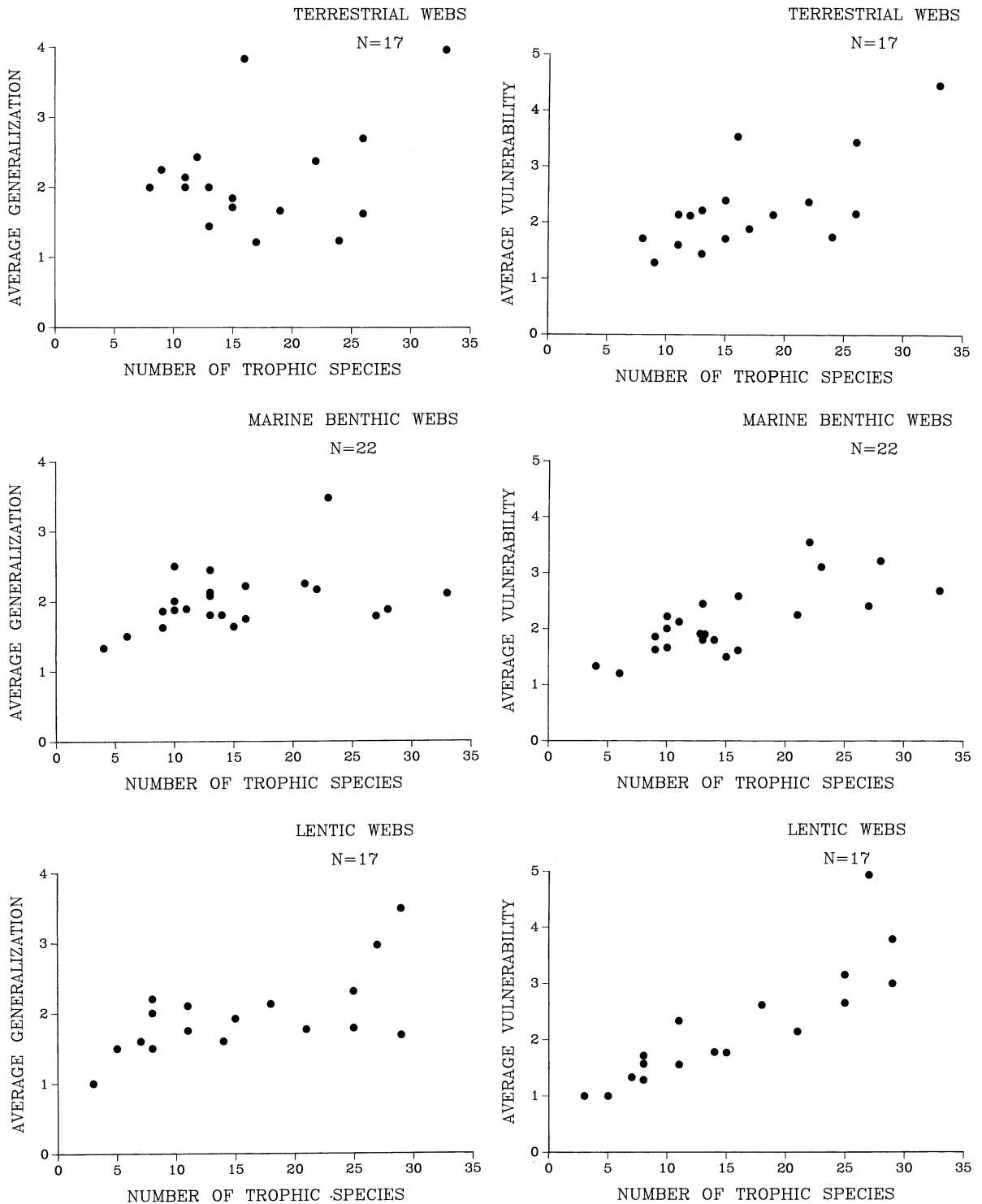
FIG. 12. Plots of web generalization (left column) and web vulnerability (right column) for terrestial, marine benthic, and lentic webs.

To examine if the tendency to conform to the hypotheses above is related to web size, I ranked conforming and nonconforming webs by S and performed Mann-Whitney U tests. Although all but 2 of 12 possible rankings associated a tendency to fit the hypothesis with a large S, only rankings for vulnerability in terrestrial webs and generalization in marine benthic webs, both consistent with the hypothesis, are statistically significant at the .05 level. So here at least is a case where S-independence is typically not falsified.
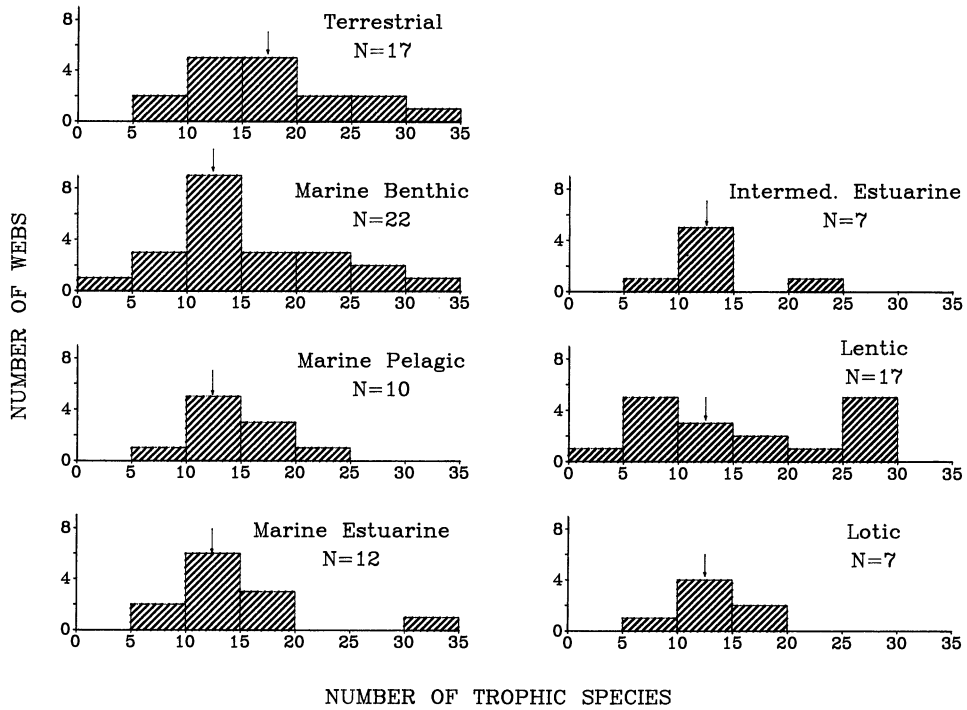
FIG. 13. Distribution of *S,* number of trophic species, by system. Vertical arrow denotes median web-size class.

Within-web variation in generality and vulnerability must be reconciled with arguments made above for individual constraints on numbers of prey species eaten and number of predator species defended against. This is not so much a problem for vulnerability, as it is assumed open-ended for appropriately large webs. However, generalization needs further rationalization. First, intraweb means for the three groups can be quite
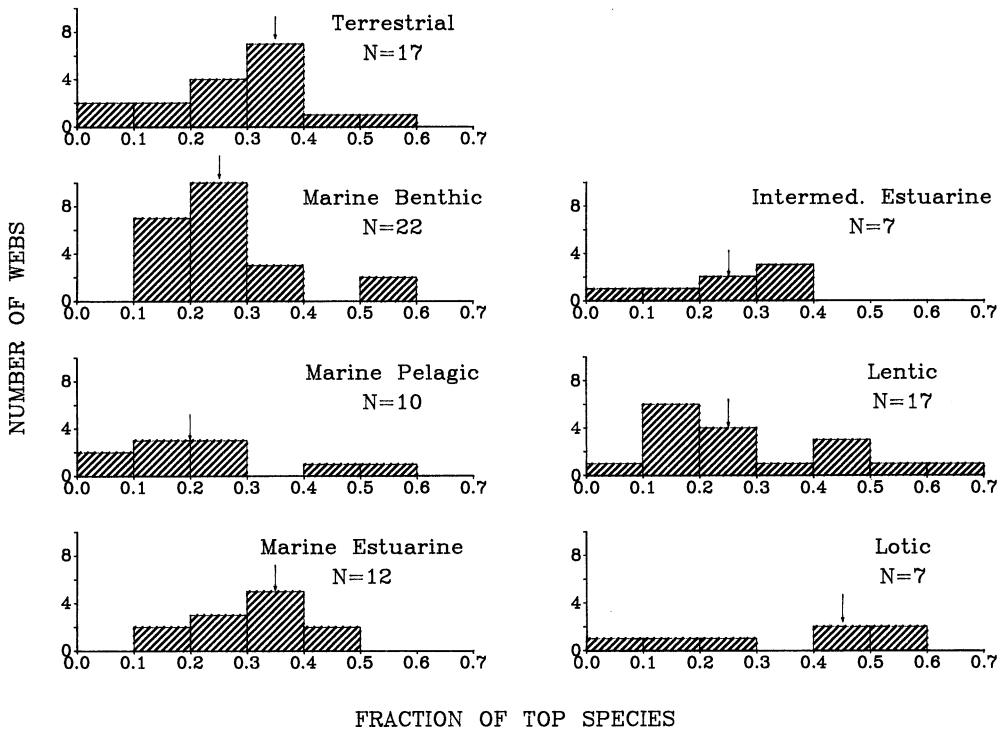

FIG. 14. Distribution of fraction top species by system. Vertical arrow denotes median fraction category.

similar despite being ranked consistently. Second, constraints may be different for different kinds of species (top vs. bottom). An especially likely such difference is with respect to prey size: larger predators, closer to the top of webs, eat a greater range of prey sizes (Wilson 1975). If the fractions of various types of predators with respect to feeding constraints are similar for webs of various sizes, the average web generalization will not vary with S. The fact that the fraction of top species increases with S would seem to disfavor this argument, all other things being equal, although "top" is not defined with respect to feeding constraints or body size. A third possibility is that species in a web are differentially saturated with respect to the kinds of species they can consume; lower species would be less saturated than upper ones, perhaps because their potential variety of prey is less. Then as S increases, lower predators come closer to saturation as their proportional representation declines (assuming it does), so that web generalization stays constant. While tending to alleviate the problem created by the fraction of top species increasing with S, this tendency creates problems of its own if too strong. The best one can say now is that within-web variation in generalization and vulnerability is not such as to foil predictions given here about S-dependence.

SIMILARITIES AND DIFFERENCES IN FOOD-WEB PROPERTIES BETWEEN KINDS OF SYSTEMS

The various kinds of systems show both surprising similarities and substantial differences in food-web properties. This section collects such information from previous sections and reports additional results. Those for lotic and intermediate estuarine systems are especially tentative, as only seven webs are available for each.

1. *Web size (S)*.—Distributions of the number of trophic species are remarkably similar between kinds of systems (Fig. 14), despite major differences in other food-web properties. Medians are nearly all between 10 and 15 species (Table 4).

2. *Web height (maximum chain length)*.—Cohen's maximum chain length is greatest in marine pelagic systems (median 5 links) and least in marine estuarine and lotic systems (median 3 links); all other systems have medians of 4 links. Cohen's mean chain length is very highly correlated with this property (see section above, Food-chain Lengths) so will be distributed similarly. These data support Wiegert and Owen's (1971) earlier observation that planktonic systems have more levels than terrestrial ones.

3. *Loose-knitness (mean minimum chain distance)*.—The web mean loose-knitness, calculated as the mean of the minimum distances (in units of links) between all pairs of species in a web which are connected directly or indirectly, is least in marine pelagic and greatest in intermediate estuarine systems (median

categories 1.8 and 2.4–2.6 links, respectively; Table 4). Both overall heterogeneity and difference between the extreme systems are marginally significant ($P = .076$ and $P < .10$ by one-way ANOVA and Tukey comparison). These figures include webs with isolated units of more than one species; such webs might be expected to have misleadingly small values, because pairs that cannot be connected have to be deleted from the average, yet these are "especially" isolated. In fact, 9 of 13 such webs are more loosely knit than their system mean, so their exclusion would underestimate isolation overall. Loose-knitness should be related to S; the greater S, the greater a given species' average distance to other species. In fact, system correlations are typically large but not overwhelming (r's range from 0.054 to 0.773; median $r = 0.547$; r for all webs combined is 0.578). These r's are unrelated to the fraction of webs with isolated units of more than one species and suggest that a normalized loose-knitness would be an interesting food-web property as well. If species were all arranged in a linear chain, expected loose-knitness would be proportional to S, so S might be a suitable normalization term, although a weaker function of S might also be desirable. In contrast, loose-knitness is only weakly correlated with chain length (overall $r = -0.076$). Mean upward reach (the number of species encountered in all possible strictly upward paths to all possible top species), however, is rather strongly positively correlated with Cohen's mean chain length (system r's 0.358–0.831; r for all webs combined is 0.633). These figures suggest that loose-knitness and upward reach are food-web properties with empirical variation going beyond necessary statistical dependencies, although much research remains to be done here.

4. *Generalization*.—The mean number of prey per predator is relatively constant (Fig. 10, Table 4); it is somewhat less in intermediate estuarine and lentic systems than in others, and it is especially similar in marine benthic and terrestrial systems (means 2.00 and 2.14, respectively). This was unexpected to me in view of the argument on the relative dominance of phytophagous specialists in terrestrial systems given above. It provides indirect support for an MS-like argument applied to terrestrial systems, although polyphagy may still be less likely to traverse several levels there than in marine webs.

5. *Vulnerability*.—The mean number of predators per prey varies between system kinds more than generalization (Fig. 11, Table 4). High values are from marine pelagic and lotic systems (median category 2.75–3.0); low values are from intermediate estuaries (median category 1.25–1.5). Generalization and vulnerability tend to be positively correlated (system r's 0.437–0.874; r for all webs combined is 0.718), as would be expected, given that their numerators are identical (Eqs. 4, 5).

6. *Fraction top species*.—The fraction top species (Fig. 14, Table 4) is lowest for marine pelagic webs

TABLE 6.   Trophic species consuming substantial amounts of nonliving organic matter (=detritivores).

	Terres-trial	Marine benthic	Marine pelagic	Marine estuarine	Inter-mediate estuarine	Lentic	Lotic
Fraction webs having 0–9% detritivores	0.41	0.09	0.90	0	0	0.12	0
Fraction webs having 0–19% detritivores	0.82	0.36	0.90	0.08	0	0.18	0.29
Median percent detritivores	10	23	0	37	33	25	30

(median category 0.2) and highest for lotic webs (median category 0.4–0.5). Marine estuarine and terrestrial systems have somewhat greater values (median category 0.3–0.4) than marine benthic, intermediate estuarine and lentic systems (median category 0.2–0.3). But these differences are slight compared to within-system variability, and overall heterogeneity is not significant ($P = .605$). This might be expected in view of the theoretical ceiling on t (Eq. 2).

7. *Fraction basal species.*—The fraction basal species (species having no trophic species as prey) is highest for estuarine (means = 0.34 and 0.29) and lotic (mean = 0.25) webs and lowest for marine pelagic webs (mean = 0.12). The latter, which are tall, have mostly intermediate species, whereas estuarine and lotic webs, which are short, have few intermediate species. Overall heterogeneity is quite significant ($P = .012$), and four pairwise comparisons are significant at $\alpha = .05$ using a posteriori tests. While all systems have a negative relation of fraction producers to S, marine pelagic and benthic systems have rather strongly positive relations for the fraction decomposers to S, and the former relation is more negative for all system kinds but lentic and intermediate estuarine.

8. *Fraction detritivores.*—Huge differences exist between systems in the fraction of species that are wholly or partly detritivores (Table 6). Marine pelagic and terrestrial systems have a much smaller prevalence of detritivores (medians 0 and 0.10, respectively) than do the other systems (medians 0.23–0.37). The figure is perhaps not surprising for marine pelagic webs, in which certain nonliving organic matter can quickly drop out of the system, but it is rather surprising for terrestrial systems. Partly the latter must be an artifact of investigator observation: 2 of 17 terrestrial webs list no detritivores. On the other hand, major differences in trophic types exist between terrestrial and nonpelagic aquatic systems. Many aquatic carnivores and herbivores are also detritivores. A striking example are filter-feeders in marine benthic systems (e.g., Menge and Sutherland 1976). Even species in marine pelagic systems may consume substantial amounts of nonliving organic matter in the form of DOM (dissolved organic matter; Stephens 1975, Kurihara and Kikkawa 1986). This is a trophic role not included in most food webs.

9. *Relation of major food-web properties to number of trophic species.*—Systems vary in the degree to which their food-web properties are related to S. To some extent, the same systems conform or do not conform to the four predictions of the last section. Three systems, terrestrial, marine benthic, and lentic, always conform. One system, lotic, is always exceptional except for the prediction about fraction basal species. Marine pelagic webs do not have significant vulnerability or fraction-top-species correlations with S. Marine estuarine webs do not fit predictions about fraction top species and predator–prey ratios. Intermediate estuarine webs are ambiguous for the relation of number of links to S. As cautioned, these results may reflect sample sizes: the three most conforming kinds of systems have the largest sample sizes, and the least conforming is tied for the smallest. On the other hand, genuine differences between kinds of food webs may exist, so that eventually it may be possible to characterize S-independent food webs and S-dependent food webs. As things stand now, only lotic webs seem in the first category, and terrestrial, marine benthic, and lentic webs seem in the second.

In conclusion, with the warning that ecologists might study food webs differently, system kinds appear to be both very similar to and very different from one another in major food-web properties. Terrestrial and certain aquatic systems, marine benthic and lentic, can be more similar to one another in many food-web properties than can certain other aquatic systems, for example, those just listed vs. marine pelagic. In particular, terrestrial and marine benthic webs are similar in generalization, vulnerability, fraction of top and basal species, loose-knitness, and maximum chain length. This suggests that the extensive experimentation used to analyze marine benthic webs may provide more of a model for the sparsely manipulated terrestrial webs than might have been thought. The major difference between terrestrial and most aquatic webs found here is the prevalence of detritivores in the latter, the theoretical consequences of which have yet to be explored. Both terrestrial and marine benthic webs, as well as lentic webs, tend to be intermediate in magnitudes of web properties, including maximum chain length. Marine pelagic webs are tall, so have small fractions of both top and basal species; they also have strong correlations between loose-knitness and S but weak ones between upward reach and mean chain length. Marine estuarine and lotic systems, and to a lesser extent intermediate estuarine systems, are short and sprawling, so have high fractions of both top and basal species; they also have weak correlations between loose-knitness and S and strong ones between upward reach and

mean chain length. These facts suggest that kinds of aquatic webs may differ substantially enough to merit their distinction in food-web analyses.

CONCLUSION: LINKS BETWEEN CONCEPTUAL LEVELS OF TROPHIC ECOLOGY

We can identify three major levels of organization at which it is reasonable to conceptualize trophic ecology (Schoener 1986b). The individual level, behavioral, physiological, and morphological, is concerned with optimal food selection (reviews in Stephens and Krebs 1986, Schoener 1987) and predator avoidance (e.g., Jeffries and Lawton 1984), as well as structural constraints on ways to eat prey and avoid predators (e.g., Wainwright 1988). The population level is concerned with the existence and types of population equilibria, as well as the trajectories of change in population numbers, all as a function of the food-resource and predator regimes. The community level deals with relatively large collections of species populations; guild and related concepts are at the lower end of this approach, while food-web ecology lies near its upper end.

The three approaches have been integrated to some degree, but they could be more integrated.

Concepts at the individual level have been used to justify the proposition that predators should have a constant number of prey (Pimm 1982), but the corresponding proposition for number of predators that a prey can defend against seems to have been missed, an omission that may have predilected an S-independent rather than S-dependent view of food webs.

Arguments about constraints on feeding generalization and predator defense are easy to justify from individual-level ecology, but models incorporating such arguments will not necessarily give stable food webs. The obvious way to examine stability is with dynamical equations, the major theoretical tool at the population level. A large literature has developed on what kinds of food webs have stable dynamics (review in Pimm 1982). This approach has produced some interesting results, for example that feeding on more than one trophic level is destabilizing (Pimm and Lawton 1978), a prediction mirrored by our result that lizards have major deleterious effects on spiders (Fig. 3, left). The dynamical theory is now viewed more cautiously by one of its principal perpetrators (Lawton 1989), as somewhat less elaborate explanations seem often to explain more completely the range of food-web phenomena. I am most sensitive to failure of the population-dynamical approach to link individual-level concepts to food-web patterns; rather it seems to start mostly from scratch, hooking up equations to correspond to various food-web structures but often allowing the individual biology to be chosen "randomly." This criticism is oversimplified, but a more reductionist approach would probably lessen differences between the two levels of explanations. An existing example of such an approach is Mithen and Lawton's (1986) use

of dynamical equations to show how prey similarity predilects prey extinction. A second sort of example, this one nonexistent but probably fairly obvious in its outcome, would explicitly specify parameters for production and available space, then examine effects on equation stability (this has been explicitly done, retrospectively, for feasibility; see above).

The community-level approach of Cohen, Briand, and Newman again seems largely to begin from scratch, rather than to draw on lower level concepts. Cohen's (1978) early discovery that most food webs corresponded to interval graphs has the interpretation that a single niche dimension is adequate to describe most trophic partitioning. Niche is a community concept. The more recent, "stochastic" models of Cohen et al. are meant to be as spare as possible with respect to biological assumptions (e.g., Cohen et al. 1985: 433); the minimally successful model, the "cascade model," assumes only upper triangularity and uniform predator–prey probabilities. As Warren and Lawton (1987) pointed out, such an assumption does have a lower level explanation in terms of body size of consumers, individuals being able to eat prey primarily smaller than themselves. However, the cascade model's assumption that all species but one have some finite probability of consuming another trophic species in the web is clearly nonbiological, because nonallochthonous basal species (producers, detritivores [webs herein] or nonliving categories [BC webs]) cannot obtain energy this way. It may be that more lower level theory is needed in the minimally satisfactory model. This theory could include models specifying rather than deriving the number of basal species, models with constraints on number of prey types that can be eaten and predators that can be defended against, models sensitive to the inability of carnivores to eat certain types of plant food (e.g., leaves), and models examining the feasibility of high prey vulnerabilities in terms of competitive exclusion.

Were the various theoretical levels more unified, explanations of food-web properties that are now viewed as alternatives might then be viewed as components of the same general theory. For example, I have argued above that the idea of Elton and Hutchinson on what limits the number of levels in food chains is based on individual- and population-level concepts, and provides the mechanism for a community- or ecosystem-level restatement of the hypothesis, e.g., certain versions of the "productivity" hypothesis.

Reductionist approaches may also help alleviate what is seen by some (e.g., Paine 1988) as a major obstacle to food-web understanding, and that is methodological difficulties with web description. Paine (1988) points out, for example, that five studies of the same system, exposed rocky shores of Pacific North America, produced rather different webs.

I see as probably the major problem with web description the decision to draw a link or not. Many

species have broad ranges of prey types included in their diet but concentrate on only a few. At what percent occurrence should a prey no longer be counted as such? This sort of question needs to be answered if precise comparisons are to be made between the degree of omnivory in terrestrial vs. marine systems, for example. Moreover, and more fundamentally, do we want to base links on dietary percentages per se? In the hypothetical alternative terrestrial food webs discusssed above (Fig. 3), arrow thickness (and by implication presence or absence) was determined not by actual consumption, which is influenced by population size, but by what boils down to the potential effect of one element on a second independently of the other elements. Obviously, such arrows can only be vetted by experiments (see also Paine 1980) or by extensive comparative observations, both hard to come by and unlikely to be obtained for most food webs in even the far future, however desirable. Still more, arrows can be drawn in two directions: do we wish to base presence and thickness of a link on percent diet of predators or percent depredation of prey or both? In some cases the latter is less feasible; direct observation of predation is often difficult to impossible, and prey depredation is usually calculated indirectly from predator diet anyway. Or should per capita effects be used, and if so, those of predators on prey or the reverse? While probably often correlated, arrow thickness need not be identical in the two directions (see also Pimm and Lawton 1977). Possibly several types of food webs should be distinguished (again see Paine 1980), some describing actual flows, others describing potential flows (e.g., per-capita effects), and some in the upward and others in the downward direction.

Another methodological difficulty is lumping vs. splitting as a function of level of biological organization and (by implication) level of a food web. Pimm (1982) argues that species at upper levels, often vertebrates, are probably more finely distinguished by investigators than those at lower levels, often invertebrates. While I agree, it is not always so; Carlson's (1968) original web for part of the Mississippi River, for example, distinguishes only 4 vertebrate "species" as opposed to 15 invertebrate ones. As Cohen and Briand (1984) point out, use of "trophic species" rather than investigator-distinguished species must alleviate the problem to some extent. In this regard, it is interesting to note that plots of log (trophic species) vs. log (investigator-distinguished species) have positive slopes less than one: they range from 0.348 (terrestrial) to 0.850 (lotic), and the slope is 0.681 for all webs combined. Thus lumping by trophic species reduces some of the variability in web size, or putting it another way, webs would be more different from one another in number of species were investigator-distinguished rather than trophic species used. Correlations of these plots, incidently, are quite high; the median r is 0.885.

Although emphasizing a lower-to-upper level theo-

retical flow, in which lower level concepts are used to build upper level ones, flow in the other direction will certainly exist as well. For example, features of the distribution of generalization and vulnerability within extant webs can structure model webs such as those Jager and Gardiner (1988) used to validate the verbal theory of HSS. Magnitudes of quantities, such as generalization, that differ between systems, can also be related to hypotheses about the prevalence of interactions in food webs (see previous section, Similarities and Differences in Food-web Properties Between Kinds of Systems).

In conclusion, we began with a discussion of how a particular, simple terrestrial food web, that on subtropical Bahamian islands, might work. Hypotheses concerning the prevalence of competition vs. predation at various levels were of special interest. This simple web was found to be not necessarily typical of terrestrial webs as a whole; it contained only four of the seven major elements in published terrestrial webs, and predictions could easily be overturned with more complex webs. Variation in food-chain length between webs was investigated, and a somewhat mutated hypothesis, the "productive space" hypothesis, was derived in part inductively from the Bahamian system, in part from considerations of minimal individual and population area (or volume) requirements. S-independence (non-relatedness to number of trophic species) of food webs was suggested to be unlikely in principle and found generally not to occur in practice, although kinds of webs may vary in this regard. The various system kinds (terrestrial, marine benthic, and so on) showed some striking similarities, e.g., in number of species, but also showed major differences, e.g., in food-chain lengths, suggesting that system distinction may be desirable when testing food-web hypotheses. New food-web properties, e.g., loose-knitness and upward reach, were sometimes found useful in such comparisons. Integration of theory at various levels is most desirable. Agreement on the conventions of web description is needed as soon as possible; perhaps a convocation of ecologists should be assembled. There is a great deal of work to be done in this central, fundamental area of ecology.

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APPENDIX

Webs used in this study. Numbers without letters refer to webs in Briand and Cohen (1987).* Numbers with letters refer to webs not considered by Briand and Cohen (1987) but in papers having one or more webs used by Briand and Cohen. For example, for web 86a see the paper having web 86 in Briand and Cohen (1987).

1. Terrestrial: 4, 23, 24, 25, 27, 28, 40, 59, 60, 61, 62, 91, 92, 94, 95, 98, 100.
2. Marine Benthic: 9, 10, 11, 12, 13, 17, 37, 43, 48, 49, 50, 52, 53, 53a (Birkeland 1974 web, p. 675), 86a (bottom fishes, Sendai Bay, p. 81), 104, 105, 106, 107, 108a, 108b (did not know which web on pp. 196–7 was used by Briand and Cohen), 109.
3. Marine Pelagic: 20, 21, 29, 30, 41, 41a (subarctic waters, Fig. 49), 41b (antarctic waters, Fig. 49), 81, 86, 87.
4. Marine Estuarine: 6, 7, 10, 51, 55, 56, 70, 110, 111, 112, 113, 113a (bottom web, Fig. 17).
5. Intermediate Estuarine: 2, 3, 5, 8, 14, 15, 57.
6. Lentic: 19, 33, 38, 39, 68, 73, 75, 76, 77, 78, 79, 80, 82, 82a (Cuvette Ia, Fig. 4), 84, 94a (Ikroavik Lake, p. 213), 101.
7. Lotic: 35, 45, 64, 65, 66, 67, 71.
8. Mixed: 22, 44, 47, 58, 74, 85.

* Webs 54, 69, 72, and 83 were unavailable.