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CONSTRUCTION AND ANALYSIS OF A LARGE CARIBBEAN FOOD WEB¹

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Abstract. We document the construction of a relatively large food web (44 species) from the island of St. Martin in the northern Lesser Antilles, and compare it with patterns observed in other, generally smaller food webs. In constructing this web, we integrate data from a variety of studies, many of which focussed on *Anolis* lizards and their vertebrate predators. In addition to determining the links between predators and prey, we estimate the frequencies of predation (the link strengths), and find an approximately bell-shaped distribution with a majority of links of intermediate frequencies. Some of the properties of this web contrast strongly with those of webs in the ECOWeB compilation. In particular, our analysis shows this web to possess an unusual richness of intermediate species (relative to top predators or basal species) and of links between those intermediate species. The number and lengths of chains are also unusually high, as is the degree of omnivory. Nor does this web match the predictions of the cascade model, which predicts even higher proportions of intermediate species and links between them, and even more numerous chains. It appears that these and other differences are not due simply to the large number of species involved here, but it is not yet clear whether they should be ascribed to the completeness with which some of the diets are known, to differences between the ways this and other webs were constructed, or to unique ecological conditions on the island of St. Martin.

Key words: *Anolis*; Caribbean; cascade model; ECOWeB; food web; Lesser Antilles; link strength; predation frequency; St. Martin; trophic relations.

INTRODUCTION

A food web summarizes the trophic relations among species by identifying the links between predators and their prey. Quantitative information about the frequency of predation or magnitude of energy flow provides a more complete picture of a community, but such information is usually not available, and many studies of food webs (e.g., Cohen 1978, Sugihara 1984, Sugihara et al. 1989, Cohen et al. 1990) focus on patterns that depend on the presence rather than the strength of links. Casting data in the form of a food web compensates somewhat for the absence of quantitative information by aiding comparisons between communities and by permitting analyses that can reveal community-level patterns. Nonetheless the relative strengths of the links are important ecologically and information about them can be useful (Paine 1980).

As we will show, many properties of food webs vary with the number of species in the web (Martinez 1991a), although the invariance of some properties remains an open issue (Briand and Cohen 1984, Sugihara et al. 1989, Schoenly et al. 1991). Because the food webs that have been collected or studied have been relatively small, many of the patterns considered to be typical

food webs may be misleading descriptions of full-scale communities (Polis 1991). In the ECOWeB data bank (Cohen 1989), a compilation of 213 food webs, the mean web size is <19 species, and >95% of the webs contain <40 species. Yet North America contains, for instance, ≈3500 species of vertebrates (Wernert 1982), 90 000 species of insects (Arnett 1985), and >16 000 species of flowering plants (Williams 1964); when groups such as fungi, nematodes, and mites are included, simple arithmetic shows that, unless there are thousands of entirely disjoint food webs in North America, most webs must contain dozens to hundreds of species. The numbers are presumably even more extreme for tropical regions. We suspect that the lack of time and resources, rather than sparseness of actual communities, has limited the compilation and study of large food webs (Polis 1991).

The data that are assembled into food webs may be heterogeneous, combining species and relations that are well known with others that are known only sketchily, taxonomically resolving some groups to species while identifying others by orders, classes, or other broad categories. When the data are collected by different workers, the different levels of resolution employed may not easily correspond to one another. The resulting web is biased by the centering of detail about certain species, the foci of the data gathered. The distinction among “community,” “source,” and “sink” webs (Cohen 1978) reflects basic differences in the collection

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TABLE 1. Sources of food web data.

Source	Focus	Methods	Location	Taxonomic resolution
Initial web	<i>Anolis watti</i> , <i>A. bimaculatus</i>	observation	St. Martin	specific for vertebrates, broad for arthropods
J. McLaughlin (<i>personal communication</i>)	kestrel and thrasher diets	emetics and observations	St. Martin (kestrel), St. Eustatius (both)	insect orders
Rummel (1984)	<i>Anolis watti</i> , <i>A. bimaculatus</i> diets	stomach contents	St. Eustatius	insect orders
Heckel (1980)	arthropods in diets of <i>Anolis</i>	trap census	St. Martin	morphospecies (approximately genera)
A. P. Dobson et al. (<i>unpublished manuscript</i>)	Nematode parasites of <i>Anolis</i>	dissection	St. Martin	species
Wetmore (1916)	bird diets	stomach contents	Puerto Rico	insect orders or families
Danforth (1939)	bird diets	stomach contents	Guadaloupe, other islands	insect orders or families

of trophic data, rather than in the structure of communities.

Although such heterogeneity in the data is not desirable, in practice it may be unavoidable. The construction of large webs, especially, seems to require the use of data gathered by a variety of workers over a long span of time and with a variety of purposes. An essential step in constructing a food web, then, consists of piecing imperfect data into a single coherent picture. Because the resulting web is often a product of patchwork and extrapolation, it seems appropriate in publication to describe explicitly the methods used in its construction, so that the biases present in the data or in the method of assembly can then be evaluated realistically (Cohen et al., 1993). Yet few published food webs reveal the steps that converted the data into the final structure.

Over the last 12 yr, one of us (J. Roughgarden) has conducted studies of *Anolis* spp. and some of their associated species on several islands in the Caribbean. In this paper we integrate data from several of those studies with the purpose of constructing and analyzing a food web of the community on the island of St. Martin in the northern Lesser Antilles. We explicitly document the steps involved in assembling our data into a large (44 species) web; additionally, we incorporate information about the relative strengths of the links we find. Knowledge of the relative strengths of the links provides the basis for a subsequent study of the effects of sampling on apparent web properties (L. Goldwasser and J. Roughgarden, *unpublished manuscript*), as well as indicating which links may be robust to different methods of data collection.

After constructing the web, we analyze it using the standard descriptions of web properties. These descriptions range from the straightforward (such as counting of trophic links between basal, intermediate, and top

species) to the conceptually or mathematically sophisticated (such as topological properties of the resource or consumer graphs). Most of these descriptions, however, yield only single summary statistics for the whole web, which are useful primarily for comparison with statistics collected from other webs. The ecologist who works with a given system, on the other hand, may want an analysis to identify parts within the web that are particularly interesting or unusual in some way, rather than simply labelling the whole web as either "typical" or "atypical." To this end, we introduce several new methods of identifying species that stand out from others within a web.

Most analyses of food webs lump any taxa that are trophically "equivalent" (sharing exactly the same predators and prey) into single trophic entities, and refer to members of the web as "trophic species," or simply "species," where the context indicates trophic rather than Linnean entities (Sugihara 1982, Briand and Cohen 1984). Lumping ignores differences in the frequencies with which supposedly equivalent species interact with their predators or prey. To explore the effects of lumping on the properties of a food web, we carry out our analysis both with the original species unaltered and with the trophically equivalent species lumped.

CONSTRUCTION OF THE WEB

Integrating the trophic data of our sources into a single web required three steps: identification of consistent trophic units, identification of the trophic links among them, and assigning a measure of the relative strengths of those links. We restricted our web to the single island of St. Martin, although we used dietary information from the nearby island of St. Eustatius for kestrels and thrashers, and data in the literature from Puerto Rico and neighboring islands for the diets of

some of the other species of birds. The values obtained from other islands, although necessary for obtaining estimates of some link frequencies, should probably be regarded with caution. Table 1 shows our sources and the nature of their data.

The initial form of the web (Fig. 1 and Table 2) establishes the basic structure and relationships among groups; these relationships derive from personal observation, previous studies (e.g., Heckel 1980, Rummel 1984; J. McLaughlin, *personal communication*), and general biological intuition. It included several links expected to exist simply on grounds of biological plausibility: nectar by hummingbirds and seeds by grassquits, for instance. The web in this form is entirely qualitative, and the resolution is clearly higher for those species, especially vertebrates, that are trophically close to the lizards. Much of the process of construction consisted of expanding the initial, size-based categories for the arthropods in this web into actual taxonomic entities, and then of quantifying the links among them.

Identification of trophic units

As is common in food webs, the vertebrate taxa are consistently identified to species, so no further refinement was necessary for them. For the arthropods, our sources varied from coarse to fine levels of resolution; we used an intermediate level. This compromise was necessary because splitting the coarse- and medium-resolution data into the finest taxonomic units throughout would have introduced a great deal of guesswork about the trophic relationships of each separate taxon; what we lost in resolution we gained keeping our results close to most of the original data. Table 3 shows how we expanded the initial, size- and location-based categories to actual taxa. Following Rummel (1984), we used insect orders in most cases, separated the Formicidae (ants) from other Hymenoptera, and distinguished between larval and adult Coleoptera, Diptera, and Lepidoptera. These taxa are known to occur in the diets of *Anolis* (Rummel 1984); other insect orders are probably present as well, but we chose to err on the conservative side and omitted them. Again following Rummel, we used higher taxonomic levels for noninsect invertebrates: Annelida, Gastropoda, Acarina, Araneida, Chilopoda, and Isopoda. None of our sources resolved these taxa any further.

We excluded a few taxonomic categories present in Rummel (1984). He records one gecko tail and one flea in the stomach of an anole, out of nearly 1500 items. These species have no other known links to the species in our web. In the absence of information about the strengths of their links to any other species, including them would have required either substantial omissions of their other links or a great deal of guesswork. Because their links to anoles are known to be weak, it seemed less inaccurate to omit these species altogether. We also ignored Rummel's records of "other insects."

A. P. Dobson et al. (*unpublished manuscript*) iden-

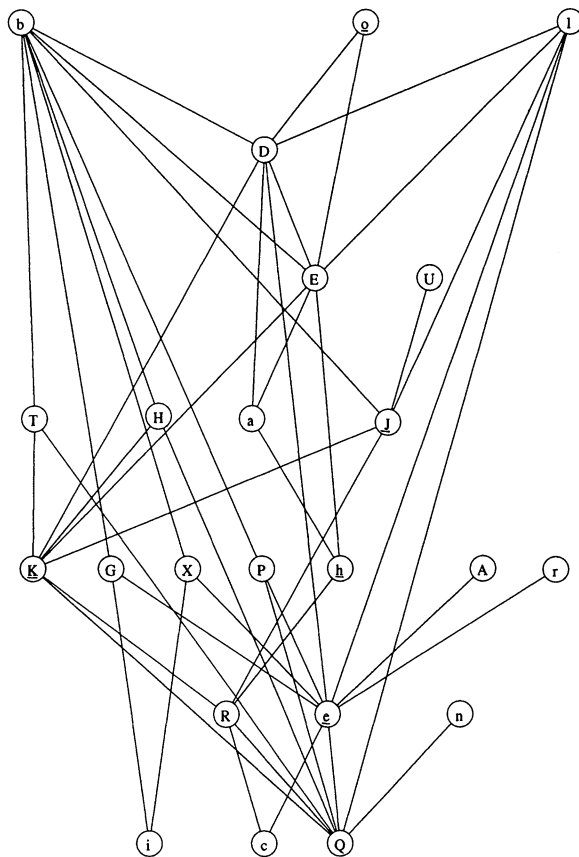


FIG. 1. The initial version of the St. Martin food web. Each species is represented by a circle with a letter, with the coding as indicated. A line connecting two species means that the higher species consumes the lower. The letter assignments and node locations in this figure anticipate those of Fig. 2, to facilitate comparison of our initial material and our results. The underlined letters represent categories that are subdivided in our analysis and in Fig. 2. A. Adult spider. D. *Anolis gingivinus*. E. *Anolis pogus*. G. Bananaquit. H. Bullfinch. J. Big floor insects. K. Small floor insects. P. Elaenia. Q. Fruit and seeds. R. Fungi. T. Grassquit. U. Gray Kingbird. X. Hummingbirds. a. Juvenile spider. b. Kestrel. c. Leaves. e. Canopy insects. h. Tiny floor insects. i. Nectar and floral. I. Pearly-eyed Thrasher. n. Scaly-breasted Thrasher. o. Nematodes. r. Yellow Warbler.

tified the species of the nematodes that parasitize *Anolis* spp. as *Thelandros cubensis*, *Alloglyptus crenshawii*, and *Mesocoelium* sp., and quantified the rates of parasitism. Of these nematodes, the first parasitizes both species of *Anolis*, and the others parasitize only *Anolis gingivinus*.

Our initial web treated plants anatomically rather than taxonomically, indicating consumption by animals of leaves, nectar, and fruits, as well as the flow of nutrients from leaves to the other two categories. None of our sources had information about the use of different plant species by different species in the web, and for our final web we had no choice but to follow this anatomy-based "taxonomy." Thus the basal "spe-

TABLE 2. The initial web. Each species is followed by a list, in parentheses, of its prey species. This format, which is particularly compact for large, sparse food webs, contains all the information contained in the graphical or matrix formats of the web (only locating the predators of a given species may require some searching). Data expressed this way can be read directly in the Scheme dialect of the computer language Lisp, in which we wrote the programs for our analysis.¹ For the purposes of the programs, we used only lowercase letters, and joined words or items that are part of a single trophic entity with hyphens and ampersands.

Vertebrates	
kestrel	(elaenia bullfinch grassquit hummingbirds bananaquit big-floor-insects anolis-gingivinus anolis-pogus)
pearly-eyed-thrasher	(anolis-pogus anolis-gingivinus fruit&seeds canopy-insects big-floor-insects)
scaly-breasted-thrasher	(fruit&seeds)
gray-kingbird	(big-floor-insects)
elaenia	(fruit&seeds canopy-insects)
bullfinch	(fruit&seeds small-floor-insects)
grassquit	(fruit&seeds [some small-floor-insects])
hummingbirds	(nectar&floral canopy-insects)
bananaquit	(nectar&floral canopy-insects [<i>not</i> gastropoda])
yellow-warbler	(canopy-insects)
anolis-gingivinus	(small-floor-insects canopy-insects juvenile-spider anolis-pogus)
anolis-pogus	(tiny-floor-insects small-floor-insects juvenile-spider)
Nonvertebrates	
nematodes	(anolis-gingivinus anolis-pogus)
canopy-insects	(fruit&seeds leaves)
big-floor-insects	(small-floor-insects fungi)
small-floor-insects	(fungi fruit&seeds)
tiny-floor-insects	(fungi)
adult-spider	(canopy-insects)
juvenile-spider	(tiny-floor-insects)
fungi	(fruit&seeds leaves)
Basal groups	
fruit&seeds	()
nectar&floral	()
leaves	()

¹ See ESA Supplementary Publication Document No. 9301 for 40 pages of source code. This document is available on 5¼" diskette or in printed form. For a copy of this document order from the Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318 USA.

cies" are not taxa at all, although they are components of basal species. We omitted the flow of nutrients among separate anatomical portions of plants, and added the categories of Roots and Wood. We also added Detritus as a basal "species."

TABLE 3. Conversion of insects from size and location classes to taxonomic units.

Size and location class	Order (or other taxon)
Big floor insects	Coleoptera adults
	Orthoptera
	Chilopoda
	Diplopoda
Small floor insects	Coleoptera larvae
	Diptera larvae
	Isopoda
	Isoptera
	Formicidae
Tiny floor arthropods	Collembola
	Mites
Canopy "insects"	Frugivores:
	Diptera adults
	Lepidoptera adults
	Other Hymenoptera
	Thysanoptera
	Herbivores:
	Lepidoptera larvae
	Hemiptera
	Homoptera
	Gastropoda

Identification of trophic links

In determining the trophic links between members of our web, we included virtually all documented links, even weak ones. In the sense of Schoenly and Cohen (1991), it is a "cumulative" food web. For each link from a predator to a size- or location-based category (Table 3), we usually included matching links from the predator to every new member taxon; it usually seemed biologically more reasonable to expect these links than to expect their absence. In some cases, however, we excluded a taxon from a predator's diet because it seemed an implausible food item. For instance, Table 3 shows that we included gastropods in the category "canopy insects"; the *Elaenia*, as a consumer of "canopy insects," received links to gastropods as well as all other corresponding orders of insects; in contrast, adult spiders, also consumers of "canopy insects," received links to the insects only and not the gastropods.

For the *Elaenia*, hummingbirds, Yellow Warbler, and grassquit, we relied primarily on Wetmore (1916) for both links and their strengths. When a link appeared in Danforth (1939) that was absent from Wetmore (1916), we included it as well, weighting its strength according to the relative numbers of stomachs examined by these two sources. We used their numbers directly, without attempting to convert their relative

masses to actual numbers of individuals. Any attempt to fine-tune these values would have been misleading, because they were collected from islands other than St. Martin. The relative strengths of these links are probably approximately correct, but there is no way of estimating from these data how close they are to the numbers actually consumed on St. Martin.

We treated ants somewhat separately. Although Table 2 classes them among the small floor insects, we included links to them from juvenile spiders, which otherwise consume only "tiny floor insects." Also, we incorporated their foraging in the canopy by including "nectar&floral" in the diets, and by including them in the diets of canopy foragers such as the Gray Kingbird. The Pearly-eyed Thrasher was already known to eat ants (J. McLaughlin, *personal communication*) but not any other "small floor insects."

In assigning prey to the taxa of arthropods (Table 4), we included in their diets items that are, in general treatments of insects (Borror et al. 1981, Arnett 1985), considered typical for each group. For instance, we included links from centipedes to all members of "small floor insects," "tiny floor insects," and juvenile spiders. We included leaves in the diets of all "canopy herbivores"; because many hemipterans are predatory (Arnett 1985: 171), we also gave them links to all canopy frugivores and herbivores, again excluding gastropods on grounds of implausibility.

We did not include the maturation of juvenile spiders to adult spiders and of larval insects to adults as trophic links in our web.

We have excluded links in which members of a trophic group consume members of the same trophic group. Cohen (1978) found that these and longer closed cycles are rare, although this point is not resolved (Polis 1991). This choice makes the later analysis of chains slightly easier; in this as in other matters, our procedures have omitted links rather than created them.

Fig. 2 shows our resulting web. The figure shows all the links but not their relative strengths.

Estimation of link strengths

We quantified the relative strengths of links as the frequency of acts of predation. The other possible measure of relative strength, flow of energy (or nutrients) from each species to its predators, would have required additional information about the relative energy (or nutritional) content of individuals of each species. The frequency of predation is, additionally, more relevant to the issue of sampling and detectability of links (L. Goldwasser and J. Roughgarden, *unpublished manuscript*) than is the flow of energy.

Links given by Rummel (1984), J. McLaughlin (*personal communication*), and A. P. Dobson et al. (*unpublished manuscript*) already indicated the relative frequency of items in the diets of the *Anolis*, thrashers, kestrels, and parasites (Table 5). However, these differences in the form and scaling of their data required

TABLE 4. Diets of nonvertebrates. Following the expansion of our size and location classes of insects into orders, we expanded the predator-prey links of the initial web (Table 2) into the following. We determined diets according to Borror et al. (1981) and Arnett (1985). Format as in Table 2.

Taxon	Diet
collembola	(fungi detritus)
orthoptera	(leaves tiny-floor-insects small-floor-insects detritus homoptera)
isoptera	(wood detritus)
hemiptera	(leaves canopy-insects [<i>not</i> gastropoda homoptera])
homoptera	(leaves)
thysanoptera	(nectar&floral leaves fungi tiny-floor-insects)
coleoptera-adult	(detritus fungi leaves nectar&floral tiny-floor-insects small-floor-insects wood)
coleoptera-larva	(roots detritus wood tiny-floor-insects)
diptera-adult	(nectar&floral fruit&seeds)
diptera-larva	(leaves detritus tiny-floor-insects)
ants	(tiny-floor-insects fungi nectar&floral fruit&seeds)
other-hymenoptera	(nectar&floral leaves canopy-herbivores [<i>not</i> gastropoda, hemiptera])
lepidoptera-adult	(nectar&floral)
lepidoptera-larva	(leaves)
adult-spider	(canopy-insects [<i>not</i> gastropoda])
juvenile-spider	(tiny-floor-insects)
annelid	(detritus)
gastropoda	(leaves detritus)
mites	(detritus fungi)
centipede	(tiny-floor-insects small-floor-insects juvenile-spider)
millipede	(detritus roots)
isopoda	(detritus)
fungi	(fruit&seeds leaves)

some early, more-or-less arbitrary decisions in coordinating the parts of the web. Such decisions were necessary: Rummel gives a count of the stomach contents, McLaughlin gives the number of items consumed per day, and A. P. Dobson et al. (*unpublished manuscript*) give the parasite loads. We began assigning predation frequencies by accepting at face value the numbers for the Pearly-eyed Thrasher. These numbers match the known predation rate of 10 *Anolis* eaten per hectare per day (McLaughlin and Roughgarden 1989). We then scaled the rates for the Kestrel to correspond to the relative predation pressures by these two species of birds. For the diets of *Anolis* we multiplied the per lizard values of Rummel (1984) by 100. We divided the rates of predation by nematodes (Dobson et al., *unpublished manuscript*) by 10.

For the remaining species for which we had quantitative data (Table 5), we assigned a sum for each species of 100, and multiplied their predation rates accordingly. Where basal species appeared in a diet, we assigned a percentage that, although arbitrary,

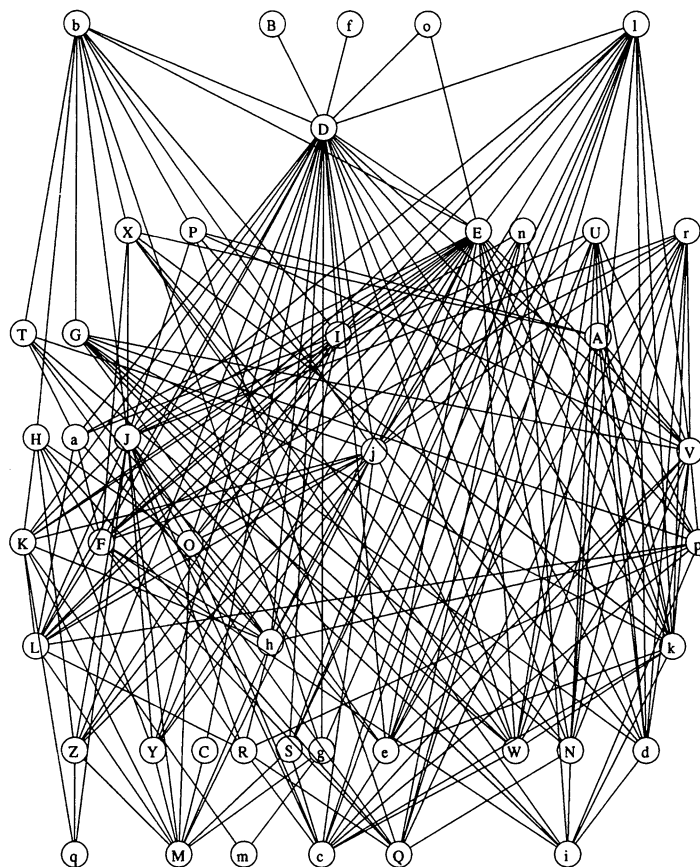


FIG. 2. The species and links in the final version of the St. Martin food web. Several features can be discerned in this otherwise tangled representation (which also demonstrates that "artistic convenience," suggested by Paine [1988] as a bias in the construction of many webs, played no role here). Because each species is shown at its minimum height (that is, consuming at least one species in the row immediately below it), the number of rows is one greater than the longest chain in the web. There are thus chains of length 8. Note, also, variation in the number of predators and prey among species: at all levels, some species have very few while others have many. Except for the three species of nematodes, the upper part of this web is much the same as in Fig. 1; most of the filling out occurs in the lower levels. A. Adult spider. B. *Alloglyptus crenshawii*. C. Annelid. D. *Anolis gingivinus*. E. *Anolis pogus*. F. Ants. G. Bananaquit. H. Bullfinch. I. Centipede. J. Coleoptera adult. K. Coleoptera larva. L. Collembola. M. Detritus. N. Diptera adult. O. Diptera larva. P. Elaenia. Q. Fruit&seeds. R. Fungi. S. Gastropoda. T. Grassquit. U. Gray Kingbird. V. Hemiptera. W. Homoptera. X. Hummingbirds. Y. Isopoda. Z. Isoptera. a. Juvenile spider. b. Kestrel. c. Leaves. d. Lepidoptera adult. e. Lepidoptera larva. f. *Mesocoelium* sp. g. Millipede. h. Mites. i. Nectar&floral. j. Orthoptera. k. Other hymenoptera. l. Pearly-eyed Thrasher. m. Roots. n. Scaly-breasted Thrasher. o. *Thaladros cubensis*. p. Thysanoptera. q. Wood. r. Yellow Warbler.

seemed reasonable according to the character of the consumer, for instance, 90% nectar&floral for hummingbirds.

For the remaining diets it was necessary to assign relative weightings to the species, to determine both their total rates of consumption and their relative representation in other predators' diets. These weightings reflect differences in the abundances of species: all else equal, rare species should appear less commonly in others' diets, and the total rate of predation (the sum of the frequencies with which it eats its prey) by a rare species should be less than the total rate of predation by a common species. Heckel (1980) surveyed the abundances of flying insects on St. Martin, and we used these abundance values directly. For the remaining in-

vertebrates we took the mean of the known rates of predation on each species and then multiplied that value by 10 or 100 (Table 6). These multiplications reflect the greater number of individuals, in general, of species at lower trophic levels. We set the total rate of predation by each remaining consumer equal to its weighting. We then scaled the prey of each consumer to sum to its weighting, by multiplying each of its prey by the appropriate constant factor.

Where basal species appeared in the diets of invertebrates, we again assigned a proportion that seemed reasonable according to the character of the invertebrate. For instance, we assigned leaves as 50% of the diets of Hemiptera (Table 6). Where more than one basal species appeared in a diet, in the absence of fur-

TABLE 5. Quantitative and taxonomic diet data. We used the following data for the frequencies of prey in the diets of these predators; the sources are indicated. Data presentation as in Table 2.

Predator	Diet	Source
kestrel	(elaenia + bullfinch + grassquit + hummingbirds + bananaquit = 11%) (big floor insects [coleoptera-adult, orthoptera, centipede, millipede] 14%) (anolis-gingivinus 60%) (anolis-pogus 15%)	J. McLaughlin, <i>personal communication</i>
scaly-breasted-thrasher	(fruit&seeds > 95%) (nectar&floral 2) (leaves 1) (other-hymenoptera 2) (gastropoda 10) (orthoptera 1) (centipede 1)	J. McLaughlin, <i>personal communication</i>
pearly-eyed-thrasher	(anolis-pogus 5) (anolis-gingivinus 5) (leaves 1) (fruit&seeds 125) (diptera-adult 1) (orthoptera 4) (ants 8) (other-hymenoptera 6) (coleoptera-adult 3) <i>otherwise</i> : (canopy insects [gastropoda, hemiptera, lepidoptera-adult, lepidoptera-larva] [not homoptera]) (big floor insects [centipede, millipede] [not thysanoptera])	J. McLaughlin, <i>personal communication</i> ; "otherwise" from Initial Web
thelandros-cubensis	(anolis-gingivinus 0.095) (anolis-pogus 0.080)	A. P. Dobson et al. (<i>unpublished manuscript</i>)
mesocoelium-sp	(anolis-gingivinus .606)	A. P. Dobson et al. (<i>unpublished manuscript</i>)
allogypus-crenshawii	(anolis-gingivinus .005)	A. P. Dobson et al. (<i>unpublished manuscript</i>)
anolis-bimaculatus [similar to anolis-gingivinus]	(annelid .08) (gastropoda .08) (centipede .02) (millipede .02) (mites .02) (juvenile-spider .10) (coleoptera-adult 1.48) (coleoptera-larva .02) (collembola .02) (ants 8.52) (diptera-adult .56) (diptera-larva .20) (other-hymenoptera 2.12) (hemiptera .02) (isoptera .54) (homoptera 1.44) (isopoda .04) (lepidoptera-adult .36) (lepidoptera-larva 9.58) (orthoptera .12) (thysanoptera .02)	Rummel (1984)
anolis-gingivinus	(anolis-pogus [very infrequent])	J. McLaughlin, <i>personal communication</i>
anolis-wattsi [i.e., anolis-pogus]	(gastropoda .01) (mites .07) (isopoda .035) (juvenile-spider .33) (centipede .01) (coleoptera-adult .70) (coleoptera-larva .01) (collembola .10) (diptera-adult 2.01) (diptera-larva .07) (hemiptera .02) (homoptera 1.68) (ants 9.55) (other-hymenoptera .58) (lepidoptera-adult .32) (lepidoptera-larva 1.18) (orthoptera .11) (thysanoptera .12) (isoptera .07)	Rummel (1984)
gray-kingbird	(fruit&seeds 56) (coleoptera-adult 56) (homoptera 6) (other-hymenoptera 43) (orthoptera 8) (hemiptera 12) (lepidoptera-adult 4) (lepidoptera-larva 10) (diptera-adult 1) (adult-spider 3)	Wetmore (1916)
grassquit	(fruit&seeds 87.4) (spider 1.2) (orthoptera 1.2) (homoptera 3.0) (lepidoptera-larva 7.2)	Wetmore (1916)
elaenia	(fruit&seeds 86) (adult-spider + lepidoptera-adult + coleoptera + hemiptera 14)	Wetmore (1916); Hemiptera from Danforth (1939)
hummingbirds	(nectar&floral) (adult-spider 11.31) (ants 3.66) (other-hymenoptera 64.63) (homoptera 14.83) (coleoptera-adult 0.83) (diptera-adult 7.14)	Wetmore 1916; ants from Danforth (1939)
yellow-warbler	(orthoptera 7.21) (ants 0.58) (homoptera 24.84) (hemiptera 3.03) (coleoptera-adult 14.62) (other-hymenoptera 8.72) (diptera-adult 8.16) (lepidoptera-adult-and-larva 11.95) (adult-spiders 18.07) (fruit&seeds 0.7)	Wetmore (1916); fruit&seeds from Danforth (1939)

ther information we assigned them equal representation. For instance, for Coleoptera larvae, we assigned 25% each to roots, detritus, and wood, and split the remaining 25% between the tiny floor arthropods, mites,

and Collembola, according to their previously established weightings.

Table 7 shows the final web, with our estimates of the relative strengths of each link indicated.

TABLE 6. Weighting of species. For the first 10 species we used the abundance data in Heckel (1980) directly. For the subsequent species we estimated relative abundances by averaging the rates of predation for all known rates of each species. We then multiplied the resulting values by 10 or 100 to reflect the high relative abundances of these smaller invertebrates.

By Heckel's abundances		
Coleoptera adult	18	
Diptera adult	142	
Hemiptera	9	
Homoptera	14	
Ants	18	
Other Hymenoptera	20	
Lepidoptera adult	2	
Orthoptera	65	
Adult spider	24	
Juvenile spider	24	
By representation in others' diets		
Frugivore canopy		($\times 10$)
Thysanoptera	7	70
Herbivore canopy		($\times 10$)
Gastropoda	3.83	38
Lepidoptera larva	218.8	219
Big floor		($\times 10$)
Centipede	1.4	14
Millipede	2	20
Small floor		($\times 10$)
Coleoptera larva	1.5	15
Isoptera	30.5	305
Isopoda	19.5	195
Diptera larva	13.5	135
Tiny floor		($\times 100$)
Mites	4.5	450
Collembola	6	600
Other		($\times 10$)
Annelid	8	80

We emphasize that many of the link strengths we have arrived at are only approximations, susceptible to revision, especially by quantitative data about the diets of the arthropods. Our assumption of equal link strengths for taxa about which no differences are known has almost certainly underestimated the variability of link strengths from one group to another. Errors in our values of the link strengths may affect the results of sampling in our subsequent study (L. Goldwasser and J. Roughgarden, *unpublished manuscript*) if the relative strengths actually differ substantially from our results. However, most of the following analysis, as is true of most approaches to web structure, uses only the presence of links and not their strengths, and is thus not affected by errors in link strength.

DESCRIPTION AND ANALYSIS OF WEB

Among the 44 "species" in this web, two pairs are trophically equivalent: *Mesocoelium* sp. and *Alloglyptus crenshawii* share the same sets of predators and prey, as do Mites and Collembola. We accordingly analyze the web in two ways: keeping all species separate, and, following Sugihara (1982), Briand and Cohen (1984), and others, replacing each of these pairs with a single,

lumped trophic unit, "Mesocoelium-sp + Alloglyptus-crenshawii," and "Mites + Collembola." The lumped version of the web thus has 42 "species." Our comparisons between this web and the webs in the ECOWeB collection are consistent in either lumping all webs being compared or lumping none.

We made two sets of comparisons between the St. Martin web and those in the ECOWeB collection. In the first set, we simply compared the St. Martin web with the mean value of each property for the collection, using the standard deviation of the values in the collection to measure the statistical significance of the difference between the St. Martin web and the collection (Sokal and Rohlf 1981: 229). Second, because the St. Martin web is already unusual in being so much larger than most of the webs in the collection, we tried to remove the effects of size from the comparisons. We use the collection to fit a regression line for each property as a function of web size; the line gave the expected value for a web of 44 (or, lumped, 42) species. Then we tested whether the St. Martin web lies within the 95 and 99% confidence intervals about the regression line.

One assumption of the regressions, that the properties vary linearly with web size, is difficult to justify in many cases, especially for properties involving proportions. The cascade model (Cohen and Newman 1985, Cohen et al. 1985, Cohen et al. 1986, Newman and Cohen 1986, Cohen and Palka 1990), although not without its own assumptions, provides a means of extrapolation without assuming linearity. Later in this section we compare the values of the St. Martin web with the predictions calculated from the cascade model (Cohen et al. 1990), for all properties for which predictions are available.

We emphasize that these comparisons are for heuristic purposes: we are not attempting to "prove" that the St. Martin web is different from other webs. Strictly speaking, it is not even clear what the ECOWeB collection is a representative sample of. The purpose of these comparisons is simply to point out in what respects this web seems to stand apart from other known webs, and to try to suggest where its differences arise. We further note that the existence of size trends in web properties is an open issue (Briand and Cohen 1984, Sugihara et al. 1989, Schoenly et al. 1991, Martinez 1991b), and that the regressions we have done here represent only a rudimentary analysis; they do not attempt to be definitive. In particular, our regressions have assumed linear responses to web size (except for the topological properties, where we assumed logistic responses), normality, and homoscedasticity. Given these caveats, Table 8 shows the results of our analysis of the St. Martin web, and the results of our comparisons between it and the ECOWeB collection.

If there are clear size trends among food webs in general and if the St. Martin web fits them, then one would expect asterisks on the left but not on the right

TABLE 7. The frequency web constructed. Each consumer is followed by a list of its prey; the name of each prey is paired with the frequency, in acts of predation per hectare per day, with which it is preyed upon by that predator. Taxon format as in Table 2. The square brackets that mark each list of prey must be converted to parentheses for use in a Lisp program.

kestrel	[(elaenia .003) (bullfinch .003) (grassquit .003) (hummingbirds .003) (bananaquit .003) (coleoptera-adult .0040) (orthoptera .0143) (centipede .0003) (millipede .0004) (anolis-gingivinus .08) (anolis-pogus .02)]
scaly-breasted-thrasher	[(fruit&seeds 95.75) (nectar&floral .50) (leaves .25) (centipede .25) (other-hymenoptera .50) (gastropoda 2.50) (orthoptera .25)]
pearly-eyed-thrasher	[(anolis-pogus 5) (anolis-gingivinus 5) (fruit&seeds 125) (leaves 1) (diptera-adult 1) (other-hymenoptera 6) (coleoptera-adult 3) (ants 8) (orthoptera 4) (centipede 1.947) (millipede 2.782) (lepidoptera-adult .278) (lepidoptera-larva 30.459) (gastropoda 5.285) (hemiptera 1.251)]
gray-kingbird	[(fruit&seeds 28) (coleoptera-adult 28) (other-hymenoptera 21.5) (orthoptera 4) (homoptera 3) (hemiptera 6) (diptera-adult .5) (lepidoptera-adult 2) (lepidoptera-larva 5) (adult-spider 1.5)]
elaenia	[(fruit&seeds 86) (adult-spider 6.3) (lepidoptera-adult .5) (coleoptera-adult 4.8) (hemiptera 2.4)]
yellow-warbler	[(orthoptera 7.21) (homoptera 24.84) (hemiptera 3.03) (coleoptera-adult 14.62) (diptera-adult 8.16) (ants 0.58) (lepidoptera-adult 5.98) (lepidoptera-larva 5.97) (other-hymenoptera 8.72) (adult-spiders 18.07) (fruit&seeds 0.7)]
bullfinch	[(fruit&seeds 90) (ants .269) (coleoptera-larva .224) (isopoda 2.919) (diptera-larva 2.02) (isoptera 4.565)]
grassquit	[(fruit&seeds 87.4) (juvenile-spider 1.2) (orthoptera 1.2) (homoptera 3.0) (lepidoptera-larva 7.2)]
hummingbirds	[(nectar&floral 90) (adult-spider 1.13) (homoptera 1.48) (ants .37) (coleoptera-adult .08) (diptera-adult .71) (other-hymenoptera 6.46)]
bananaquit	[(nectar&floral 90) (diptera-adult 2.98) (lepidoptera-adult .042) (lepidoptera-larva 4.60) (other-hymenoptera .42) (thysanoptera 1.47) (hemiptera .189) (homoptera .29)]
thelandros-cubensis	[(anolis-gingivinus 0.095) (anolis-pogus 0.080)]
mesocoelium-sp	[(anolis-gingivinus .606)]
alloglyptus-crenshawii	[(anolis-gingivinus 0.005)]
anolis-gingivinus	[(annelid 8) (gastropoda 8) (mites 2) (juvenile-spider 10) (centipede 2) (millipede 2) (isopoda 4) (coleoptera-adult 148) (coleoptera-larva 2) (collembola 2) (diptera-adult 56) (ants 852) (diptera-larva 20) (hemiptera 2) (homoptera 144) (isoptera 54) (other-hymenoptera 212) (lepidoptera-adult 36) (lepidoptera-larva 958) (orthoptera 12) (thysanoptera 2) (anolis-pogus 1)]
anolis-pogus	[(gastropoda 1) (mites 7) (juvenile-spider 33) (centipede 1) (isopoda 35) (coleoptera-adult 70) (coleoptera-larva 1) (ants 955) (collembola 10) (diptera-adult 201) (diptera-larva 7) (hemiptera 2) (homoptera 168) (other-hymenoptera 58) (lepidoptera-adult 32) (lepidoptera-larva 118) (isoptera 7) (orthoptera 11) (thysanoptera 12)]
collembola	[(fungi 1200) (detritus 1200)]
orthoptera	[(leaves 180) (detritus 60) (ants 0.20) (coleoptera-larva 0.18) (diptera-larva 1.54) (isopoda 2.24) (isoptera 3.52) (mites 5.18) (collembola 6.92) (homoptera 0.16)]
isoptera	[(wood 610) (detritus 610)]
hemiptera	[(leaves 18) (diptera-adult 5.47) (thysanoptera 2.70) (homoptera .54) (lepidoptera-adult .08) (lepidoptera-larva 8.44) (other-hymenoptera .77)]
homoptera	[(leaves 56)]
thysanoptera	[(nectar&floral 70) (leaves 70) (fungi 70) (collembola 40) (mites 30)]
coleoptera-adult	[(detritus 8) (fungi 8) (leaves 8) (nectar&floral 8) (wood 8) (collembola 11.30) (mites 8.47) (coleoptera-larva .28) (isopoda 3.67) (isoptera 5.74) (diptera-larva 2.54)]
coleoptera-larva	[(roots 15) (detritus 15) (wood 15) (collembola 6.42) (mites 8.57)]
ants	[(collembola 10.28) (mites 7.71) (fungi 18) (nectar&floral 18) (fruit&seeds 18)]
other-hymenoptera	[(nectar&floral 20) (leaves 20) (lepidoptera-larva 37.63) (homoptera 2.40)]
lepidoptera-adult	[(nectar&floral 8)]
lepidoptera-larva	[(leaves 476)]
diptera-adult	[(nectar&floral 284) (fruit&seeds 284)]
diptera-larva	[(leaves 180) (detritus 180) (collembola 102.85) (mites 77.14)]
adult-spider	[(diptera-adult 28.69) (other-hymenoptera 4.04) (thysanoptera 14.14) (lepidoptera-adult .40) (lepidoptera-larva 44.24) (hemiptera 1.82) (homoptera 2.83)]
juvenile-spider	[(ants 1.62) (collembola 53.96) (mites 40.47)]
annelid	[(detritus 320)]
gastropoda	[(leaves 76) (detritus 76)]
mites	[(detritus 900) (fungi 900)]

TABLE 7. Continued.

centipede	[(collembola 19.29) (mites 14.47) (ants .58) (coleoptera-larva .48) (diptera-larva 4.34) (isopoda 6.27) (isoptera 9.81) (juvenile-spider .77)]
millipede	[(detritus 40) (roots 40)]
isopoda	[(detritus 780)]
fungi	[(fruit&seeds 55) (leaves 55)]
fruit&seeds	()
nectar&floral	()
leaves	()
wood	()
roots	()
detritus	()

of the central column. Generally, however, when St. Martin is statistically different from one ECOWeB value, it is different from the other also. Similarly, lumping rarely affects the statistical significance of differences between the St. Martin web and those of the ECOWeB collection.

Standard, whole-web counts

These measures compare the number of predators and prey, and the proportions of top predators, intermediate species, and basal species. Although the differences are not statistically significant, the St. Martin web has proportionally more intermediate species than is typical. This difference may be due partially to the vertebrate-centered bias in our data, as well as an artifact of the use of anatomical elements rather than real taxa for the basal species in the St. Martin web. However, even when basal species are excluded, the proportion of intermediate species in the St. Martin web (0.789 unlumped, 0.805 lumped) is higher than the mean proportion of intermediate species in the other webs (0.595 unlumped, 0.618 lumped). Also, the low ratio of predators to prey (close to unity) is due to the preponderance of intermediate species (which are members of both categories).

Lumping had little effect on these measures because one of the trophically equivalent pairs was among top predators and the other was among intermediate species.

Links and chains

The St. Martin web stands out with a strikingly high number of links per species, and this high ratio seems to have consequences in many of the unusual features that follow. The links also seem to be distributed much more between intermediate species than is typical of other webs. If we again exclude the basal species and their links (and look only at top-to-intermediate and intermediate-to-intermediate links), we find that only 28% of the remaining links are from top predators to intermediate species, far fewer than the 59% found typically. However, given the large proportion of intermediate species in this web, the proportion of intermediate-to-intermediate links is not unexpectedly

large. Although this web is relatively rich in both links and intermediate species, it is not disproportionately rich in links among those intermediate species.

This web contains 3816 chains (distinct paths from a top predator to a basal species). This number may appear startlingly high—indeed, it is much higher than either the mean or expected number of chains from the ECOWeB collection—but a simple example can show how rapidly the number of chains in a web can increase with even reasonable numbers of species and links. Consider a web with five trophic levels, five species per level, in which every consumer preys on all five species on the next lower level. Such a web contains 25 species, 4 links per species, 5 prey items per predator, and a mean chain length of 4. Each of these values is less than the corresponding value for the St. Martin web. The number of distinct chains, calculated by taking powers of 5, is $5^4 = 3125$, only slightly fewer than the number of chains in the St. Martin web. If, in comparison, each of the five predators at each level preyed on only three species in the next level (2.4 links per species, still above the ECOWeB value), the number of chains would be only $5 \times 3^4 = 405$. The key value here is the average number of links per species: a large number of chains is a consequence of having many prey items per predator in a web that is at least moderately large.

In addition to being numerous, the chains in the St. Martin web are atypically long (Briand and Cohen 1987): the mean chain length is 4.8 and the maximum chain length 8. There are 20 chains of length 8 in this web; using parentheses to indicate alternative paths and arrows to point from predator to prey, these chains can be shown as: (Kestrel, Pearly-eyed Thrasher, *The-landros cubensis*, *Mesocoelium* sp., *Alloglyptus crenshawii*) → *A. gingivinus* → *Anolis pogus* → Centipede → Juvenile Spider → Ants → (Mites, Collembola) → Fungi → (Fruit&Seeds, Leaves). It should be noted, though, that all 20 of these longest chains rely on the infrequent link of *A. gingivinus* consuming *Anolis pogus*.

Lumping the trophically equivalent species reduces the number of chains and their mean length only moderately. The longest chains still contain eight links, and there are eight of them.

One web in the ECOWeB collection, number 103,

TABLE 8. The St. Martin food web and its differences from the ECOWeB collection. The central data column shows the value of each property of the St. Martin web. For each property, the first row (marked "s") comes from an analysis with all species kept separate; the second row (marked "l") from one that lumps species that are trophically equivalent. The left-hand data column shows the mean value of each property for the 213 webs in the ECOWeB collection. The right-hand data column shows the expected value of each property for a web the size of the St. Martin web, based on a linear regression of the ECOWeB data. In most cases, the handling of the data, that is, the lumping of trophically equivalent species, the inclusion of discretionary links, and the treatment of outliers does not affect the significance of the results, but differences are both frequent enough and, in some cases, large enough to point out the need for care and thought in carrying out any analysis of web properties.

Property		ECOWeB mean		St. Martin web		Expected by ECOWeB size trends†	
Standard, whole-web counts							
Ratio of predators to prey	s	1.43		1.06		1.67	*(d-)
	l	1.18		1.03		1.15	
Proportion of top predators	s	0.325		0.182		0.370	*(d-)(t-)
	l	0.301		0.167		0.265	
Proportion of intermediate species	s	0.482		0.682		0.447	
	l	0.490		0.690		0.547	(d*)(t**)
Proportion of basal species	s	0.193		0.136		0.183	(t**)
	l	0.209		0.143		0.188	(t**)
Links and chains‡							
Number of links per species	s	1.87	**	4.95	**	2.27	**
	l	1.72	**	4.88	**	2.68	**
Proportion of links top-to-intermediate	s	0.360		0.234		0.374	
	l	0.348		0.244		0.341	
Proportion of links top-to-basal	s	0.131		0.032		0.152	
	l	0.124		0.034		0.056	(d*)(t**)
Proportion of links intermediate-to-intermediate	s	0.252		0.550		0.231	
	l	0.253		0.532		0.307	(t*)
Proportion of links intermediate-to-basal	s	0.257		0.183		0.243	
	l	0.275		0.190		0.295	
Connectance	s	0.273		0.230	(t*)	0.132	**
	l	0.312		0.238	(t*)	0.077	**
$S \times C$ (species times connectance)	s	4.016	**	10.14	**	4.67	**
	l	3.744	**	10.00	**	5.43	**
Number of chains	s	72.0	**	3816	**	190.7	** (t*)
	l	56.4	**	2442	**	238.2	**
Mean chain length	s	2.61	*	4.78	*	2.71	
	l	2.59	*	4.49		3.35	**
Standard deviation in chain length	s	0.67		1.22		0.82	**
	l	0.68		1.21		1.02	**
Maximum chain length	s	3.74	**	8	*	4.23	*(d-)
	l	3.74	**	8		5.48	**
Index of omnivory	s	0.157	**	0.595	**	0.156	
	l	0.163	**	0.577	**(d*)	0.222	*(t**)
Percent of species omnivorous	s	0.266	*	0.636	*	0.275	
	l	0.270	(t-)*	0.619		0.369	**
Predator-prey asymmetries							
Mean number of prey per consumer	s	2.41	(d**)(t**)*	5.74	*	3.36	**
	l	2.21	**	5.69	*	3.87	**
Standard deviation in prey per consumers	s	1.65	**	4.99	*(t-)	2.62	**
	l	1.31	**	4.86	**	2.67	**
Mean number of consumers per prey	s	3.04		6.06		4.03	**
	l	2.46	**	5.86	**(t*)	3.74	**
Standard deviation in consumers per prey	s	1.94		3.41		3.68	**
	l	1.42	*	3.37		3.00	**
Topological properties§							
Chordal?	s	93.9%		No		83.8%	**
	l	93.9%		No		36.8%	**
Interval?	s	88.3%		No		63.0%	**
	l	88.3%		No		8.1%	**

TABLE 8. Continued.

Property		ECOWeB mean	St. Martin web	Expected by ECOWeB size trends†	
Without holes in consumer space?	s	81.7%	No	68.7%	**
	l	81.7%	No	33.9%	**
Connection properties					
Proportion intermediate links by predator only	s	0.29	0.38	0.26	
	l	0.30	0.37	0.33	
Proportion intermediate links by prey only	s	0.24	0.13	0.33	**
	l	0.26	0.14	0.40	**
Proportion intermediate links by both	s	0.40	0.49	0.42	
	l	0.35	0.48	0.40	

* The statistical significance of each comparison (all two-tailed) is indicated by asterisks between the St. Martin column and the column with which it is being compared. ** $P < .01$; * $.01 < P < .05$; no asterisks indicates $P > .05$. The statistical significance of the slope of the regression (Sokal and Rohlf 1981: 474) is indicated to the right of the right-hand data column.

† Many of the webs in ECOWeB include "discretionary" links, which reflect predation records that are uncertain, varying, or only suspected; they are indicated in the data matrices by negative values. Given these discretionary links, we analyzed ECOWeB in two ways: by including all indicated links, both negative and positive, and by omitting negative links. The differences between these analyses were almost always negligible, and the results in the table come from the analyses that included all links. We indicate the instances where omitting the discretionary links affects the statistical significance of our results with a "d" and the significance level without the discretionary links.

Because the large webs are a priori outliers, we repeated our analyses by omitting the five webs that have > 50 species (nos. 123, 167, 181, 182, and 210). We indicate the instances where omitting the large webs affects the statistical significance of our results with a "t" and the significance level without the large webs.

‡ For the chain properties, we omitted those webs with cycles (numbers 21, 30, 100, 116, 123, 127, 128, 180), because chain lengths are not well defined when a series of links can pass through a species more than once.

§ For the topological properties, the central data column shows whether the St. Martin web possesses the property in question, and the left column shows the proportion of webs in the collection with that property. Because these properties are binary rather than real valued, we used a logistic regression to obtain the relationship between web size and the probability of having the property (Wilkinson 1989, Collett 1991). The right-hand column shows the calculated probability that a web the size of the St. Martin web has the property. The asterisks indicate whether the confidence intervals for the slope include 0.0. Employing a logistic regression avoided the need to divide the webs into size classes and construct regressions on proportions within those classes; that approach might have created artifacts because the large size classes have few webs.

is also extreme in its chain properties: it has 23 species, 5.78 links per species, and 3671 chains; it possesses chains of length 10. Hall and Raffaelli (1991) studied another web with extreme chain properties: it has 92 species, 4.45 links per species, 5518 chains, and a modal chain length of 5.

There are several ways to measure the level of omnivory, the predation by one species on other species of a variety of trophic levels. Here we employ two measures. For the first, we assign to each species the set of paths from it down to a basal species; the length of each path is the number of links down to the basal species. Each species' set of path lengths has a mean and standard deviation. The mean simply indicates the position, high or low, of the species within the web, but the standard deviation measures the extent to which the species eats prey at a variety of levels. We take as our index of omnivory the mean, over all species in the web, of the standard deviations in their path lengths. For example, if all of a species' paths to basal species are the same length, then its standard deviation is zero; a web of only such species has an omnivory index of zero. The more variation in the lengths of the paths, the higher the standard deviations and the higher the index of omnivory. For the St. Martin web, the index of omnivory is significantly higher than either the mean or the expected values of the ECOWeB collection.

For our second measure of omnivory we calculated

simply the proportion of species that consumed prey from more than one trophic level. Again, the St. Martin web has a higher level of omnivory than do those in ECOWeB, although the difference is not as striking. The contrast between this measure and the previous one suggests that the omnivorous species in the St. Martin web consume prey from a particularly wide range of trophic levels. The result with our second measure also accords with Polis's (1991) finding of unexpectedly high proportions of omnivorous species in a very large (but also highly aggregated) food web in the Coachella Valley. Although Hall and Raffaelli (1991) used a different index of omnivory than the ones we use here, they also found a high level of omnivory in their web.

It is worth pointing out the difference between the standard deviation in chain length and our index of omnivory; only for the latter property does the St. Martin web differ statistically from the ECOWeB collection. The index of omnivory includes variation in the height of all species in the web, while the standard deviation in chain length incorporates variation only in the heights of top predators. Paths from basal species only partly up the web are not explicitly included in any strict chain property, although such paths may constitute subsets of chains. The unusually high index of omnivory for the St. Martin web suggests that it may have a relatively high degree of variability in feeding

levels among its lower species as well as among its higher ones.

Predator-prey asymmetries: new measures of variability within a web

Trophic links are not distributed uniformly throughout a food web: some species have more kinds of prey than others, and some species have more kinds of predators than others. The variation among species in the number of links to predators and to prey can indicate how clustered the links may be within the web, as well as point to species with an unusually large number of links to either predators or prey. Species with many kinds of prey are, of course, generalists, and those with few kinds of prey are specialists; but there are no analogous terms for species with either relatively large or small numbers of predators.

In the St. Martin food web, the mean number of prey for each consumer species is 5.74, with a standard deviation of 4.99 (unlumped). Two species, *Anolis pogus* and *A. gingivinus*, are outliers, ~3 standard deviations above the mean, with 19 and 22 kinds of prey, respectively. The mean number of predators for each species of prey is 6.06, and the standard deviation is 3.41. There are no outliers for the number of predators for each species of prey.

Within the ECOWeB collection, it seems more common for the standard deviation in the number of consumers for each prey species to be greater than the standard deviation in the number of prey for each consumer species. This pattern indicates that species tend to vary more in the number of predators to which they are subject than in the number of prey they consume. In the St. Martin web, however, this trend is reversed, and species vary more in the number of prey they consume than in the number of predators that eat them.

The extreme number of prey for both species of *Anolis* is probably an artifact of two aspects of the data collection. First, the lizards were the central interest in many of the source studies, and the greater number of hours spent attending them probably resulted in a more complete sampling of their trophic relations. Second, those studies focused more on sampling the lizards' prey than their predators, and, indeed, we found the lizards to be unusual only in their number of prey, not their number of predators.

The converse of the first point is that species that appear with few links may have been inadequately sampled, although some species may certainly be true specialists. Nonetheless, the distribution of the numbers of prey species per consumer has not been explored within communities in general. At the very least, species with particularly few links to either predators or prey may serve as flags to the investigator that more data may be needed to confirm or disprove that point. Thus unusual values for these properties can both draw attention to an unusual web or unusual parts within a

web as well as provide a check on the completeness of the data.

Topological properties

Cohen (1978) found that a greater proportion of webs possess the interval property than would be expected by chance. For a web with this property, the resources that consumers use can be arranged in an abstract "consumer space" in a single line, without any loops or branchings. Unlike most of the webs in the collection, the St. Martin web is not interval.

A necessary but not sufficient condition for intervality is that a web be chordal (= "triangulated"; a chordal graph is also called a "rigid circuit graph" and possesses a "perfect elimination ordering"; Sugihara 1982, 1984). A nonchordal graph has loops in consumer space that bar intervality; chordality would otherwise allow the loops to fold up into a single line. Sugihara (1982) found that a greater proportion of webs are chordal than would be expected by chance. He suggested that chordality is a more meaningful property than intervality, and found that most noninterval webs fail because they are not chordal. The St. Martin web, consistent with Sugihara's hypothesis, fails intervality by being not chordal. Most webs in the ECOWeB collection, however, are chordal.

Sugihara (1984) found that the species in most food webs are closely packed, without holes between the species, in an abstract "resource space." The St. Martin web, again unlike most of the webs in the collection, possesses many holes, both one-dimensional and of higher dimensions.

The lack of intervality and chordality and the presence of holes, which make this web appear unusual compared with the majority of webs in the ECOWeB database, may be a consequence of the size of this web, rather than a reflection of any unusual ecological properties. To recast this point, we suspect that the high incidence of chordality, intervality, and the lack of holes in most of the webs is a consequence of the small size of most of the webs. As Sugihara notes, sufficiently small webs satisfy these properties by default, in a trivial consequence of their simplicity. As webs become larger and their geometry more complicated, the opportunities to fail some criterion increase markedly (Cohen and Palka 1990). It should be noted, however, that Cohen (1978) and Sugihara (1982) find statistical significance in their results even when taking the size of the webs into account.

Connection properties

The relationship between a web's consumer graph and its resource graph is not immediately evident: species that are connected in one need not be connected in the other. The consumer graph connects species that share at least one prey item, so it necessarily omits basal species; the resource graph connects species that

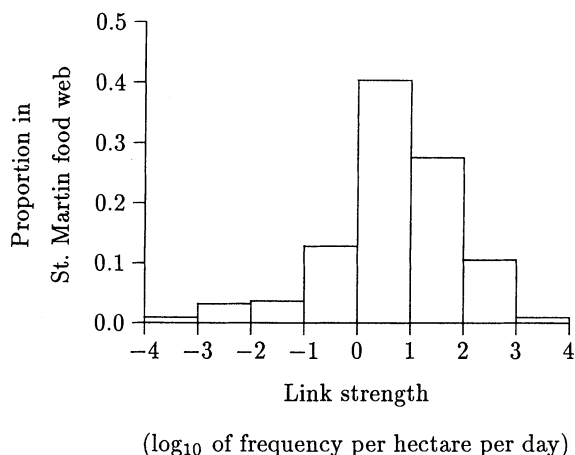


FIG. 3. The frequency distribution of link strengths in the St. Martin food web.

share at least one predator, and omits top predators. Thus the two graphs have the potential for congruence only for intermediate species. Among any pair of intermediate species there are four possibilities: that they share both predator and prey (and are connected in both graphs), that they share a predator only (and are connected in the resource graph only), that they share prey only (and are connected in the consumer graph only), or that they share neither predator nor prey (no connection in either graph).

We can restrict our attention to only those intermediate species that are connected in at least one of the graphs. In the absence of further information, one would probably expect many intermediate species to be linked by both predators and prey: intuitively, if a pair is similar enough to consume a common resource, they are probably similar enough for some predator to consume both of them.

In the St. Martin web, this expectation is, in a general way, borne out. Among pairs of intermediate species that are connected in at least one graph, more species share both predators and prey (are connected in both graphs), than either share a predator only (are connected in the resource graph) or share a prey only (are connected in the consumer graph). This pattern seems to be true among the webs in the ECOWeB collection as well, although less strongly. The St. Martin web seems unusual in having very few intermediate species that share prey without sharing a predator. Curiously, also, the St. Martin web runs counter to a statistically significant size trend within ECOWeB for this property.

Link strengths

Fig. 3 shows the distribution of link strengths within the web. The strong central tendency in the distribution contrasts with Paine's (1980, 1992) findings that predator-prey networks tend to have many weak links and only a few strong ones. This difference may be real or only apparent, for two reasons. First, these studies deal

with different quantities. Paine's (1992) experimental results measure the effects, including indirect ones, of the presence of single species on the abundances of others. In contrast, we calculate the frequency of each pairwise interaction; frequencies of interactions are only one of many kinds of factors that affect abundance, and in complex systems there need not be a one-to-one relationship between the interaction frequencies and their effects on abundance (Levins 1975, Puccia and Levins 1985, Goldwasser, *in press*). Second, even assuming a close relationship between link frequency and effect on abundances, our distribution is compatible with those found by Paine only if his distributions are in fact bimodal. The scale for link strengths in Fig. 3 is logarithmic, so the strongest links represent interactions that are considerably more frequent than the others. The central peak of the distribution thus represents a majority of interactions that are much less frequent than the minority of strong interactions on the right-hand tail. This description may qualitatively match Paine's results, except for our inclusion of a minority of extremely infrequent links on the left-hand tail, depending on the actual central tendency in his distributions.

The paucity of information about link strengths in general seems particularly unfortunate because the distribution of link strengths may be both a fundamental characteristic of communities as well a possible connection between their web properties and their dynamics.

Comparisons with the cascade model

The cascade model (Cohen and Newman 1985, Cohen et al. 1985, Cohen et al. 1986, Newman and Cohen 1986, Cohen and Palka 1990) reproduces many of the properties observed in webs of the ECOWeB collection, and, because its predicted values vary nonlinearly with web size, it provides an additional means of extrapolating from the ECOWeB collection to relatively large webs. This model generates webs by assuming that there exists a linear ordering of species, and that there is a constant, uniform probability that each species might consume any species below it on the list. In addition, no species can consume any species above it on the list: cycles are impossible. Although these assumptions are difficult to justify biologically, similarities between observed webs and webs thus generated give the model a phenomenological justification.

Because the predictions of this model are specific to both the size of a web and the number of links per species (or the probability of a link between any two species), one of the unusual features of the St. Martin web, its relatively large number of links, is simply incorporated as a parameter into the cascade model. (We found that, for most properties, the high probability of links between species has a larger effect on the predictions than does the number of species.) Thus similarity between the web and the predictions would not

necessarily imply resemblance between the web and the rest of the ECOWeB collection, except in some underlying structure that the cascade model captures. In fact, though, the predictions of the model rarely match the observed values. Interestingly, the predictions are in the opposite direction from those taken directly from the ECOWeB collection, that is, they seem more extreme than the St. Martin web itself.

Predictions exist only for webs in which all trophically equivalent species have been lumped, so that is the only kind of comparison we make here. For these predictions, we took the number of species, S , to be 42, and the probability that a species consumes any species below it on the list, p , to be 0.238; for these values, the parameter $c = p/S = 10.0$, and the observed and predicted number of links equal 205 (Cohen et al. 1990: 84–85; in contrast, the ECOWeB collection gives a value of c around 3.72). The cascade model predicts top, intermediate, and basal species in the proportions 0.100, 0.800, and 0.100, that is, a higher proportion of intermediate species than is observed either in the St. Martin web or in the ECOWeB collection. The proportion of top predators in the cascade model has a standard deviation of 0.032, so the difference between the St. Martin web (0.167) and the predictions is statistically significant at $P < .05$. The model's standard deviation in the proportion of basal species also equals 0.032, so this difference is not statistically significant. The cascade model predicts that the ratio of predators to prey equals 1.00, which is close to the value in the St. Martin web (1.03). The cascade model predicts top-to-intermediate links, top-to-basal links, intermediate-to-intermediate links, and intermediate-to-basal links in the proportions 0.164, 0.020, 0.652, and 0.164, which represents an unusually high proportion of links among intermediate species (the St. Martin web has 0.532) and unusually low proportions of links with other levels. In general, the St. Martin web has more species and links at both its top and the bottom, and fewer in its center, than is predicted by the cascade model.

The cascade model predicts 8258 chains (Cohen et al. 1990: 119), far more than are observed (2442), and a mean chain length, 8.077, that is nearly twice what is observed (4.49). The predicted standard deviation in chain length is 2.454, again double what is observed (1.21). For the expected maximum chain length (Cohen et al. 1990: 160–163), the cascade model gives a wide range, between 6 and 20, for the median of the probability distribution for maximum chain length; the value for the St. Martin web is near the low end of this range. In general, the St. Martin web has fewer and shorter chains than is predicted by the cascade model.

Further evidence that this web does not match the cascade model is given by a comparison of two numbers that the cascade model predicts should be equal (Cohen et al. 1990: 157): the mean chain length (here, 4.49) and the number of predators plus the number of prey of each species, averaged over the whole web (here,

9.91). This and the other comparisons, although usually lacking statistical significance levels, are marked enough to indicate that the St. Martin web differs fundamentally from similarly sized webs generated by the cascade model. Intuitively, it might be thought of as shorter and wider than predicted, although it is relatively taller and thinner than the webs of the ECOWeB collection.

The cascade model predicts that the probability of having either the interval or the chordal property is virtually zero for a web with these parameters (Cohen et al. 1990: 197, 201); this prediction matches the observed lack of both properties in the St. Martin web. Cohen and Palka (1990) note that, because the cascade model predicts a marked decline in both intervality and chordality with web size, the investigation of large, relatively complete webs is likely to turn up many that are neither interval nor chordal.

The comparisons in this section emphasize two points. First, the differences between the predictions of the cascade model and the expectations based directly on ECOWeB (either with or without the linear regressions) demonstrate that extrapolations to large web sizes are not robust to differences among models. Second, the differences between the St. Martin web and any set of predictions demonstrate that this web fits no current model. Whether this lack of fit should be ascribed to shortcomings of the models or to features peculiar to this web cannot be determined at present.

DISCUSSION

One of our goals in so explicitly documenting the construction of a food web for St. Martin has been to provide a means for assessing the findings as well as the merits and shortcomings of constructing food webs in the first place. We suggest that the construction of almost any food web may, of necessity, encounter these or similar shortcomings. We offer this assessment in the order of results, procedures, and then objectives, to reflect an increasing generality in the issues raised.

Assessment of results

The size of the St. Martin web developed here distinguishes it at the outset: it is larger than 95% of those in the ECOWeB collection. However, if only its size were unusual, then the central column of Table 8 would have asterisks on its left side and not on its right. Because the asterisks on the left and right are almost always paired, the patterns in this web do not seem to represent simply a linear scaling up from webs already known. Nor does this web match the scaling of properties predicted by the cascade model.

The recent study by Polis (1991) also suggests that large food webs may yield novel information. Although his analysis uses a high as well as arbitrary level of aggregation, his findings, based on thousands of species and their trophic relationships in the Coachella Valley,

suggest that many widely accepted generalizations about food webs may not be robust to extensive data collection. Interestingly, for many web properties (such as the number of links per species, the proportion of intermediate species, the number of chains, the mean and maximum chain lengths, the number of prey per consumer, and the number of consumers per prey) the Coachella Valley web and the St. Martin web differ from the ECOWeB collection in the same direction. In most cases the values from the Coachella Valley web are even more extreme than those of the St. Martin web, which suggests that, in and of itself, the extent of the data collected may directly bias the patterns that are discovered (L. Goldwasser and J. Roughgarden, *unpublished manuscript*). Similarly, Hall and Raffaelli (1991) ascribed the unusually long chains in their web, which is also unusual in its large number of chains and its high level of omnivory, to the completeness of their data.

There are two biases that stem from the data that we have used. First, our original data centered about *Anolis* and their predators, so the web seems richer in links near them. There is an apparent (and probably misrepresentative) loss of detail, taxonomic resolution, and variability in the strength of interaction further from the lizards. By using data that were centered about two trophic levels rather than one, however, we may have reduced this effect slightly. Second, we classified the basal species (plants) by parts rather than taxa, severely limiting the richness we could find at the base of the web. These biases may have reduced the accuracy of our estimates of the standard, whole-web properties and of the proportions of links between different trophic levels.

Assessment of procedures

One source of bias in our procedures stems from our allocation of frequencies of interaction equally in the absence of further information. This procedure is not likely to yield the actual frequencies of predation, but is intended, conservatively, only to give reasonable estimates of their relative frequencies. We were interested in preserving as much of the original variability of the true web as possible, but we did not wish to create variability where we had no evidence for it. Thus we are likely to have underestimated the actual variability among species in rates of predation.

Because we included every known or suspected link in this web, we constructed a single cumulative food web rather than a series of changing, "time-specific" food webs (Schoenly and Cohen 1991). Pooling our data was unavoidable because of the incompleteness in its reporting, but it removed the possibility of seeing any changes in the web over time. One consequence of our inclusiveness is that the picture is static: it does not suggest a way of looking at or modeling the community in a dynamic way. Nor does the analysis suggest any processes by which the community arrived at ei-

ther the common or the unusual features of its structure. Although time-specific webs make more stringent demands on the data, they may answer this problem somewhat by permitting the depiction of changes in trophic relationships through time.

The comparison between web properties with trophically equivalent species initially separate and then lumped showed that the lumping procedure had a fairly minor effect for all measures and descriptions of this web. The similarity between the lumped and unlumped versions may be due to the small number of trophically equivalent species in this web. In turn, the small number of trophically equivalent species may be due to the relative completeness with which we determined links between species. Our earlier, less complete version of this web contained fewer links and more apparently equivalent species. This observation suggests that "trophic equivalence" among species may reflect lack of knowledge as much as similarity of ecological relationships. With greater knowledge of trophic relationships in a web, the question of whether to lump equivalent species in an analysis may become moot as more differences among species become apparent. Also, if the different link strengths are taken into account, the notion of trophic equivalence becomes less well defined.

We imposed a taxonomic boundary by resolving the insect groups to the level of orders. This boundary represents a compromise between the differing levels of resolution in our sources (Table 1). It increases the uniformity in resolution among the insect taxa, at the expense of discarding some of the data. This kind of sifting, which differs from the more generalized effects of changing resolution throughout the web (e.g., Martinez 1991a), seems unavoidable when combining data from partially overlapping sources. Any attempt to integrate a variety of sources is likely to face the dilemma of finding a level of resolution that minimizes both lumping existing groups, which throws away information, and splitting other groups, which introduces guesswork.

We also imposed a boundary on the web as a whole by omitting, for instance, Rummel's (1984) records of the gecko and the flea. Although these omissions helped avoid guesswork or further omissions, they raise a serious issue. The data themselves indicate that these species are trophically connected to others that we have not included: this web is part of a much larger network, and whatever compartmentalization exists is incomplete (Pimm 1982). The implication of our finished product, that this web is a closed, complete entity that does not interact significantly with the outside world, is thus misleading. This point, which probably applies to any web anywhere, is more than a casual one. A growing body of evidence suggests that the openness of ecological systems strongly affects their dynamics and structure (Roughgarden et al. 1988). Representing communities as self-contained food webs runs the risk

of omitting what may be crucial features for understanding how they work.

Assessment of objectives

We initially characterized a food web as a means of summarizing data about trophic relations, but, having come this far, we confess to a slight uneasiness with the enterprise. A food web does not seem to be a neutral receptacle: our attempt to bring disparate data within a single picture imposed a degree of taxonomic and temporal uniformity that may misrepresent both the true web and the state of our knowledge about it. Despite our depiction of it, the web is probably open rather than closed; nontrophic and spatial interactions may play important roles; links differ in variability, scale, and dependence on one another. Much ecological theory shows that these differences may strongly affect the stability and other properties of the system. On one hand, information about these differences is rarely available; on the other hand, it would be difficult to represent such information, explicitly or implicitly, in a web. The depiction of ecological relationships in terms of food webs seems vulnerable to Colwell's (1984) characterization of some of the older ecological models as reminiscent of the elaborate and quaint schemes of medieval philosophers.

We note that these reservations are caveats, not dismisals. Incorporating frequencies of trophic interactions, as we have done, adds to the information that the web can convey, and constructing a series of time-specific webs, as Schoenly and Cohen (1991) do, can suggest something of the dynamics within communities. In general, explicitly documenting the decisions made in constructing a web can mitigate the effects of simplifying a complex collection of data.

Given the tentative nature of a constructed web, it seems worth focusing an analysis on web properties that are relatively robust to minor alterations in the structure of the web. Also, because comparisons among a variety of webs introduce yet another level of heterogeneity that cannot be controlled, the web properties that prove most useful may be those that point toward features and differences within a web (such as our measures of predator-prey asymmetries) rather than between webs (such as the whole-web and topological properties). Ecologists who do not study food webs *per se* may find more use for measures that help focus on unusual features in their own systems, independent of the between-web comparisons that are of particular interest to food web specialists.

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