

TEMPORAL VARIATION IN FOOD WEB STRUCTURE: 16 EMPIRICAL CASES¹

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Abstract. Analysis of food web structure and temporal dynamics is essential to understanding energy flow and population dynamics of species, and may contribute to conservation, wildlife management, and disease and pest control. This report synthesizes all the observational studies of food web dynamics to which we have access.

Most published food webs are static and cumulative: they depict information gathered over many occasions. A web observed over a single, relatively short time period is time specific. Here we analyze the relation between cumulative and time-specific versions of webs in 16 published cases. Fourteen of the 16 webs are from detritus-based habitats that harbor large fractions of arthropod species: carcasses, tree fluxes, felled logs, treeholes, dung pads, and an acidic pond. The other two webs describe soybean fields and the arctic tundra. These webs are presented here in a consistent format and are analyzed in four ways.

First, we quantified temporal trends and levels of variation in nine web properties: the percentages of species in the web that are top predators (%*T*), intermediate species (%*I*), and basal species (%*B*); the ratio of number of prey species to number of predator species (*P*); the mean chain length (μ); the product of species richness and connectance ($S \times C$); and the numbers of total species, newly arriving species, and local extinctions. In most webs %*I* and %*T* fluctuated widely; the latter generally increased in time or remained constant, while the former correspondingly decreased or remained constant. Since the number of basal species usually varied little, changes in %*B* were inversely associated with changes in species richness over successional and seasonal time scales. Predictable changes in *P*, μ , and $S \times C$ accompanied the changes in %*B*, %*I*, and %*T*. The numbers of total species, new arrivals, and local extinctions displayed no consistent increasing or decreasing trends.

Second, we compared cumulative and time-specific webs from the same habitat to determine which properties, if any, of time-specific webs might be predicted from cumulative webs. In cumulative webs, *P*, μ , and %*T* came closest to the median of the values from time-specific webs, followed by %*I*, $S \times C$, and %*B*. Cumulative webs, which usually appear in general ecology textbooks, overestimate $S \times C$ and underestimate %*B* relative to time-specific versions. In five studies cumulative webs were completed when the last or next-to-last samples were taken; additional sampling in these cases would probably have uncovered more species.

Third, opportunistic species were removed from four time-specific webs to determine how these species influenced web structure. Removing one top-feeding opportunistic species from each web caused a dramatic rise in %*T*, small reductions in %*I*, $S \times C$, μ , and *P*, and a negligible rise in %*B*. A single opportunistic species, even though it makes only rare and brief visits to a habitat, can dramatically reshape web structure.

Fourth, properties of cumulative and time-specific versions of the 16 food webs were compared to properties of cumulative webs in two published web catalogs. The cumulative versions of the 16 webs grossly resemble the cumulative webs in both prior catalogs, but the median $S \times C$ is greater and the median %*B* is lower in the 16 cumulative webs than in either prior catalog. Even for these two statistics, the median value for the 16 cumulative webs falls well within the range of variation of both prior catalogs. The time-specific webs in the 16 cases differ from those of the two prior catalogs somewhat more than do the cumulative webs. Comparisons between time-specific and cumulative versions of a web, one system at a time, are more sensitive than rough comparisons between collections of webs because the methods used to define species and links are (usually) consistent within a study.

Key words: arthropod-rich food webs; community structure and assembly; cumulative vs. time-specific food webs; detritus-based systems; food web dynamics; food web structure; opportunistic species; predator-prey relationships; successional and seasonal variation in food webs; temporal variability; top predators.

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INTRODUCTION

Food webs summarize predator-prey relationships in ecological communities. Studies of large collections of published webs have provided several new generalizations about the organization of ecological communities (Cohen 1978, Pimm 1982, Briand 1983, Schoener 1989, Sugihara et al. 1989, Cohen et al. 1990a; for a recent review, see Lawton 1989). These generalizations are open to criticism in part because the underlying data are frequently of poor quality (e.g., see Paine 1988); the data often blur spatial and temporal heterogeneity in web structure. Most reported webs are vague about the duration of the period of observation. Here we assemble, describe, and analyze the first substantial collection of webs in which changes over time are reported in detail.

The analysis of web structure and dynamics is essential to a realistic understanding of the population dynamics of species, energy flow, and other ecological processes. Though these dynamic processes are of greater intrinsic interest than web structure for some ecologists, the study of one or a few species in theoretical or experimental isolation provides little or no useful guidance, in many instances, to the organization and likely behavior of species embedded in real communities. Moreover, an understanding of webs may contribute to diverse practical applications, such as conservation and wildlife management, pest and disease vector control, and medical (including forensic) entomology (Schoenly 1991).

Food web dynamics can be approached in three ways: theoretically, experimentally, and observationally. There are numerous theoretical studies of web dynamics (e.g., Pimm and Lawton 1977, Yodzis 1981, 1984, Post and Pimm 1983, Cohen and Newman 1988, Cohen et al. 1990b), but most dynamic models lack detailed empirical foundations. A realistic general dynamic theory of webs does not yet exist. Few experimental studies of web dynamics are available (e.g., Drake 1985, Pimm and Kitching 1987, Jenkins and Kitching 1990). Several observational field studies of individual habitats have demonstrated that webs can vary substantially in time and in space (Brooks and Dodson 1965, Beaver 1985, Kitching 1987, Warren 1989, Winemiller 1990; see also Crowder et al. 1988, Frost et al. 1988, Lodge et al. 1988, and Porter et al. 1988).

This report synthesizes all the observational studies of food web dynamics to which we have access. The observed patterns in the temporal dynamics of webs may provide empirical guidance to future theoretical developments.

Most published webs depict information gathered cumulatively, over many occasions and sometimes several locations. We will call a web gathered over many occasions within spatial limits specified by an author a "cumulative" web. Cumulative webs present

static images of trophic interactions and they routinely appear in general ecology textbooks (e.g., Odum 1983, Krebs 1985, Begon et al. 1986, Ricklefs 1990). We will call a web observed in one place over a single, relatively short time period, a "time-specific" web. Our analysis of the relation between cumulative and time-specific webs has four parts. First, using published time-specific web data, we quantify temporal variation in nine properties. Second, we compare cumulative and time-specific webs from the same habitat to determine which properties, if any, of time-specific webs might be predicted from cumulative webs. Does a cumulative web differ greatly from the time-specific webs that it cumulates? Third, we hypothetically remove opportunist species from time-specific webs to determine how much these rare but potentially important species influence web structure. Fourth, we compare properties of cumulative and time-specific webs to properties of webs in two published catalogs (Cohen et al. 1990a, Schoenly et al. 1991).

DATA SOURCES, METHODS, AND FOOD WEB STATISTICS

Sixteen food webs from eight published studies are included in this analysis (Table 1). Most webs are based on detritus that supports large numbers of arthropod species. All but two of the eight studies (Naumov 1972, Warren 1989) were part of investigations on insect trophic structure (Schoenly 1990, Schoenly et al. 1991), and in these six studies all webs but one (Robinson 1953) were classified by one of us (Schoenly et al. 1991) as community webs (as originally defined by Cohen 1978). Robinson's (1953) web is classified as a source web (the source is tree flux, or oozing sap).

In all the webs except that of Sdobnikov (1958), both vertebrates and invertebrates are identified to species and genus. Hence, the taxonomic resolution is uniform across trophic levels. In approximately one-half of these webs, predator-prey links are simply present or absent, but not otherwise quantified. Three studies include relative abundances or species biomasses (Valiela 1974, Kitching 1987, Warren 1989). In studies of small and relatively short-lived dungpats and carcasses (Valiela 1974, McKinnerney 1978), the interval between consecutive samples is short, usually only a single day. In studies of larger and more perennial habitats, like soybean fields (Mayse and Price 1978) and rotting logs (Savely 1939), the interval between samples varies from several weeks to one year.

McKinnerney (1977, 1978) studied carrion communities at three locations in the Chihuahuan Desert: Hueco Mountains, Texas (26 time-specific samples); White Sands National Monument, New Mexico (39); and Aden Crater, New Mexico (11). Prey and predator lists were collected for invertebrate species but not for vertebrates at White Sands and Aden Crater; carrion-frequenting vertebrates were not studied at the Hueco Mountains site. At Aden Crater, carcasses were sam-

pled less frequently than carcasses at the other sites, a higher proportion of species were vertebrates, and prey of vertebrates were not reported. We therefore elected to exclude the Aden Crater data set from this analysis.

The authors determined trophic links using varied methods. All the authors used direct field observation. Some studies (Savely 1939, Mayse and Price 1978, McKinnerney 1978, Warren 1989) also used literature accounts of the same or related species in different locations. In addition, Savely (1939), Robinson (1953), and Warren (1989) analyzed gut contents of some species. Valiela (1974) and Warren (1989) also performed laboratory feeding trials on selected sets of predators and prey. Details on the method(s) used by Sdobnikov (1958, cited by Naumov 1972: 549) to construct his arctic tundra webs are unavailable to us.

We constructed cumulative and time-specific webs from each study in the form of matrices, each containing one column per predator and one row per prey. When species A eats species B there is a '1' in column A and row B; otherwise there is a '0.' Where the reported data made it possible to do so, we constructed site-specific cumulative webs by cumulating over time the trophic links of reported time-specific and site-specific webs (Naumov 1972, Valiela 1974, Mayse and Price 1978, Kitching 1987, Warren 1989). Where the original report presented only a cumulative web and time-specific species lists (Robinson 1953, McKinnerney 1977, 1978), we constructed time-specific webs by assuming that a feeding link from prey A to predator B was present in the time-specific web if and only if such a link was present in the cumulative web and species A and B occurred together at the time of observation. Savely (1939: appendix) listed diets and times of occurrence of species in a form substantially equivalent to our Table A4 and Table A5. (He also graphed one time-specific web for pine logs.) We constructed cumulative and time-specific webs from his list.

McKinnerney (1978) and Mayse and Price (1978) gave detailed information about the distribution over time of sampling effort and field observations. In the other studies, temporal variation in web structure is an unknown compound of variation in the observer's sampling effort and variation in the underlying web. As have others before (e.g., R. T. Paine, as cited in Cohen 1978: 121; Winemiller 1990), we urge that future studies of temporal change in webs give explicit reports of sampling effort over time.

Our reconstructions of prey records, time data, and species lists for all 16 webs appear in the Appendix. Cumulative and time-specific webs from each study will be available in version 2 of ECOWeB. One set of time-specific webs from each of four published reports (Savely 1939, Valiela 1974, Mayse and Price 1978, McKinnerney 1978) is already available in version 1 of ECOWeB (Cohen 1989).

Warren (1989) drew time-specific web graphs for two

sites (the margin and open water) in a pond at Skipwith observed on each of five sampling dates. Warren observed the relative abundance, life-history stage, and length of organisms. In his data, unlike the data from all the other studies, the simultaneous presence of two species A and B does not automatically imply a feeding relation between them, even if there is a feeding relation between them in the cumulative web, because "not all sizes or stages of particular species can feed on all sizes or stages of another species" (P. H. Warren, *personal communication*, 4 April 1990).

Because of inconsistencies between field workers in the reporting of cannibalism, we elected simply to exclude cannibalistic links. This decision accords with the practice of some other investigators (e.g., Pimm 1982: 125; Cohen et al. 1990a, Schoenly et al. 1991). Reported cannibalistic links are included in the Appendix but were dropped prior to our analyses.

The only reported cases of mutual predation (i.e., species A eats species B and simultaneously species B eats species A) occurred in the Queensland tree-hole webs of Kitching (1987: 281, Fig. 1). There each of three species (numbered 6, 7, and 8 in our Table A6) is reported to prey on both of the other two. This reported mutual predation is also consistent with the feeding relations reported for these three species in a more recent report by the same author (Jenkins and Kitching 1990: 200, Fig. 1) but was not reported consistently in three other studies (Kitching 1983: 216, Fig. 8, Kitching and Pimm 1985: 133, Fig. 4a, Kitching and Beaver 1990: 152, Fig. 9.2). R. L. Kitching (*personal communication*, 12 July 1990) stated that his 1987 analysis used "a slightly different form of presentation than the earlier descriptive papers and did not require the same degree of detail in the web used." We included these links of apparent mutual predation in the Appendix. However, as we did for cannibalism, we excluded all links among these three species prior to analysis to make Kitching's data more comparable to the data in the seven other reports.

There were no predatory cycles of length 3 (i.e., A eats B, B eats C, and C eats A) or longer in any of the webs. Consequently, after the exclusion of cannibalism and of Kitching's report of mutual predation, all webs were acyclic.

Quantitative measures of web structure were calculated for each time-specific web and, where applicable, each cumulative web. These statistics are based on investigator-defined species and links, not on trophic species and trophic links obtained by lumping (lumping is defined by Briand and Cohen [1984]). The first six statistics (a-f) apply to both time-specific and cumulative webs:

a) %T, the percentage of top predators in the web, i.e., 100 times the number of species with no reported predators divided by *S*, the total number of species reported in the web (Briand and Cohen 1984);

b) %I, the percentage of intermediate species, i.e.,

TABLE 1. Structural statistics of time-specific and cumulative versions of 16 food webs.

Food web	N*	% top species (%T)			% intermediate species (%I)			% basal species (%B)			Prey/Predator (P)		
		Range†	Med.‡	Cum.§	Range	Med.	Cum.	Range	Med.	Cum.	Range	Med.	Cum.
Carrion; Hueco Mts., USA	27	4-86	55	34	0-92	41	64	4-25	6	2	0.17-1.0	0.48	0.67
Carrion; White Sands, USA	40	67-92	83	76	0-22	7	20	5-33	7	4	0.08-0.50	0.20	0.25
Elm flux; Sheffield, United Kingdom	25	29-50	33	25	25-57	50	63	14-33	17	12	0.66-1.0	0.89	0.86
Pine logs; N. Carolina, USA	5	57-70	65	61	26-38	32	35	3-5	5	4	0.31-0.45	0.37	0.41
Oak logs; N. Carolina, USA	5	54-76	67	70	21-40	29	26	3-6	5	4	0.25-0.49	0.35	0.32
Treeholes; Australia, site 1	5	13-38	29	10	24-49	32	60	38-40	38	30	1.0-1.40	1.17	1.29
Treeholes; Australia, site 2	5	10-43	31	9	28-60	31	64	29-43	31	27	0.80-1.29	1.13	1.25
Treeholes; Australia, site 4	5	29-44	37	40	23-33	29	30	30-43	33	30	0.83-1.75	0.93	0.86
Treeholes; Australia, site 5	5	29-38	34	30	24-40	26	40	30-43	38	30	1.0-1.25	1.0	1.0
Treeholes; Australia, site 10	5	25-33	29	33	33-37	35	33	33-38	36	33	1.0-1.20	1.1	1.0
Treeholes; Australia, site 11	5	14-50	29	40	12-43	35	30	33-43	38	30	0.80-1.50	1.1	0.86
Soybean; Illinois, USA	3	29-33	31	33	57-60	59	60	7-14	11	7	0.71-0.83	0.77	0.71
Arctic tundra; USSR	3	45-50	48	45	33-40	37	40	15-17	16	15	0.60-0.65	0.62	0.65
Dung; New York, USA	3	37-45	39	41	52-61	57	57	2-3	3	2	0.57-0.64	0.61	0.60
Pond; United Kingdom, open water site	6	17-38	21	18	54-79	73	78	4-8	6	4	0.67-0.87	0.83	0.85
Pond; United Kingdom, pond margin site	6	19-26	25	24	70-77	72	73	3-5	4	3	0.76-0.84	0.79	0.78

* The number of time-specific webs plus the cumulative version.

† Range of variation in the time-specific versions.

‡ Median in the time-specific versions.

§ Value for the cumulative version.

|| C = connectance, the ratio of actual links to possible links in a food web.

100 times the number of species with both predators and prey, divided by S ;

c) %B, the percentage of basal species (pure autotrophs and detritus), i.e., 100 times the number of species with no reported prey, divided by S ;

d) P , the ratio of the number of prey species to the number of predator species (Cohen 1977);

e) μ , the mean chain length of the web, i.e., the average length (counting links, not counting species) of all maximal food chains from a basal species to a top predator (Cohen 1978);

f) $S \times C$, the product of species richness S and connectance C , where $C = L/[S(S-1)/2]$ and L is the number of predator-prey links reported in the web (Briand 1983). Thus $S \times C = 2L/(S-1)$ is very nearly twice the ratio of links to species.

The following characteristics pertain only to time-specific webs:

g) S , the total number of species (species richness), defined as the number of investigator-defined species observed in a particular time-specific web.

h) The number of newly arriving species, defined as the number of investigator-defined species who were not observed in any previous time-specific web. For the first time-specific web, the number of newly arriving species is defined to equal the number of total species.

i) The number of local extinctions, defined as the number of investigator-defined species that are present in the current time-specific web and are absent from the next time-specific web, the *first* time that such species disappear.

By definition, the statistics on new arrivals and local extinctions pertain to the first interval during which species are present in the web. For example, if a species is present in a first time-specific web, is absent from a second, reappears in a third, and is absent from a fourth, it is not counted as a newly arriving species at the time of the third time-specific web, and it is not counted as a local extinction at the time of the fourth web.

RESULTS

Temporal variation in food web properties

Food web structure varies substantially over time (Figs. 1-7). We shall summarize this variability using the median, over all 16 webs, of the range of each statistic over the time-specific versions. Among the trophic positions %I varies most, with a median range of 21, followed closely by %T at 18, and %B at 6 (Table 1). Large fluctuations in both %I and %T reflect extensive reshuffling of species with different diets and residence times in the community. Since the number

TABLE 1. Continued.

Mean chain length (μ)			Total no. species (S)			No. links (L)			$S \times C \parallel = 2L / (S - 1)$			Reference(s)
Range	Med.	Cum.	Range	Med.	Cum.	Range	Med.	Cum.	Range	Med.	Cum.	
1.0-3.30	1.77	2.55	4-28	16	47	3-92	36	195	2.0-8.06	4.4	8.48	McKinnerney (1977, 1978)
1.0-1.65	1.25	1.65	3-20	14	25	2-39	22	50	2.0-4.22	2.62	4.17	McKinnerney (1977, 1978)
1.5-2.25	2.20	2.17	4-7	6	8	3-9	7	11	2.0-3.0	2.8	3.14	Robinson (1953)
2.0-2.55	2.34	2.43	36-86	55	112	47-156	75	192	2.57-3.67	2.82	3.46	Savelly (1939)
2.09-2.64	2.41	2.47	48-88	81	139	70-117	116	199	2.69-2.99	2.90	2.88	Savelly (1939)
2.0-2.67	2.0	2.75	5-8	8	10	4-11	9	19	2.0-3.14	2.57	4.22	Kitching (1987)
2.0-2.77	2.0	2.76	7-10	7	11	7-16	10.5	21	2.33-3.56	2.96	4.2	Kitching (1987)
1.67-1.89	1.75	1.8	7-10	9	10	6-11	9.5	12	1.98-2.75	2.35	2.67	Kitching (1987)
1.5-1.9	1.64	1.9	7-10	8	10	5-13	6.5	13	1.67-2.89	1.86	2.89	Kitching (1987)
1.67-1.89	1.8	1.89	6-9	8	9	6-11	8	11	2.0-2.75	2.29	2.75	Kitching (1987)
1.67-2.0	1.8	1.8	7-9	8	10	7-9	7.5	12	2.0-2.33	2.27	2.67	Kitching (1987)
2.0-2.27	2.14	2.27	7-15	11	15	10-35	22.5	35	3.33-5.0	4.17	5.0	Mayse and Price (1978)
1.79-1.91	1.86	1.91	12-20	16	20	23-54	39	54	4.18-5.68	4.93	5.68	Naumov (1972, after Sdobnikov 1958)
3.23-3.59	3.41	3.51	29-43	36	46	86-211	149	218	6.14-10.1	8.1	9.69	Valiela (1974)
2.04-3.85	3.17	3.76	13-24	18	28	29-110	69	134	4.83-9.65	8.12	9.93	Warren (1989)
3.72-4.57	4.03	4.81	26-34	26	37	75-194	136	262	7.9-12.52	10.9	14.6	Warren (1989)

of basal species in most webs varies little, changes in %B are inversely associated with changes in S .

We now present detailed graphs and describe temporal variation in web structure, one property at a time, for seven of the most frequently sampled cases (McKinnerney 1977, Hueco Mountains and White Sands sites; Robinson, 1953, elm flux; Savelly 1939, oak and pine logs; Warren 1989, margin and open water sites; Figs. 1-7). Temporal variation in the remaining nine cases (Kitching 1987, six sites; Mayse and Price 1978, Naumov 1972, Valiela 1974) is summarized in Table 1.

In a rabbit necrovore study of McKinnerney (1978) in the Hueco Mountains, Texas, %T and %I change dramatically, with values spanning nearly the entire possible range for these properties (Fig. 1a,b). High numbers of both new arrivals and local extinctions are strongly influenced by the quality and availability of carcass resources, and account for a substantial fraction of the total variation. Early successional species, such as carrion-breeding flies, that are at first intermediate species later become top predators after their natural enemies leave the carcass. As the time since carcass deposition increases, detritivorous species become more numerous than predators. As a result, P , μ , and $S \times C$ also decrease (Fig. 1d-f). Similar trends in %T, %I, P , μ , and $S \times C$ are observed on carrion in White Sands

(McKinnerney 1978) (Fig. 2) and in decaying oak logs and pine logs (Savelly 1939) (Figs. 4 and 5).

The elm flux web of Robinson (1953) has fewer species and seasonal rather than successional turnover of species. Compared to the webs of McKinnerney and Savelly, variation in all properties is dampened considerably in the flux web (Fig. 3a-f). This reduced variation may be largely attributable to an uninterrupted presence of flux material—a sap oozing from branch scars of elms—and the nearly continuous presence of four arthropod species (numbered 1, 2, 4, and 7 in the Appendix) that live and breed in the flux material year round. This web appears to owe its low level of temporal variability to a relatively stable basal resource, elm flux.

According to Warren (1989), both the margin and the open water of an acidic pond at Skipwith Common held increasing numbers of species from mid-March to early October (Figs. 6g and 7g). Accompanying these changes were increases in μ and $S \times C$, slight decreases in %B, and varying trends in %T, %I, and P (a-f in Figs. 6 and 7). More litter and more species were found in the pond margin than in open water. Warren (1989) hypothesized that higher energy input in the pond margin may have contributed to the observed differences between the two sites in species richness and food-chain lengths.

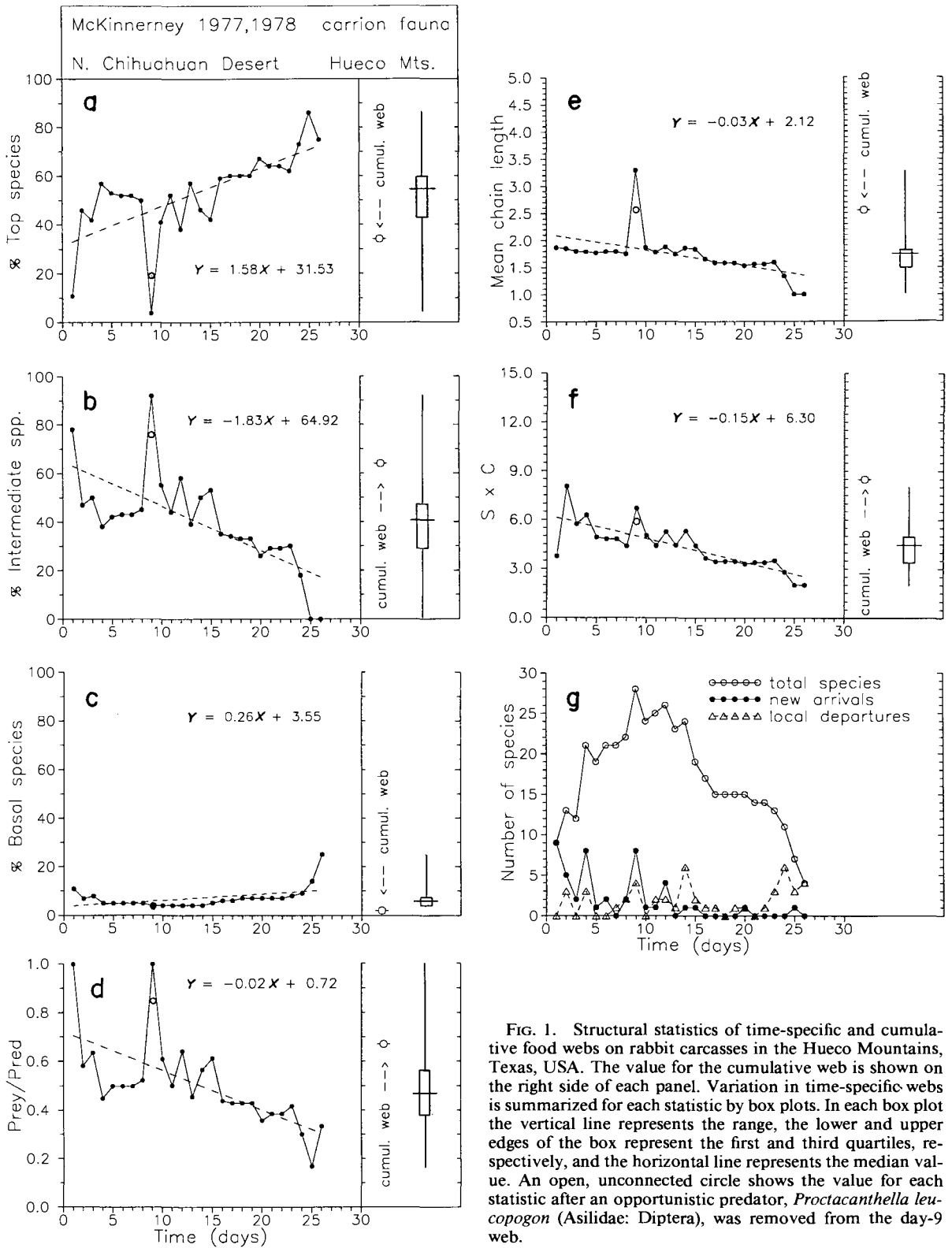


FIG. 1. Structural statistics of time-specific and cumulative food webs on rabbit carcasses in the Hueco Mountains, Texas, USA. The value for the cumulative web is shown on the right side of each panel. Variation in time-specific webs is summarized for each statistic by box plots. In each box plot the vertical line represents the range, the lower and upper edges of the box represent the first and third quartiles, respectively, and the horizontal line represents the median value. An open, unconnected circle shows the value for each statistic after an opportunistic predator, *Proctacanthella leucopogon* (Asilidae: Diptera), was removed from the day-9 web.

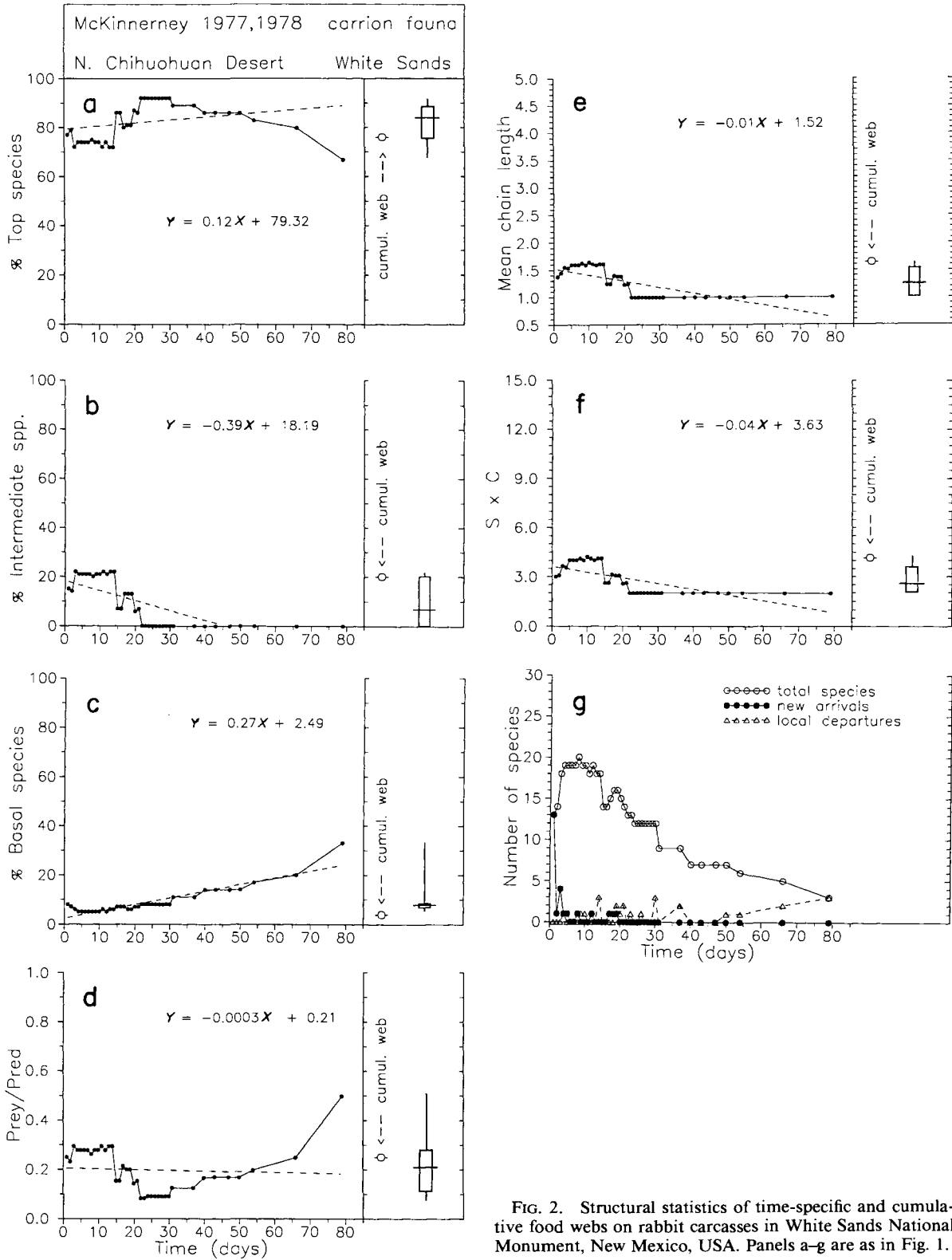


FIG. 2. Structural statistics of time-specific and cumulative food webs on rabbit carcasses in White Sands National Monument, New Mexico, USA. Panels a-g are as in Fig. 1.

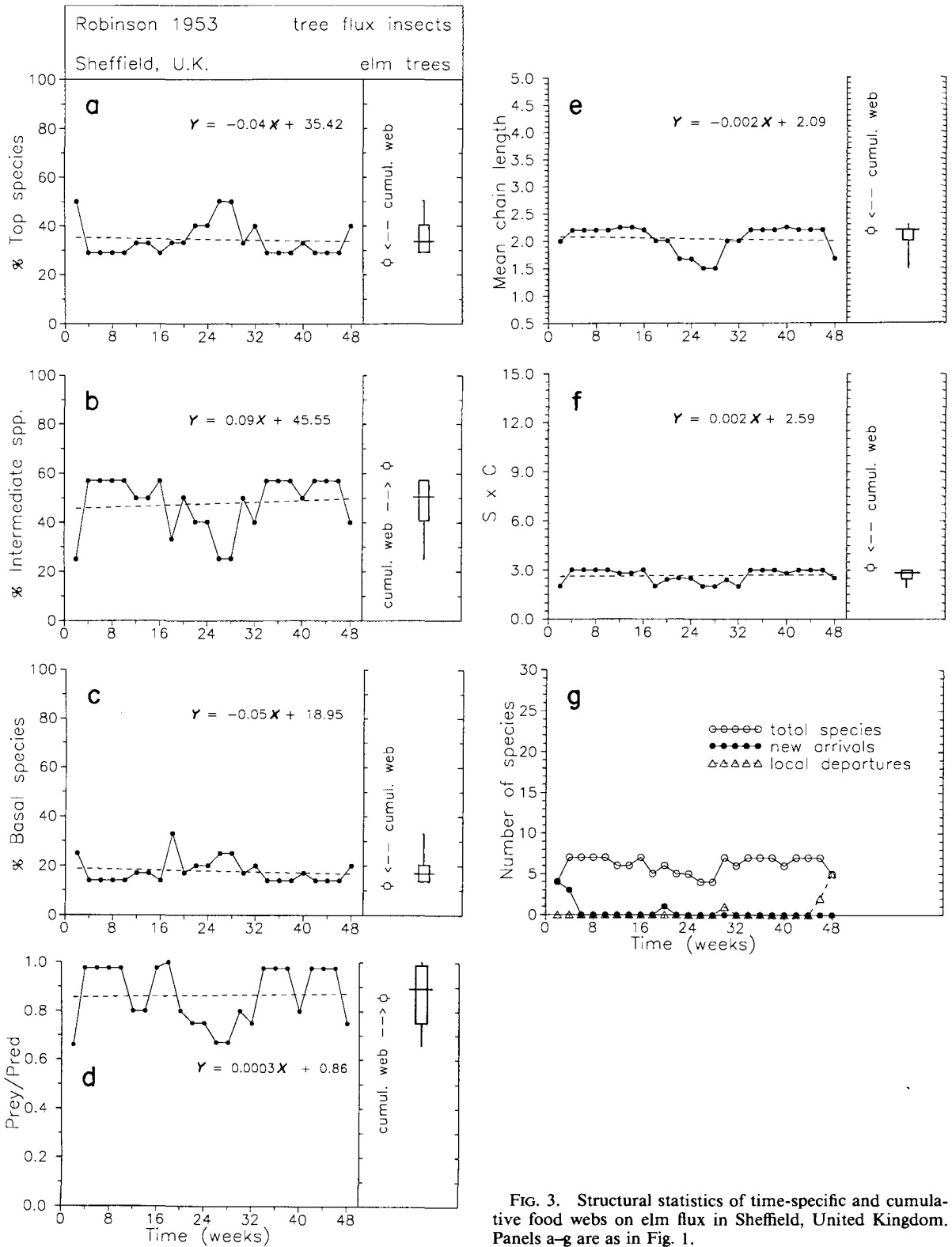


FIG. 3. Structural statistics of time-specific and cumulative food webs on elm flux in Sheffield, United Kingdom. Panels a-g are as in Fig. 1.

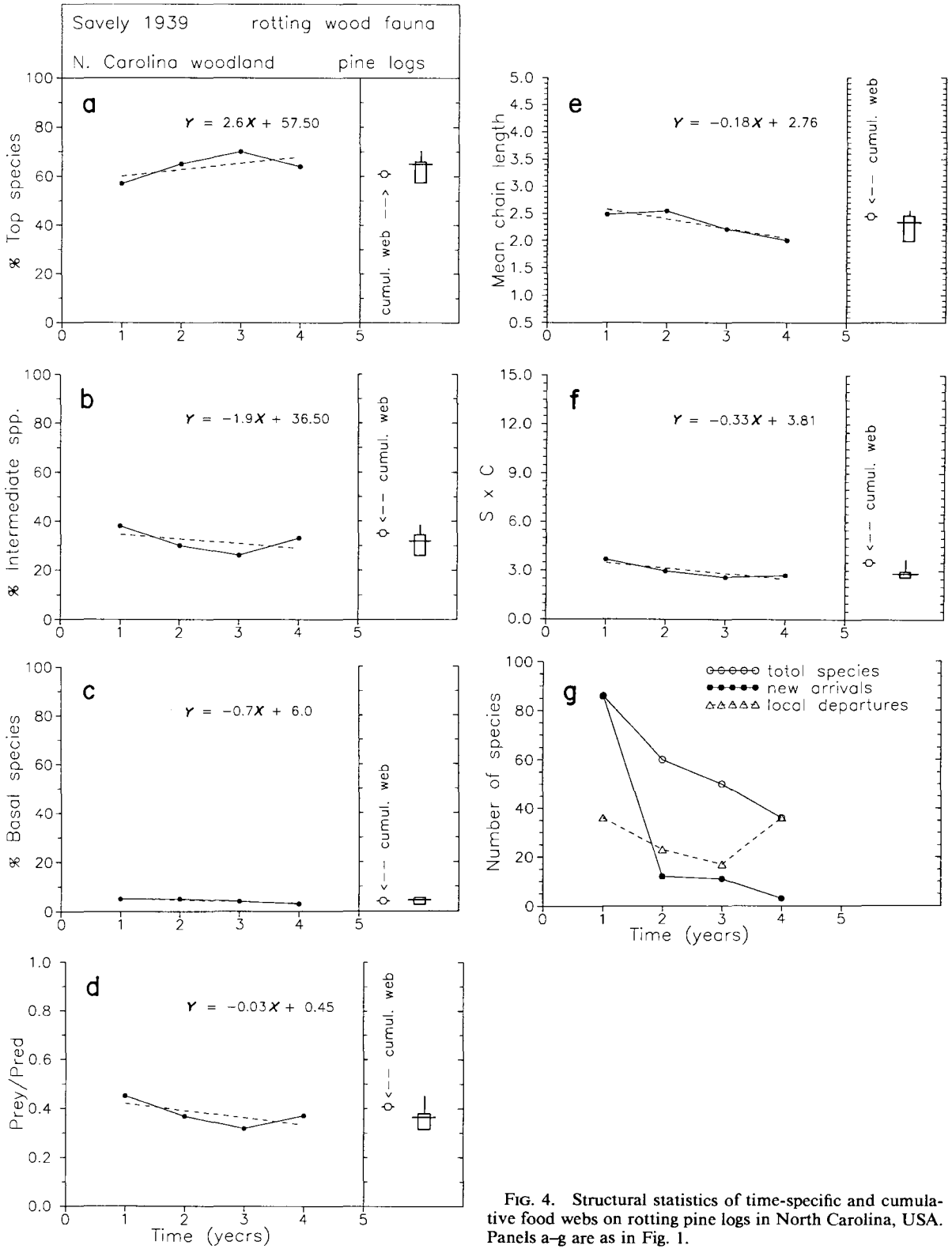


FIG. 4. Structural statistics of time-specific and cumulative food webs on rotting pine logs in North Carolina, USA. Panels a-g are as in Fig. 1.

Several overall temporal patterns emerge. We shall describe these patterns in qualitative terms, without attempting to attach levels of statistical significance to the slopes of the regressions shown in Figs. 1–7, because successive data points within each panel in these figures are not statistically independent.

In six of the seven webs pictured the proportion of top species either increases or is nearly constant over time; in the exceptional cases (Warren's open water site, Fig. 6a), %*T* decreases very slightly. Except for the White Sands carrion study, there is little increasing or decreasing temporal trend in %*B*. It follows that where %*T* increases and %*B* is roughly constant in time, %*I* must decrease. These patterns determine the behavior of the prey/predator ratio $P = (\%B + \%I)/(\%I + \%T) = (\%B + \%I)/(100 - \%B)$, for if %*B* is constant and %*I* is decreasing in time, then *P* must be decreasing in time. This is indeed generally the case (d in Figs. 1–7), again with the not very strong exception of Warren's open water site (Fig. 6d). Further, if %*T* increases, %*B* is roughly constant, and %*I* decreases in time, and if the presence or absence of a link between any two species does not depend on time, then μ should decrease in time, since there are relatively fewer intermediate species among which a food chain can travel before terminating in a top species. Indeed, μ remains constant or decreases with time in Figs. 1–5 (series e). In Figs. 6e and 7e the regressions of mean chain lengths increase slightly with time amid substantial fluctuations in the individual points, giving only weak evidence for a real increase in mean chain lengths. The temporal pattern of $S \times C = 2L/(S - 1)$ (f in Figs. 1–7) corresponds exactly to the temporal pattern of μ ; in each case, both $S \times C$ and μ increase, or both decrease, or both are nearly constant in time. Careful comparison of $S \times C$ and μ , study by study, shows that even minor fluctuations in one variable are often reflected in the other.

The correspondence between $S \times C$ and μ has a simple but rough (not exact) explanation. Any chain of *n* links contains *n* + 1 species, so the longer a chain is, the higher the ratio of links to species for that chain. (For example, a chain of one link has a links-to-species ratio of 0.5, while a chain of four links has a links:species ratio of 0.8.) Therefore, the higher the mean chain length, the higher is the mean links:species ratio over all chains, counting each link and each species as many times as it occurs in a chain. The mean links:species ratio over all chains does not correspond exactly to $S \times C = 2L/(S - 1)$, because the latter counts each link and each species exactly once, but it is not surprising that the mean links:species ratio over all chains and $S \times C$ vary similarly.

Thus the temporal patterns in %*B*, %*I*, and %*T* (series a–c of Figs. 1–7) largely or approximately determine the temporal patterns of the prey:predator ratio *P*, the mean chain length μ , and $S \times C$.

Changes over time in the numbers of total species, newly arriving species, and local species extinctions followed a diversity of patterns (g in Figs. 1–7). The numbers of total species showed a unimodal peak in two cases (McKinnerney's webs, for which reported sampling effort was nearly uniform over time), three cases of increasing trend (g in Figs. 5–7), one case of decreasing trend (Fig. 4g), and one case of essentially no trend (Fig. 3g). As a whole, the number of total species displayed no systematic trend. If most observers (other than McKinnerney and Mayse and Price) had systematically increased or systematically decreased their sampling effort over time, one might have expected a similar systematic pattern in the number of total species reported (superimposed on possible successional or seasonal effects on the number of total species). The absence of such systematic patterns in the number of total species, plus the presence of systematic patterns in some other features, such as the percentage of top species, suggests that these systematic patterns in other features are genuine, and not artifacts of changes in sampling effort.

The numbers of newly arriving species and local species extinctions similarly displayed no systematic increasing or decreasing trend over time, as a whole (g in Figs. 1–7). These statistics describe the great majority of the appearances of species in these webs, because in most webs most species were present for a single interval (Table 2). For example, in the Hueco Mountains 94% of the 47 species observed appeared only for a single interval, never reappearing after once going locally extinct; the remaining 6% of species were reported as present in two intervals of time-specific webs. Only in the elm flux web of Robinson (1953) were less than half of the species present for a single interval.

The cumulative web is determined when the last new species arrives. In three of the seven webs illustrated (Savely 1939, oak logs and pine logs; Warren 1989, open water site), the cumulative webs were completed when the last samples were taken (g in Figs. 4–6), and in two other webs (Hueco Mountains rabbit carrion, McKinnerney 1978; pond margin, Warren 1989), in the next-to-last sample (g in Figs. 1 and 7). However, in the White Sands carrion web and the elm flux web the cumulative web was reached before one-half of the samples had been taken (day 19 and week 20, respectively; g in Figs. 2 and 3).

These observations strongly suggest that additional sampling might have uncovered additional species in the first five cases mentioned. It seems very unlikely that the cumulative webs in these cases really include all the species that visit these communities. But it is possible that some species arrive only as a resource (carcass, log, or dungpat) is almost completely consumed; Schoenly and Reid (1987) refer to such species in carrion as members of the "endpoint fauna."

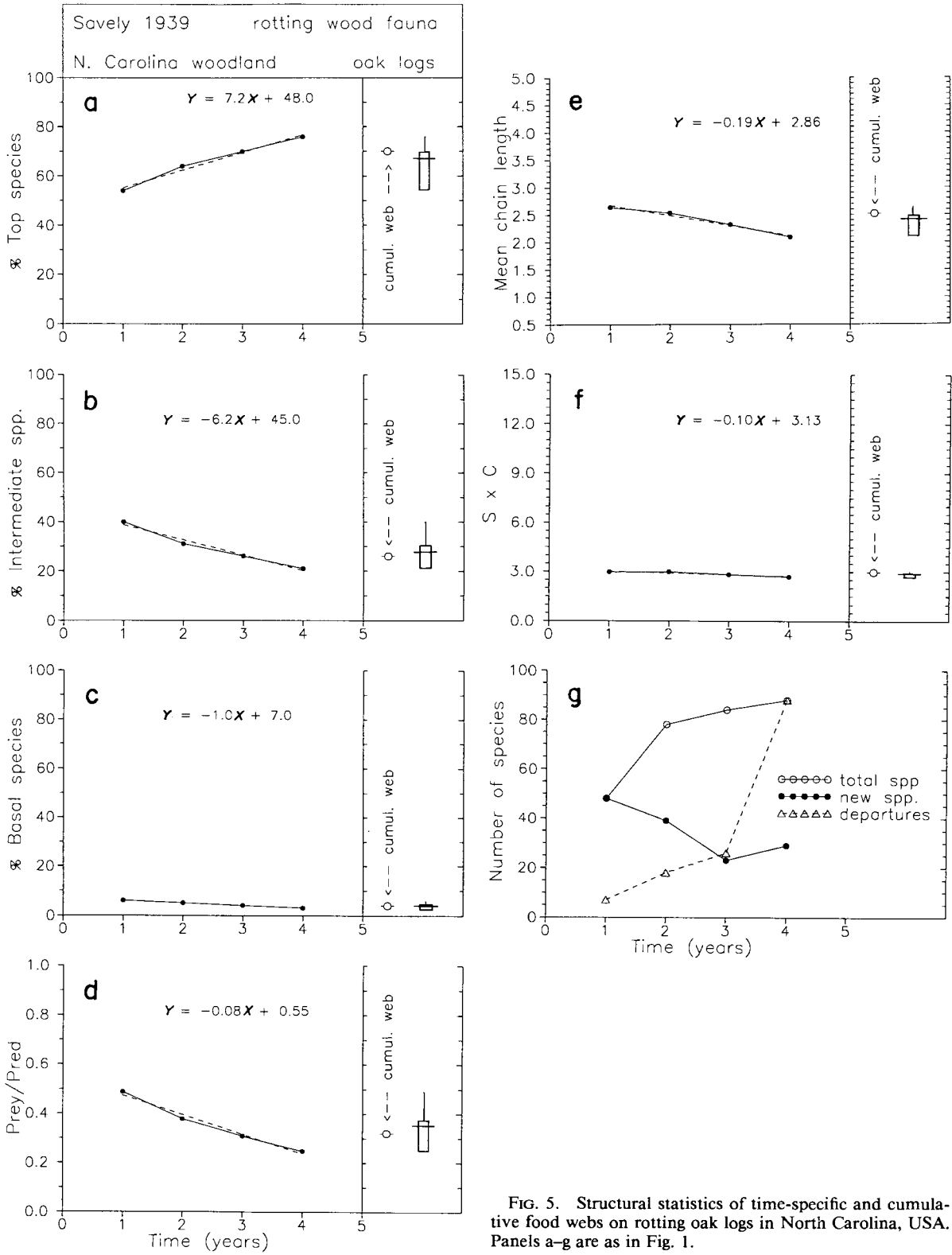


FIG. 5. Structural statistics of time-specific and cumulative food webs on rotting oak logs in North Carolina, USA. Panels a-g are as in Fig. 1.

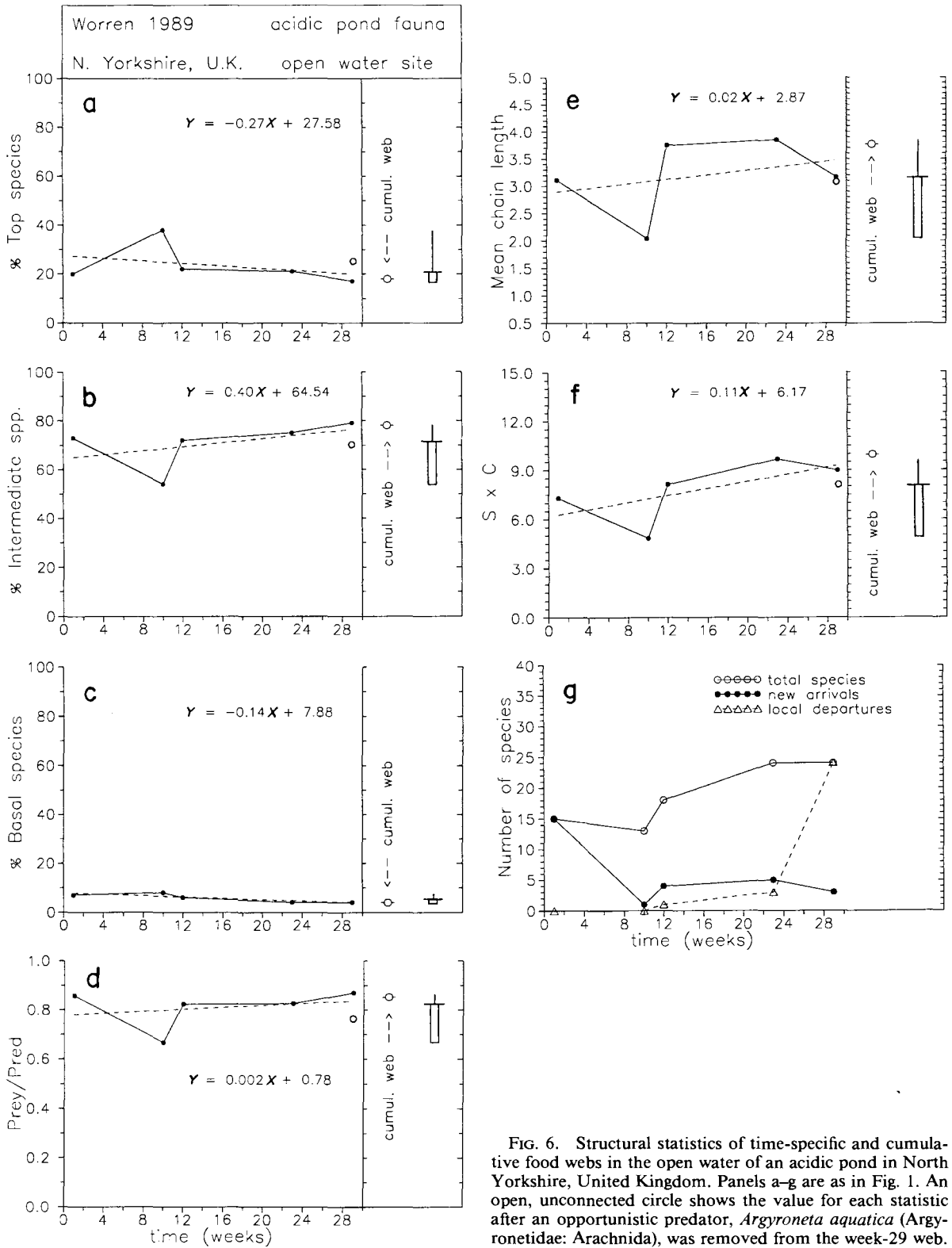


FIG. 6. Structural statistics of time-specific and cumulative food webs in the open water of an acidic pond in North Yorkshire, United Kingdom. Panels a-g are as in Fig. 1. An open, unconnected circle shows the value for each statistic after an opportunistic predator, *Argyroneta aquatica* (Argyronetidae: Arachnida), was removed from the week-29 web.

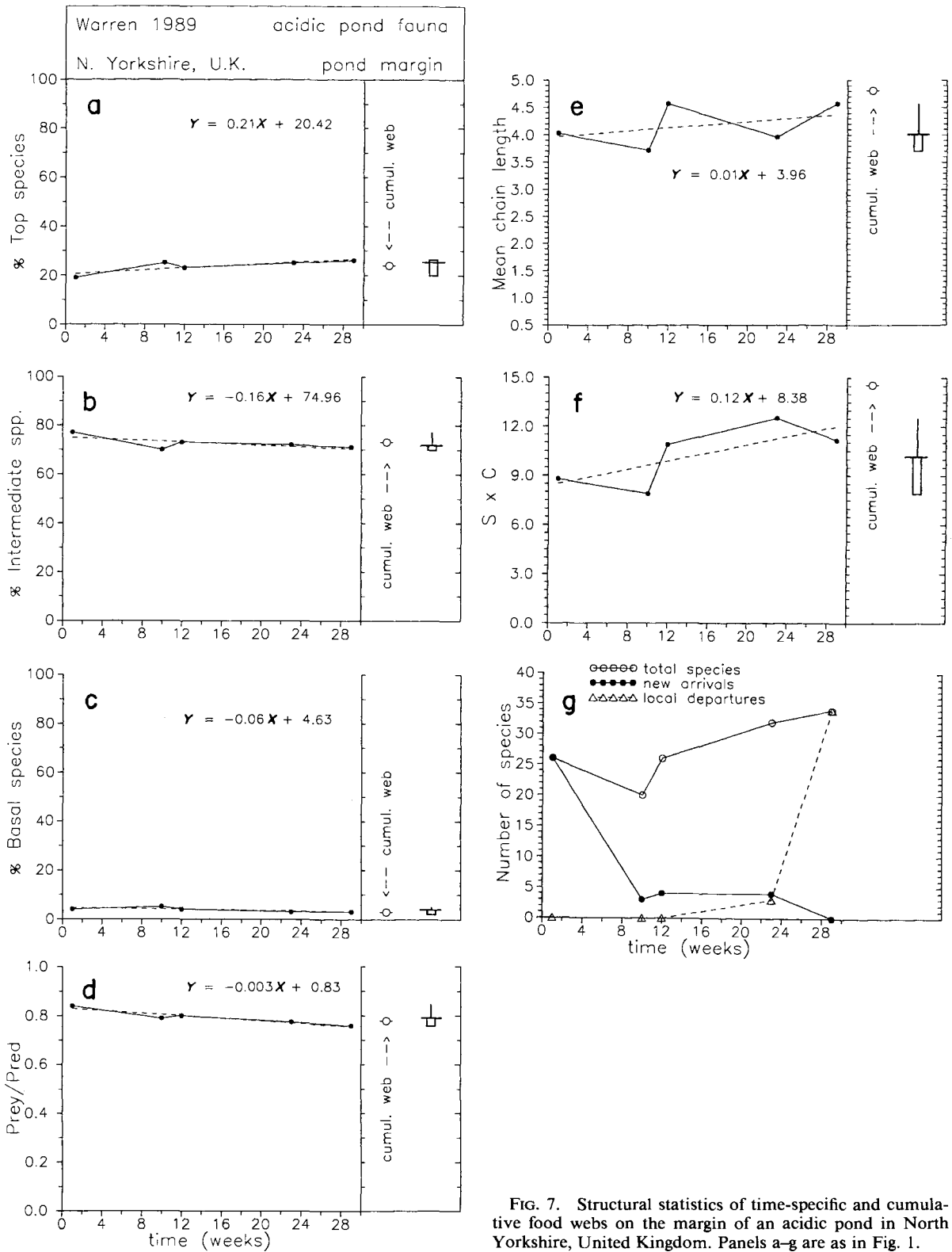


FIG. 7. Structural statistics of time-specific and cumulative food webs on the margin of an acidic pond in North Yorkshire, United Kingdom. Panels a-g are as in Fig. 1.

TABLE 2. Frequency of observation and frequency of appearance of species in 16 food webs.

Food web	Number of investigator-defined taxa (<i>S</i>)	Number of time-specific webs	Average interval between time-specific webs*	Number of intervals taxon was observed			
				1	2	3	4
				(% of taxa)			
Carrion; Hueco Mts., USA	47	26	1 d	94	6	0	0
Carrion; White Sands, USA	25	39	2.0 d	88	12	0	0
Elm flux; Sheffield, United Kingdom	8	24	2 wk	38	50	0	12
Pine logs; N. Carolina, USA	112	4	1 yr†	100	0	0	0
Oak logs; N. Carolina, USA	139	4	1 yr†	99	1	0	0
Treeholes; Australia, site 1	10	4	1.7 mo	80	20	0	0
Treeholes; Australia, site 2	11	4	1.7 mo	73	27	0	0
Treeholes; Australia, site 4	10	4	1.7 mo	80	20	0	0
Treeholes; Australia, site 5	10	4	1.7 mo	100	0	0	0
Treeholes; Australia, site 10	9	4	1.7 mo	100	0	0	0
Treeholes; Australia, site 11	10	4	1.7 mo	90	10	0	0
Soybean; Illinois, USA‡	15	2	9 wk
Arctic tundra; USSR‡	20	2	6 mo
Dung; New York, USA‡	46	2	4 d
Pond; United Kingdom, open water site	28	5	7.0 wk	86	14	0	0
Pond; United Kingdom, pond margin site	37	5	7.0 wk	62	35	3	0

* When time-specific webs were reported at fixed intervals, the average interval is reported without a decimal point. When time-specific webs were reported at irregular intervals, the average interval is reported with a decimal point.

† See Tables A4 and A5.

‡ The number of intervals observed was calculated only for studies with four or more time-specific webs.

Cumulative vs. time-specific webs

The 16 cumulative webs had from 8 to 139 investigator-defined species (Table 1). The median number of species was 17.5. The webs had from 11 to 262 links, with a median of 43 links. The number of investigator-defined species is greater than or equal to the number of lumped trophic species, and the number of links

among investigator-defined species is greater than or equal to the number of links among trophic species (Cohen et al. 1990a).

We now compare each property in each cumulative web with the range of values of that property in time-specific versions of the same web (Table 1). If the cumulative value falls outside the range from the corresponding time-specific webs, then we shall say that

TABLE 3. Comparison of cumulative and time-specific versions of the same web.

Food web	% change*					<i>S</i> × <i>C</i> †
	Percentage top species (% <i>T</i>)	Percentage intermediate species (% <i>I</i>)	Percentage basal species (% <i>B</i>)	Prey/Predator (<i>P</i>)	Mean chain length (μ)	
Carrion; Hueco Mts., USA	-38	56	-67	40	44	93
Carrion; White Sands, USA	-8	186	-43	25	32	59
Elm flux; Sheffield, United Kingdom	-24	26	-29	-3	-1	12
Pine logs; N. Carolina, USA	-6	9	-20	10	4	23
Oak logs; N. Carolina, USA	4	-10	-20	-9	2	-1
Treeholes; Australia, site 1	-66	88	-21	10	38	64
Treeholes; Australia, site 2	-71	106	-13	11	38	42
Treeholes; Australia, site 4	8	3	-9	-8	3	14
Treeholes; Australia, site 5	-12	54	-21	0	16	55
Treeholes; Australia, site 10	14	-6	-8	-9	5	20
Treeholes; Australia, site 11	38	-14	-21	-22	0	18
Soybean; Illinois, USA	6	2	-36	-8	6	20
Arctic tundra; USSR	-6	8	-6	5	3	15
Dung; New York, USA	5	0	-33	-2	3	20
Pond; United Kingdom, open water site	-14	7	-33	3	19	22
Pond; United Kingdom, pond margin site	-4	1	-25	-2	19	34
Median	-6%	8%	-21%	-1%	6%	21%
Range	109	200	61	62	45	94

* % change = [(cumulative value - median time-specific value)/median time-specific value] × 100. Positive numbers indicate that the cumulative value exceeded the median time-specific value.

† *S* = species richness, and *C* = connectance = the ratio of actual links to possible links in a food web.

TABLE 4. Comparison of webs before and after a single opportunistic species was removed.

Food web property*	McKinnerney (1977) (Hueco Mts. site, day 9)			Kitching (1987) (site 1, time 1)			Kitching (1987) (site 2, time 1)			Warren (1989) (open water, week 29)		
	With <i>P. leucopogon</i>	Without <i>P. leucopogon</i>	% change	With <i>L. fletcheri</i>	Without <i>L. fletcheri</i>	% change	With <i>L. fletcheri</i>	Without <i>L. fletcheri</i>	% change	With <i>A. aquatica</i>	Without <i>A. aquatica</i>	% change
% <i>T</i>	4	19	375	13	29	123	10	33	230	17	26	53
% <i>I</i>	92	77	-16	49	29	-41	60	33	-45	79	70	-11
% <i>B</i>	4	4	0	38	42	11	30	33	10	4	4	0
<i>P</i>	1.00	0.85	-15	1.4	1.25	-11	1.29	1.0	-22	0.87	0.77	-11
μ	3.30	2.55	-23	2.67	2.0	-25	2.77	2.0	-28	3.17	3.08	-3
$S \times C$	6.72	5.94	-12	3.14	2.33	-26	3.56	2.75	-23	8.96	8.00	-11

* *T* = top species, *I* = intermediate species, *B* = basal species, *P* = prey/predator, μ = mean chain length; *S* = species richness, and *C* = connectance (the ratio of actual links to possible links in a food web).

the cumulative web is a bad fit to the time-specific data. Table 1 reveals that in 21 out of 96 comparisons (22%) the fit is bad. The $S \times C$ statistic has seven bad fits, followed by %*B* (6), %*T* and %*I* (3 each) and μ (2). The prey-to-predator ratio was the only property for which no bad fits were found. In 1 of the 16 webs (Kitching 1987: site 1), cumulative values give bad fits for nearly every property (Table 1).

To display the magnitude as well as the direction of differences between cumulative and time-specific webs, Table 3 lists the percent by which each cumulative statistic deviates from the time-specific median value, for each web. In cumulative webs, *P*, μ , and %*T* provide the closest fit to time-specific data, followed by %*I*, $S \times C$, and %*B*. %*B* in cumulative webs always underestimates the median %*B* in time-specific webs, sometimes by as much as two-thirds. The statistics μ , %*I*, and $S \times C$ in cumulative webs usually overestimate the corresponding medians in time-specific webs. There is no systematic trend in the signs of the percentage changes of *P* and %*T*.

Opportunist species

We define a top-feeding opportunist as a top predator with wide feeding habitats, observed in only one time-specific web by an author. Such opportunists may be described as incidental species because they are sometimes represented by only a single individual.

Top-feeding opportunists are reported in one-fourth to one-third of the webs collected here and may occur (unreported) in others. The potential significance of opportunist species in altering web structure can be illustrated in at least three of these studies (McKinnerney 1977, Kitching 1987, Warren 1989).

During a 26-d study of carrion in the Hueco Mountains (McKinnerney 1977), the robber fly *Proctacanthella leucopogon* (Williston) appeared and left on day 9 as a single individual. This species was a potential predator on "all the taxa present concurrently, except beetles and ants" (M. Conley, *personal communica-*

tion, 8 September 1989; G. Forbes, a Ph.D. student working on robber flies in the region, confirmed Conley's findings, 8 September 1989). It was the only top predator on day nine. If *P. leucopogon* and its 17 prey links are removed from the day-9 web, five properties change markedly (see open, unconnected circles in Fig. 1). Compared to the day-9 web with *P. leucopogon*, the web without it had a 5-fold increase in %*T* and 1.2-fold drops in all other structural statistics except %*B* (Table 4). Deleting *P. leucopogon* from the day-9 web tightens the linear relationships of each web property with time (Fig. 1).

Kitching (1987) recorded eggs and tadpoles of the leptodactylid frog *Lechriodus fletcheri* (Boulenger) in Australian treeholes at two study sites during 3 mo of the year (time period 1, see Appendix). This species is cannibalistic and preys on all other treehole inhabitants except ostracods and algophagid mites (Kitching 1987). Compared to the webs with *L. fletcheri*, the versions without it showed the same qualitative changes as the day-9 carrion web of McKinnerney (1977): %*I*, *P*, μ , and $S \times C$ decreased, whereas %*B* increased (Table 4).

When the water spider *Argyroneta aquatica* (Clerk) and its prey links were removed from the open-water, week-29 Skipwith pond web of Warren (1989), %*T* changed by 53%, whereas %*B* and μ varied little (Fig. 6: open unconnected circles). Only one individual of *A. aquatica* appeared in the pond during week 29 even though this generally rare species "breeds in all the ponds and ditches at Skipwith" (J. H. Lawton, *personal communication*, 31 July 1990).

Each hypothetical removal of a top-feeding opportunist species created a shorter web with fewer links per species, a smaller ratio of prey to predator species, and a larger percentage of top predators (Table 4). Other parallel cases in which a single top-feeding opportunist species may briefly reshape web structure include the salamander *Plethodon glutinosus* (Green), in rotting oak logs and pine logs. However, Savely (1939) gave no prey lists for salamanders.

TABLE 5. Summary food-web statistics of the Schoenly-Beaver and Briand-Cohen collections and of the cumulative and time-specific webs.

Food web property	Schoenly et al. (1991) (<i>N</i> = 41 webs*)		Cohen et al. (1990a) (<i>N</i> = 113 webs)		Cumulative webs (<i>N</i> = 16 webs)		Time-specific webs (<i>N</i> = 16 systems)	
	Range	Medi- an	Range	Medi- an	Range	Medi- an	Range	Medi- an
% top species (% <i>T</i>)	8-95	39.0	6-55	23.5	9-76	33.5	21-83	33.5
% intermed. species (% <i>I</i>)	0-92	47.0	26-83	55.6	20-78	48.5	17-73	35.0
% basal species (% <i>B</i>)	2-53	16.0	4-40	18.8	2-33	9.5	3-38	13.5
Prey/predator (<i>P</i>)	0.05-1.73	0.75	0.50-1.42	0.96	0.25-1.29	0.82	0.2-1.17	0.81
Mean chain length (μ)	1.0-4.28	2.0	1.0-5.92	2.63	1.65-4.81	2.39	1.25-4.03	2.0
$S \times C = 2L/(S - 1)\dagger$	1.75-9.03	3.92	2.0-12.1	3.65	2.67-14.6	4.19	1.86-10.9	2.86

* Includes only cumulative webs; the remaining 20 of the 61 community webs in this collection are time specific.

† S = species richness, C = connectance (the ratio of actual links to possible links in a food web), and L = the number of predator-prey links in the food web.

Comparison of cumulative and time-specific food webs with prior catalogs

We now compare the 16 sets of cumulative and time-specific webs with two prior collections of community webs described by Schoenly et al. (1991) and Cohen et al. (1990a). The sets of webs in Table 5 are without overlap. The 41 cumulative community webs of the Schoenly-Beaver collection used in Table 5 do not share any webs with the 16 cumulative webs listed in Table 1. Time-specific versions have been excluded from the webs of the Schoenly-Beaver collection in Table 5. There is also no overlap between the webs, all of which are community webs, of the Briand-Cohen collection and the cumulative webs in Table 1. Thus there is no correlation among the Schoenly-Beaver, Briand-Cohen, and cumulative collections caused by shared webs. The Schoenly-Beaver webs are not lumped into trophic species, whereas the Briand-Cohen webs are lumped into trophic species. Like the Schoenly-Beaver webs, the cumulative and time-specific webs are unlumped.

We deal first with the cumulative webs, then with the time-specific webs. By the crude statistics used in Table 5, the cumulative webs grossly resemble the webs in both prior catalogs. (Notice that the medians of the percentages of top, intermediate, and basal species need not add to 100.) For all six statistics a-f, the range of variation among the cumulative webs heavily overlaps the range of variation in the catalogs. For four of the six statistics the median value for the cumulative webs falls between the median value for the two catalogs. The two exceptions are the $S \times C$ product, the median of which (4.19) is greater in the cumulative webs than in either prior catalog, and %*B*, the median of which (9.5%) is lower in the cumulative webs than in either prior catalog. Even for these two statistics, the median value for the cumulative webs falls well within the range of variation of both prior catalogs.

This gross comparison glosses over the substantial differences between the two prior catalogs and between both of them and the cumulative webs (compare the

three median values of %*T* and %*B*, for example). The differences are partly due to the presence or absence of lumping, the inclusion (Cohen et al. 1990a) or exclusion (Schoenly et al. 1991) of vertebrate top predators, the inclusion of one source web here (Robinson 1953), and other methodological differences among the original observers and between cataloguers. The differences may also be partly due to intrinsic variation among webs. Given the methodological differences, a more refined comparison seems premature now.

We now consider the time-specific webs. In Table 5, the variation in %*T* among the time-specific webs is summarized by the range and median, over the 16 systems, of the median of %*T* for each system shown in Table 1. Thus, among the 16 systems the smallest median %*T* shown in Table 1 is 21% and the largest median %*T* is 83%; these values are shown as the range of %*T* in Table 5 for the time-specific webs, even though *individual* time-specific webs may have had lower or higher values of %*T*. Similarly, the median %*T* shown in Table 5 is actually the median of the 16 medians shown in Table 1. The variation of the other statistics of time-specific webs in Table 5 are computed similarly.

For all six statistics a-f, the median of the medians for the time-specific webs falls well within the range of variation of both prior catalogs, and the range of variation among the time-specific webs heavily overlaps the range of variation in the catalogs. Nevertheless, even by these gross measures, the time-specific webs differ from those of the two prior catalogs somewhat more than do the cumulative webs. The median of the medians for the time-specific webs does not fall between the medians of the Schoenly-Beaver and Briand-Cohen collections for %*I*, %*B*, or $S \times C$. That the time-specific webs are not very different from the cumulative webs by the measures shown in Table 5 reflects the limited sensitivity of those measures. Comparisons between time-specific and cumulative versions of a web, one system at a time, as in Table 3, are more appro-

priate and more sensitive because the methods used to define species and links are (usually) consistent within a study.

DISCUSSION

Whenever food webs are studied over different temporal and spatial scales, previously concealed variation emerges. Kitching (1987) and Warren (1989) superimposed time- and site-specific data over a single cumulative or "regional" web. Like Kitching and Beaver (1990), we examined temporal variation in web structure, one property at a time. In the future, the combination of temporal and spatial variation should be examined more closely, along with information on the relative abundances or biomasses of species such as was reported by Kitching (1987), Warren (1989), and Winemiller (1990).

Properties of cumulative vs. time-specific webs

A time-specific food web represents a subset of the predator-prey interactions recorded during an observation period. Comparison of time-specific webs with cumulative webs from the same habitat reveals that some properties depend on the temporal scale at which observations are made. In three cases here, cumulative and time-specific webs taken from the same environment differed dramatically. Some properties of time-specific webs, such as P , $%I$, and μ , could be more accurately estimated from cumulative data than other properties, such as $S \times C$ and $%B$. In nearly every one of the 16 webs studied here, $S \times C$, which is roughly twice the ratio of links to species, was consistently larger and $%B$ was consistently smaller in cumulative webs than in time-specific versions. These findings strongly suggest that cumulative webs, which routinely appear in general ecology textbooks, overestimate $S \times C$ and underestimate $%B$ relative to time-specific versions.

We offer the following tentative explanation of why $%B$ is smaller in cumulative webs than in time-specific versions. In most webs, the same organisms are basal species in most time-specific versions. While there is typically little turnover among the basal species, there is typically much more turnover among the intermediate and top species. Consequently, when all the time-specific webs are cumulated, the number of basal species increases little compared to the number in any time-specific web, while the number of top and intermediate species may increase substantially compared to the number in any time-specific web. Thus the fraction of basal species is smaller in cumulative webs.

The low turnover of basal species in the detritus-based webs is a consequence of counting the detritus, which is always present, as one or more species. In other webs, the low turnover of basal species is due to the continuous presence of plants.

In addition to varying in time and in space, reported webs vary conspicuously in the taxonomic and trophic

resolution of their trophic groups. Sugihara et al. (1989) found that eight commonly reported properties (including five studied here) were generally robust to trophic lumping when 61 webs from the Schoenly-Beaver collection were progressively reduced to one-half their original, unaggregated number of species or to ten species, whichever was larger. However, as webs were lumped trophically, $S \times C$ and $%B$ changed systematically more than the other statistics: $S \times C$ tended to decrease and $%B$ tended to rise. Equivalently, with more refined (and therefore larger numbers of) species, $S \times C$ increased and $%B$ decreased. This pattern of variation parallels that in our investigation of temporal variation, and may have the same explanation.

Another parallel finding is that, in both studies, the fraction of intermediate species $%I$ is more variable than either $%B$ or $%T$ (Table 1 and Table 3). Thus some properties fluctuate similarly as the number of trophic species is reduced either by trophic lumping or by time-specific observation. The class of web properties for which this is generally so, and a general explanation, remain to be determined.

Opportunist species

The concept of "tourist" species, introduced by Moran and Southwood (1982: 292), differs from the concept of "opportunist" species defined here. According to Moran and Southwood, "tourists" are "*non-predatory* [our italics] species which have no intimate or lasting association with the plant but which may be attracted to trees for shelter and sustenance (honeydew and other substances), or as a site for sun-basking and sexual display. Since they fall victim to local predators, tourists may become part of the trophic web of the arboreal community." By contrast, we define an opportunist as a predator with wide feeding habitats, observed in only one time-specific web by an author, which upon appearing becomes a top predator. By definition, the primary trophic role of a tourist species, if it has any at all in the community under observation, is as a prey species, while the necessary trophic role of an opportunist species is as a predator.

Our analysis of opportunist species helps answer a question raised by Roughgarden et al. (1989: 6): "How are ecosystem structure and function influenced by the rare but important events that may occur every century or so?" We showed that the hypothetical removal of a single top-feeding opportunist species in four webs caused a dramatic rise in $%T$, small reductions in $%I$, $S \times C$, μ , and P , and a negligible rise in $%B$. In each case we assumed that none of the other species altered its diet qualitatively after the opportunist was removed. This assumption may not be realistic. Nevertheless, these naive calculations show that a single opportunistic species, even if it makes only rare and brief appearances in a habitat, can dramatically reshape web structure.

Roughgarden et al. (1989: 6) also asked: "What is

the role of 'tourist' species (in Southwood's phrase), which occasionally wander into a food web but are not a permanent part of it?" While our results do not pertain to tourist species, as defined by Southwood, we have shown that a transient opportunist species can be important to community structure. It remains to be shown what effects a transient top-feeding opportunist has on population dynamics and other ecological processes. The recognition that transient top-feeding opportunists exist and are trophically linked to many other species is an early step toward measuring any such effects.

Our results pertain to only top-feeding opportunist species. It would be highly informative to repeat these hypothetical removals on different species of top-feeding opportunists and on different types of opportunist species (e.g., intermediate-feeding opportunists vs. top-feeding opportunists) in the same web to see if our results hold for opportunist species feeding at similar as well as at different trophic positions.

Questions for future work

Many open questions remain to be resolved by future empirical work. Before posing specific questions, let us describe some improvements we would like to see in future reports of the temporal dynamics of a web. The spatial boundaries of the study site would be completely specified in physical terms and would not be changed by the observer during the study. A systematic plan of time-specific sampling effort would be chosen in advance (perhaps following a pilot study), and would be reported in detail, along with a yield-effort curve (Cohen 1978: 120–121) for species and for links. Organisms would be identified to species; further, life-cycle stages of a single species with different diets or different predators would be treated as separate trophic species. All transient organisms observed within the boundaries of the study site would be reported. The presence or absence of a trophic link between any two species would be determined afresh for each time-specific web; it would *not* be assumed that species A always (or alternatively never) eats species B when they occur together on the basis of observations made at one time. Both abundance and body size would be reported for each species; this would allow wide use of sensitive descriptors, such as prey-predator density ratios (Lockwood et al. 1990). Laboratory feeding trials and stomach content analyses would supplement observational records on predator and prey behavior. Accompanying each time-specific web would be detailed data on physical and chemical factors in the environment that might affect web structure and population dynamics, such as temperature, salinity, wave action or turbulence, and light availability in aquatic habitats, or temperature, moisture, and nutrient availability in terrestrial habitats.

A sufficiently large number of webs satisfying these

desiderata would make it possible to answer the following specific questions.

First, if A eats B at time t_1 , under what conditions is it true that A eats B at all $t_2 \neq t_1$? Equivalently, how generally valid is the assumption we used to construct time-specific webs from time-specific species lists and a cumulative web? Warren (1989) showed that not all life-history stages of a given predator feed on all stages or abundance levels of its established prey. How do the levels of abundance and the life-cycle development of predators and prey affect web structure in most communities?

Second, in food webs, are spatial and temporal variation interchangeable? In certain physical systems the observation of a single system over a long time period reveals variation that is identical to that found by observing many systems of the same kind at different places at the same time. This interchangeability of temporal and spatial variability is called ergodicity (not to be confused with the usual demographic use of the term). In this sense of the word "ergodic" are webs ergodic?

Third, how long does a community need to be observed before its cumulative web is (nearly) complete? Are there community characteristics that can be measured in advance that will aid in predicting the necessary duration of observation? In a large web of Little Rock Lake, carefully constructed from the reports of at least seven specialists, Martinez (1991) identified 182 taxa by using all the information available up to 1985. A year later, after a specialist in macrophytes had joined the study at Little Rock Lake, the number of macrophytic taxa jumped from zero to 17 and the total number of taxa jumped from 182 to 260; there were substantial increases in every major category of taxon except the microbiological catch-all called "Fine Organic Matter." There is every reason to believe that additional specialists might further increase the number of reported taxa. This example shows that even under very favorable conditions of prolonged collaborative research, it may be difficult to specify a web completely. But it may not take forever to describe a web with, say, 95% completeness. The question is: how long, and how can we know how long?

Fourth, if a web contains data on the strengths of the interactions between species and an approximate version of the web is assembled by ignoring any interaction whose strength falls below a certain arbitrarily chosen threshold level (called the 'link threshold'), how does the structure of the approximate version depend on the link threshold? To answer this question, Wine-miller (1990) analyzed the stomach contents of neotropical fishes in Venezuela and Costa Rica and used a manual on North American freshwater invertebrates (Pennak 1978) to determine the prey of invertebrate predators. He constructed sink webs for 13 sites and evaluated the effects of the link threshold on several web properties. He found that the approximate webs

obtained by using different link thresholds at a given site varied extensively in the numbers of links, connectance, compartmentation (Pimm and Lawton 1980), and mean numbers of links per species. Because Winemiller (1990) did not directly investigate the food habits of the invertebrate predators in this study, it is possible that many trophic links at lower trophic levels went unreported. The question Winemiller studied deserves further investigation.

Fifth, how are population dynamics, energy and material flows, and other ecological processes affected by the rare appearance of top-feeding and other types of opportunist species?

Sixth, how do exogenous physical and chemical factors affect web structure and dynamics? For example, what are the web effects of major physical perturbations, such as El Niño in marine and freshwater habitats or fire in terrestrial habitats? In short, how are webs coupled to the abiotic environment?

In addition to empirical questions, theoretical questions abound. We mention only two. First, how can a simple model be constructed that provides a unified, quantitatively accurate account of the temporal trends observed here? It would be nice if the model were not totally ad hoc but were related to at least one of the models previously proposed for web statics (e.g., Cohen and Newman 1985, Cohen et al. 1990a) or dynamics (e.g., Pimm 1982, Post and Pimm 1983, Carpenter 1988, Cohen et al. 1990b).

Second, what explains the difference between the apparently low turnover rates of basal species, the higher turnover rates of top species, and the still higher turnover rates of intermediate species? Are these turnover rates related to body size or other life-history characteristics of species? These turnover rates seem to be the key to explaining the differences between time-specific and cumulative webs, and may contribute to explaining the temporal patterns in the fractions of top, intermediate, and basal species.

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APPENDIX

Reconstructions of prey records, time data, and species lists for 16 food webs that appear in eight published studies (see Table 1). For some details of our reconstruction methods, see *Data sources, methods, and food web statistics*.

TABLE A1. Cumulative food web of the rabbit necrovores-predator community reported by McKinnerney (1977, 1978) for the Hueco Mountains, Texas, for days 1-26 following carcass placement on day 1.* Numbers in the column "Time in web" refer to the day(s) each species was found. Species considered incidental by McKinnerney are not included. McKinnerney did not study carrion-feeding vertebrates at this site.

Species	Time in web (days 1-26)	Prey species
1. <i>Boottetix argentatus</i> Bruner	20	47
2. <i>Taeniopoda eques</i> (Burmeister)	25	47
3. <i>Sinea complexa</i> Caudell	9	4, 5, 8-12, 14, 15, 18, 19, 21-29, 31, 35
4. <i>Saprinus discoidalis</i> LeConte	4-24	9, 22, 24, 26, 28
5. <i>S. pennsylvanicus</i> Paykul	9	9, 22, 24, 26, 28
6. <i>Nicrophorus marginatus</i> Fab.	4-8	47
7. <i>N. carolinus</i> L.	4-8	47
8. <i>Silpha truncata</i> Say	3-22	22, 24, 26, 28, 47
9. <i>S. truncata</i> larvae	8-11	47
10. staphylinid (Aleocharinae)	11-23	18-21, 23, 27, 29
11. <i>Dermestes vulpinus</i> Fab.	4-24	47
12. <i>Necrobia rufipes</i> (DeGeer)*	6-23	19
13. <i>Nitidula ziczac</i> Say	14	47
14. <i>Eleodes entricatus</i> Hald.	8-14	47
15. <i>Trox punctatus</i> Aermar	4-24	47
16. <i>Proctacanthella leucopogon</i> (Wiliston)*	9	3, 18-29, 40-43
17. <i>Promachus giganteus</i> Hine*	12	18, 19, 21-24, 26-29, 38-43
18. <i>Euxesta</i> sp.	3-19	47
19. <i>Piophilina</i> sp.	6-16	47
20. <i>Trupanea actinobolo</i> (Loew)	15-24	47
21. <i>Musca domestica</i> L.	1-24	47
22. <i>M. domestica</i> larvae	1-14†	47
23. <i>Cochliomyia macellaria</i> (Fab.)	1-24	47
24. <i>C. macellaria</i> larvae	1-14†	47
25. <i>Phaenicia sericata</i> (Mg.)	4-9	47
26. <i>P. sericata</i> larvae	4-14†	47
27. <i>Oxysarcodexia ochripyga</i> (Wulp)	1-23	47
28. <i>O. ochripyga</i> larvae	1-14†	47
29. <i>Goniochaeta plagiodes</i> Tns.*	9-17	9
30. <i>Idiasta</i> sp.	5-7	22, 24, 26, 28
31. <i>Pogonomyrmex desertorum</i> Wheeler	4-25	19, 21-28, 47
32. <i>P. rugosus</i> Emery	2	21-28, 47
33. <i>Conomyrma insana</i> (Buckley)	2-4	21-28, 47
34. <i>Pheidole</i> sp.	2	21-28, 47
35. <i>Solenopsis xyloni</i> McCook	1-25	19, 21-28, 47
36. <i>Iridomyrmex pruinosum</i> (Roger)	2-4	21-28, 47
37. <i>Myrmecocystus mimicus</i> Wheeler	2	21-28, 47
38. <i>Rygius annulatus</i> (Say)	12, 13	47
39. <i>Calliopsis hirsutifrons</i> Cockerell	12, 15	47
40. <i>Nomia tetrazonata</i> Cockerell	9, 12	47
41. <i>Lasioglossum morilli</i> (Cockerell)	9-26	47
42. <i>Dialictus microlepiodes</i> (Ellis)	9-26	47
43. <i>Dialictus</i> sp.	9-26	47
44. <i>Apis mellifera</i> L.	11	47
45. <i>Trachrhinus</i> sp.	4	22, 24, 26, 28, 47
46. <i>Misumena</i> sp.	10, 14, 15	18-24, 26-29, 39, 41-43
47. Carcass	1-26	

* M. Conley (formerly M. McKinnerney) corrected two errors in her published data (*personal communication*, 5 September 1989). In her Fig. 4 (1978), tachinids (species 29 above) eat prey 9 (not prey 22, 24, 26, 28) and consumer 12 eats prey 19 (not dermestid larvae). Also, in the day-9 and day-12 webs, asilid flies (spp. 16 and 17, respectively) are potential predators on "all the taxa present concurrently, except beetles and ants" (confirmed by G. Forbes, *personal communication*). Another predator of the day-9 web, *Sinea complexa* (Reduviidae: Hemiptera), reportedly ate flies, beetles, and ants (McKinnerney 1977). However, the likelihood that this species ate the highly mobile asilid fly *Proctacanthella leucopogon* was small (M. Conley, *personal communication*, 24 May 1990); therefore, both the day-9 and cumulative webs are acyclic (no cannibalistic or mutual predation links were found).

† For these larvae, information on total residence time in the web was not available in McKinnerney (1977, 1978). M. Conley (*personal communication*, 5 September 1989) reported that her data "were very inadequate on larvae; field ID [identification] is virtually impossible for most of them. . . ." Instead, total residence times on dipteran larvae were taken from rabbit necrovores data collected by Schoenly and Reid (1983) from a desert-scrub habitat in the Northern Chihuahuan Desert near the study sites of McKinnerney (1978). M. Conley (*personal communication*, 16 July 1990) found no mention in her 1976 field notebooks of dipteran larvae occurring on rabbit carcasses beyond day 14, thereby confirming Schoenly and Reid's endpoint estimates of dipteran larva residence times in these carcasses; however, she reports that ". . . there might be maggots in the rabbit carcasses at the later stages during earlier summer or later fall, when temperatures are lower and desiccation is not as complete in the early period."

TABLE A2. Cumulative food web of the rabbit necrofore-predator community reported by McKinnerney (1977, 1978) for White Sands National Monument, New Mexico, for days 1-31, 37, 40, 43, 47, 50, 54, 66, and 79 following carcass placement on day 1. Numbers in the column "Time in web" refer to the day(s) each species was found.*

Species	Time in web (days 1-31, 37, 40, 43, 47, 50, 54, 66, 79)	Prey species
1. <i>Saprinus discoidalis</i> LeConte	2-26	17-19
2. <i>S. pennsylvanicus</i> Paykul*	19, 21	17-19
3. <i>Nicrophorus marginatus</i> Fab.	4	25
4. <i>Dermestes vulpinus</i> Fab.	3-23	25
5. <i>Embaphion contusum</i> Lec.	18, 19	25
6. <i>Eleodes hispilabris</i> Blais	1-31, 37, 40, 43, 47, 50, 54, 66	25
7. <i>Trox scutellaris</i> Say	1-30	25
8. <i>T. nodosus</i> Robinson	1-30	25
9. <i>T. suberosus</i> Fab.	1-30	25
10. <i>Euxesta</i> sp.	1-31, 37, 40, 43, 47, 50, 54, 66	25
11. <i>Diacrita plana</i> Steyskal	12, 20	25
12. <i>Coenosia</i> sp.	3-9	25
13. <i>Cochliomyia macellaria</i> (Fab.)	3-21	25
14. <i>Sarcophaga utilis</i> Aldrich	1-31, 37	25
15. <i>Oxysarcodexia ochripyla</i> (Wulp)	1-31, 37	25
16. Isoptera (unspecified)	17-19	25
17. <i>C. macellaria</i> larvae	3-14†	25
18. <i>S. utilis</i> larvae	1-14†	25
19. <i>O. ochripyla</i> larvae	1-14†	25
20. <i>Idiasta</i> sp.	8, 10	17-19
21. <i>Pogonomyrmex apache</i> Wheeler	1-31, 37, 40, 43, 47, 50, 54, 66, 79	13, 16-19, 25
22. <i>Myrmecocystus mimicus</i> Wheeler	1-31, 37, 40, 43, 47, 50, 54, 66, 79	13, 16-19, 25
23. <i>Solenopsis xyloni</i> McCook	5-31, 37, 40, 43, 47, 50, 54	13, 16-19, 25
24. <i>Iridomyrmex pruinosum</i> (Roger)	1-31, 37, 40, 43, 47, 50	13, 16-19, 25
25. Carcass	1-31, 37, 40, 43, 47, 50, 54, 66, 79	

* Species considered incidental by McKinnerney are not included. Species 2 and its reported prey (species 17-19) do not occur jointly on any day. We included these species and their trophic links in our cumulative web to preserve the author's original species list and web data. McKinnerney reported several vertebrate species as probable carrion feeders at various times in the succession but did not specify the carrion insects they may have also consumed: *Holbrookia maculata* Girard, *Sceloporus undulatus* (Bosc), *Uta stansburiana* Baird and Girard, *Cnemidophorus inornatus* Baird, *Cathartes aura* (Linnaeus), *Bubo virginianus* (Gmelin), *Canis latrans* Say, *Mephitis mephitis* (Schreber), and *Conepatus mesoleucus* (Lichtenstein). These vertebrates are not included in this web.

† For these larvae, information on total residence time in the web was not available in McKinnerney (1977, 1978). Instead, total residence times on dipteran larvae were estimated from rabbit necrofore data collected by Schoenly and Reid (1983) from a desert-scrub habitat in the Northern Chihuahuan Desert near the study sites of McKinnerney (1978). M. Conley (personal communication, 16 July 1990) found no mention in her 1976 field notebooks of dipteran larvae occurring on rabbit carcasses beyond day 14, thereby confirming Schoenly and Reid's endpoint estimate of dipteran larvae residence times in these carcasses; however, she reports that "... there might be maggots in the rabbit carcasses at the later stages during earlier summer or later fall, when temperatures are lower and desiccation is not as complete in the early period."

TABLE A3. Cumulative food web of the brown elm flux community in Sheffield, United Kingdom, as reported by Robinson (1953) for the months January through December. Numbers in the column "Time in web" refer to the week(s) each species was found during the year, starting with January; for example, week 10 refers to the second week in March.

Species	Time in web (weeks 2-48)	Prey species
1. <i>Phaomia</i> sp. larvae	4-20, 30-46	3-5
2. <i>Thamiarea hospita</i> Maerk larvae, adults	2-48	5-7
3. <i>Systemus</i> sp. larvae*	2-18, 30-46	5
4. <i>Brachyopa insensilis</i> Collin larvae	4-16, 20-48	8
5. <i>Dasyhelea obscura</i> Winnertz larvae	2-16, 34-48	8
6. <i>Aulacigaster leucopeza</i> (Meigen) larvae	20-30	8
7. <i>Hericia hericia</i> Kramer (all stages)	4-10, 16-24, 30-38, 42-48	8
8. Tree flux	2-48	

* Cannibalistic species.

TABLE A4. Cumulative food web of the felled pine log community reported by Savely (1939) from a North Carolina woodland. Numbers in the column "Time in web" refer to the year(s) each species was found in pine logs of different ages (years 1-4); fourth-year logs refer to all logs aged over 3 yr (Savely 1939). We omitted questionable links. Savely (1939) observed salamanders, *Plethodon glutinosus* (Green), in pine logs > 3 yr old, but reported no specific prey that they eat.

Species	Time in web (years 1-4)	Prey species
1. <i>Entomobrya</i> sp.	1-4	109, 110
2. <i>E. ligata</i> Nic.	1-4	109, 110
3. <i>E. corticola</i> Nic.	1-4	109, 110
4. <i>Pseudachorutes</i> sp.	1-2	109, 110
5. <i>Isotoma sensibilis</i> Tlb.	1-4	109, 110
6. <i>Tomocera flavescens</i> Tlb.	1-2	109, 110
7. <i>Reticulitermes flavipes</i> Koll.	2-3	111
8. <i>Parcoblatta</i> sp.	1-4	110
9. <i>heteropteran</i> (undet.)	1	55, 63, 64, 66-70
10. <i>Epiptera</i> sp.	1	110
11. <i>Tachymenis flavicauda</i> (Say)	1-4	1-6, 101-106
12. <i>Saprinus</i> sp.	1-2	73-78
13. <i>Plegaderus</i> sp.	1-3	110
14. <i>Cylistix cylindrica</i> (Payk.)	1-2	75
15. <i>Platysoma lecontei</i> Mars.	1-4	71-78
16. <i>Platysoma parallelum</i> Say	1-2	63-70
17. <i>Thanasimus dubius</i> Fab.	1	63-70
18. <i>Copidita thoracica</i> Fab.	3	109
19. <i>Boros unicolor</i> Say	1-2	109
20. <i>Dendroides bicolor</i> Newm.	1-2	109
21. <i>Alaus myops</i> Fab.	1-4	20, 46, 47, 49, 52, 55
22. <i>Ischiodontus</i> sp.	1-2	109
23. <i>Orthostethus infuscatus</i> Germ.	3-4	109
24. <i>Melanotus</i> sp.	1-4	109
25. <i>Elater verticinus</i> Beauv.	1-4	109
26. <i>Megapenthes limbalis</i> (Hbst.)	2-3	109
27. <i>Buprestis lineata</i> Fab.	1-2	111
28. <i>Buprestis</i> sp.	1-3	111
29. <i>Chalcophora</i> sp.	1	112
30. <i>Chrysobothris</i> sp.	1	112
31. <i>Temnochila virescens</i> (Fab.)	1	30, 51, 55, 63-69
32. <i>Rhizophagus cylindricus</i> (Lec.)	1	51, 62-70
33. <i>Brontes dubius</i> Fab.	1-3	110
34. <i>Mycetophagus pini</i> Zieg.	1-2	110
35. <i>Colopterus semitectus</i> Say	1	110
36. <i>Synchita</i> sp.	2-3	109
37. <i>Uloma punctulata</i> Lec.	3-4	109
38. <i>Xylopinus rufipes</i> (Say)	2-4	109
39. <i>Scotobates calcaratus</i> (Fab.)	3-4	109
40. <i>Bolitotherus cornutus</i> (Panz.)	1	110
41. <i>Platydema flavipes</i> Fab.	1-3	110
42. <i>Hypulus concolor</i> (Lec.)	2	109
43. <i>Stephanopachys rugosus</i> Oliv.	1-2	111
44. <i>Stelidota geminata</i> Say	1	110
45. <i>Passalus cornutus</i> Fab.	3-4	109
46. <i>Pseudolucanus capreolus</i> (L.)	3-4	109
47. <i>Derobrachus brunneus</i> (Forst.)	4	109
48. <i>Asemum moestum</i> Hald.	1	111, 112
49. <i>Rhagium lineatum</i> Oliv.	1	112
50. <i>Xylotrechus sagittatus</i> (Germ.)	1	112
51. <i>Callidium antennatum</i> Newm.	1	112
52. <i>Acanthocinus obsoletus</i> (Oliv.)	1	112
53. <i>A. nodosus</i> (Fab.)	1	112
54. <i>Eupogonius tomentosus</i> Hald.	1	112
55. <i>Monochammus titillator</i> (Fab.)	1	112
56. <i>Leptura</i> sp.	2-4	109
57. <i>Rhyncolus</i> sp.	1-3	110
58. <i>Cossonus corticola</i> Say	1-3	110
59. <i>Pissodes memorensis</i> Germ.	1	112
60. <i>Pachylobins picivorus</i> Germ.	1	112
61. <i>Hyllobius pales</i> Hbst.	1	112
62. <i>Platypus flavicornis</i> Fab.	1	110
63. <i>Ips grandicollis</i> Eichh.	1	112
64. <i>I. calligraphus</i> Germ.	1	112
65. <i>Xyleborus fitchi</i> Hopk.	1	110
66. <i>Orthotomicus coelatus</i> (Eichh.)	1	112

TABLE A4. Continued.

Species	Time in web (years 1-4)	Prey species
67. <i>Pithyophthorus annectens</i> Lec.	1	112
68. <i>P. pullus</i> Simm.	1	112
69. <i>Dendroctonus valens</i> Lec.	1	112
70. <i>D. tenebrans</i> (Oliv.)	1	112
71. Chironomid larvae (unsp.)	3-4	110
72. Cecidomyiid larvae (unsp.)	3-4	110
73. <i>Xylophagus fasciatus</i> Walker	1	49
74. Dolicopodid larvae (unsp.)	2-4	110
75. <i>Lonchaea</i> sp.	1-2	110
76. <i>Theresia monohammi</i> (Ins.)	1	55
77. <i>Sciara coprophila</i> Lint.	1-2	107
78. <i>Sarcophaga repax</i> Walker	1	55
79. <i>Sirex nigricornia</i> Fab.	1	111
80. <i>Oryssus</i> sp.	1	30
81. <i>Coeloides pissodis</i> Ashm.	1	59
82. <i>Camponotus herculeanus</i> DeG.	1-3	108
83. <i>Leptinothorax curvispinosus</i> Mayr	1-4	108
84. <i>Ponera coarctata</i> Emery	1-4	108
85. <i>Lasius umbratus</i> Nyl	1-2	108
86. Lumbricid (unsp.)	3-4	109
87. <i>Polygyra thyriodius</i> Say	4	110
88. <i>Euconulus chersinus</i> Say	2-3	110
89. <i>Zonitoides arboreus</i> Say	2-4	110
90. <i>Philomyces carolinensis</i> (Bosc.)	3-4	110
91. <i>Cambala annulata</i> Say	3-4	109
92. <i>Fontaria coriacen</i> Koch.	2-4	109
93. <i>Polydesmus serratus</i> (Say)	4	109
94. <i>Geophilus varians</i> McNeil	1-4	108
95. <i>Linotaenia bidens</i> (Woods)	1-4	108
96. <i>Cryptops hyalina</i> Say	1-3	108
97. <i>Bothropolys multidentatus</i> Newport	1-3	108
98. <i>Chelanops oblongus</i>	1-2	101-106, 108
99. <i>C. virginnae</i>	1-2	108
100. <i>Chelifer cancroides</i> (L.)	1-2	108
101. <i>Uropoda</i> sp.	1-4	110
102. <i>Parasitus</i> sp.	1-2	108
103. <i>Dendrolaelaps</i> sp.	1-2	108
104. <i>Pergamasus</i> sp.	1-2	108
105. Tyroglyphid (unsp.)	2-3	110
106. Oribatid (unsp.)	2-3	110
107. Dead cerambycid	1-2	
108. Various larvae (unsp.)	1-4	109, 110-112
109. Rotting wood	1-4	
110. Fungi	1-4	109, 111, 112
111. Sapwood	1-3	
112. Phloem	1-2	

TABLE A5. Cumulative food web of the felled oak log community reported by Savely (1939) from a North Carolina woodland. Numbers in the column "Time in web" refer to the year(s) each species appears in oak logs of different ages (years 1-4); fourth-year logs refer to all logs > 3 yr old (Savely 1939). We omitted questionable links.*

Species*	Time in web (years 1-4)	Prey species
1. <i>Entomobrya ligate</i> Nic.	1-4	134, 135
2. <i>Lepidocyrtus cyaneus</i> Tlb.	1-3	134, 135
3. <i>Isotoma sensibilis</i> Tlb.	1-4	134, 135
4. <i>Pseudistoma sensibilis</i> Tlb.	1-3	134, 135
5. <i>Pseudachorutes</i> sp.	2-3	135
6. <i>Neosmithurus clavatus</i> (Banks)	2-4	135
7. <i>Reticulitermes flavipes</i> Koll.	2-4	134
8. <i>Zorotypus hubbardi</i> Caudell	2-3	135
9. <i>Parcoblatta</i> sp.	1-4	135
10. <i>Epiptera</i> sp.	2-3	135
11. <i>Tachyta nana</i> (Gyll.)	1-4	1-6, 122-132
12. <i>Canosoma crassus</i> (Grav.)	1-4	135
13. <i>Thoracophorus costalis</i> Er.	1-3	135
14. <i>Coproporus ventriculus</i> Say	3-4	135
15. <i>Trachysectus confluentus</i> Say	3-4	135
16. <i>Actium</i> sp.	4	122-125, 128, 130
17. <i>Acritus exiguus</i> (Er.)	1-2	135
18. <i>Bacanius punctiformis</i> Lec.	2-3	135
19. <i>Epiurus regularis</i> Beauv.	2-4	135
20. <i>Epiurus</i> sp.	2-4	135
21. <i>Platysoma lecontei</i> Mars	2-4	80-83, 85
22. <i>Chariessa pilosa</i> Forst.	1-3	2, 4, 36-38, 80-85
23. <i>Mordellistena</i> sp.	2-3	134
24. <i>Glipodes sericans</i> Welsh.	3	134
25. <i>Dendroides bicolor</i> Dru.	2-4	134, 135
26. <i>Elater nigricollis</i> Hbst.	2-4	134
27. <i>Orthostethus infuscatus</i> (Germ.)	3-4	134
28. <i>Deltometopus amoenicornis</i> (Say)	4	134
29. <i>Alaus oculatus</i> L.	1-4	54, 60, 64, 69, 72
30. <i>Melanopus</i> sp.	1-3	134
31. <i>Elaterinae</i> (undet.)	2-4	134
32. <i>Chrysobothris femorata</i> (Oliv.)	1	137
33. <i>Agrilus</i> sp.	1-2	137
34. <i>Dicerca</i> sp.	2	137
35. <i>Rhysodes americanus</i> Lap.	4	134
36. <i>Silvanus embellis</i> Lec.	1-2	135
37. <i>S. planatus</i> Germ.	1-2	135
38. <i>Brontes dubius</i> Fab.	1, 4	135
39. <i>Megalodacne fasciata</i> (Fab.)	1-4	135
40. <i>Triplax thoracica</i> Say	4	135
41. Mycetyphagid (undet.)	4	135
42. <i>Synchita fuliginosa</i> Melsh.	2	134
43. <i>Solydium lineola</i> Say*	3	78
44. <i>Hymenorus</i> sp.	4	134
45. <i>Haplocephala bicornis</i> Oliv.	2-3	135
46. <i>Platydemia subcostatum</i> Lap.	2-4	135
47. <i>P. ruficorne</i> Sturm.	2-4	135
48. <i>P. ruficolle</i> Cast. & Brill.	2-4	135
49. <i>Uloma imberbis</i> Lec.	3-4	134
50. <i>Dioedus punctatus</i> Lec.	3-4	134
51. <i>Scotabates carcaratus</i> (Fab.)	3-4	134
52. <i>Merinus laevis</i> Oliv.	2	134
53. <i>Xylopinus saperdoides</i> (Oliv.)	3-4	134
54. <i>Alobates pennsylvanicus</i> (DeG.)	2-4	134
55. <i>Meracantha contracta</i> (Beauv.)	4	134
56. <i>Strongylium crenatum</i> Makl.	4	134
57. <i>Synchroa punctata</i> Newm.	2-4	134, 135
58. <i>Phloeotrypa vaudouere</i> Muls.	2-3	134
59. <i>Cis</i> sp.	2	135
60. <i>Pseudolucanus capreole</i> (L.)	3-4	134
61. <i>Platycerus quercus</i> Web.	4	134
62. <i>Ceruchus piceus</i> (Web.)	4	134
63. <i>Dorcus (brevis</i> Say?)	4	134
64. <i>Polymoecus brevipes</i> Lec.	4	134
65. <i>Cloetus globosus</i> (Say)	4	134
66. <i>Trichiotinus bidens</i> Fab.	4	134
67. <i>Phileurus valgus</i> L.	4	134

TABLE A5. Continued.

Species*	Time in web (years 1-4)	Prey species
68. <i>Passalus cornutus</i> Fab.	2-4	134
69. <i>Derobrachus brunneus</i> (Forst.)	4	134
70. <i>Leptura proxima</i> Say	4	134
71. <i>Xylotrechus colonus</i> (Fab.)	1	137
72. <i>Romaleum atomarium</i> (Drury)	1-3	137
73. <i>Neoclytus scutellaris</i> Oliv.	1	137
74. <i>Graphisurus fasciatus</i> DeG.	1-2	137
75. <i>Eupsalis minuta</i> Drury	3-4	134
76. <i>Euparius marmoreus</i> Oliv.	3	135
77. <i>Platypus quadridentatus</i> Oliv.	3	135
78. <i>Orthotomicus coelatus</i> Eichh.	1	137
79. <i>Scolecocampa liburna</i> Geyer	3-4	134
80. <i>Lonchaea</i> sp.	1-2	135
81. Mycetophilid larvae (undet.)	2-4	135
82. Cecidomyid larvae (undet.)	3-4	138
83. Dolycopodid larvae (undet.)	2-4	138
84. Tachinid larvae (indet.)	1	72
85. <i>Megaselia</i> sp.	1-2	80, 81, 83, 84
86. <i>Tremex columb</i> L.	1-2	136
87. <i>Atanycolus simplex</i> (Cress.)	1	32
88. <i>Atanycolimorpha</i> sp.	2	72
89. <i>Sparhius floridanus</i> Ashm.	1	32
90. <i>Doryctes</i> sp.*	2	64-67
91. <i>Augochlora pura</i> Say	4	139
92. <i>Camponotus herculeanus</i> DeG.	1-4	133
93. <i>Crematogaster lineolata</i> Say	1-4	133
94. <i>Leptothorax curvispinosus</i> Mayr	1-4	133
95. <i>Ponera coarcta</i> Emery	1-4	133
96. <i>Proceratium croceum</i> Wheeler	1-4	133
97. <i>Formica exsectoides</i> Forel	3	133
98. <i>Pheidole</i> sp.	4	133
99. Lumbricid (undet.)	3-4	134
100. <i>Strobilops gena</i> Pilsbry	3-4	134, 135
101. <i>Polygyra fallax</i> Say	4	134, 135
102. <i>P. tridentata</i> Say	4	134, 135
103. <i>P. thyroideus</i> Say	4	134, 135
104. <i>Zonitoides arboreus</i> Say	2-4	134, 135
105. <i>Euconulus chersinus</i> Say	2-4	134, 135
106. <i>Retinella indentata</i> Say	2-4	134, 135
107. <i>Philomyces carolinensis</i> (Bosc.)	3-4	134, 135
108. <i>Cambala annulata</i> (Say)	3-4	134
109. <i>Fontaria coriacea</i> Koch	4	134
110. <i>Polydesmus serratus</i> Say	4	134
111. <i>Spirostephon lactarium</i> (Say)	3-4	134
112. <i>Linotaenia bidens</i> (Woods)	1-3	133
113. <i>Geophilus varians</i> (McNeil)	1-3	133
114. <i>Scolopendra viridis</i> Say	2-4	133
115. <i>Cryptops hyalina</i> Say	2-4	133
116. <i>Otocryptops sexspinosus</i> (Say)	2-4	133
117. <i>Bothropolys multidentatus</i> Newport	2-4	133
118. <i>Chthonius spinosus</i>	1-2	133
119. <i>Chthonius longipalpus</i>	1-2	133
120. <i>Chelanops</i> sp.	3	133
121. <i>Chelanops dentatus</i>	4	133
122. <i>Podothrombium</i> sp.	4	133
123. <i>Allothrombium pulvinus</i> Ewing	4	133
124. <i>Zetes</i> sp.	3-4	135
125. <i>Schelorabates</i> sp.	4	135
126. <i>Uropoda</i> sp.	1-3	135
127. <i>Discopoma</i> sp.	1-3	135
128. <i>Pergamasus</i> sp.	1-4	133
129. <i>Seilus</i> sp.	2-3	133
130. <i>Megisthanus</i> sp.	1-4	133
131. <i>Dendrolaelops</i> sp.	1-3	133
132. Trypoglyphid sp.	2	133
133. Various larvae	1-4	134-138
134. Rotting wood	1-4	
135. Fungi (red rot)	1-4	134, 136, 137
136. Sapwood	1-2	

TABLE A5. Continued.

Species*	Time in web (years 1-4)	Prey species
137. Phloem	1-3	
138. Microorganisms	2-4	
139. Pollen	4	

*Species 43 and 90 and their prey (species 78 and 64-67, respectively) do not occur jointly on any day though Savely reports them as predators and prey in his appendix. We included these species and their trophic links in our cumulative web to preserve the author's original species list and food web data. Savely (1939) observed salamanders, *Plethodon glutinosus* (Green), in oak logs >3 yr old, but reported no specific prey they eat.

TABLE A6. Cumulative food web of treehole communities of box forest (mostly *Tristania conferta* and *Agrodendron actinophyllum*) in southeast Queensland, Australia, reported by Kitching (1987) for six study sites and four sampling periods. Each time period represents 3 mo; period 1: January, October, and December 1982, period 2: January to March 1983, period 3: April to June 1983, and period 4: July to September 1983. According to Jenkins and Kitching (1990), species 6, 7, and 8 are mutual predators.*

Species	Time in web (periods 1-4)	Prey species
A. Site 1		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	2	11
3. Algophagid mites	...	11
4. Mosquito larvae	1, 3, 4	11, 12
5. Ostracods	...	12
6. <i>Anatopynia pennipes</i> Freeman	1, 3, 4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i> Lee and Reye	3, 4	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	1-4	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> (Boulenger)†	1	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	
B. Site 2		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	2, 4	11
3. Algophagid mites	1	11
4. Mosquito larvae	1, 3, 4	11, 12
5. Ostracods	...	12
6. <i>Anatopynia pennipes</i>	1-4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i>	1-4	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	1, 2, 4	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> †	1	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	
C. Site 4		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	1, 2, 4	11
3. Algophagid mites	1, 2	11
4. Mosquito larvae	2-4	11, 12
5. Ostracods	1-4	12
6. <i>Anatopynia pennipes</i>	1-4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i>	1, 2, 4	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	...	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> †	...	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	

TABLE A6. Continued.

Species	Time in web (periods 1-4)	Prey species
D. Site 5		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	2-4	11
3. Algophagid mites	1-3	11
4. Mosquito larvae	1, 2	11, 12
5. Ostracods	1-4	12
6. <i>Anatopynia pennipes</i>	1-4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i>	...	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	2	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> †	...	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	
E. Site 10		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	1-4	11
3. Algophagid mites	1-4	11
4. Mosquito larvae	1-3	11, 12
5. Ostracods	...	12
6. <i>Anatopynia pennipes</i>	1-4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i>	1	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	...	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> †	...	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	
F. Site 11		
1. <i>Prionocyphon niger</i>	1-4	10
2. <i>Clogdia</i> sp.	1-4	11
3. Algophagid mites	1, 2, 4	11
4. Mosquito larvae	1-3	11, 12
5. Ostracods	1	12
6. <i>Anatopynia pennipes</i>	1-4	1, 2, 4, 7, 8
7. <i>Culicoides angularis</i>	4	1, 2, 4, 6, 8
8. <i>Arrhenurus</i> sp.	...	1-4, 6, 7
9. <i>Lechriodus fletcheri</i> †	...	1, 2, 4, 6-8
10. Large particle detritus	1-4	
11. Small particle detritus	1-4	
12. Suspended organic matter	1-4	

* Kitching (*personal communication*, 12 July 1990) reports that "... mutual predation probably does happen [between these species] although not with symmetrical strength."

† Cannibalistic species.

TABLE A7. Cumulative food web of the soybean arthropod community in east central Illinois reported by Mayse and Price (1978) for weeks 3 and 12 of the study. According to the authors, this list excludes some of the more uncommon arthropods found in this system. We include both observed and probable feeding links.*

Species	Time in web (weeks 3 and/or 12)	Prey species
1. Predatory red mites (undet.)†	3, 12	5, 8-10
2. <i>Orius insidiosus</i> (Say)†	12	8-13, 15
3. <i>Nabis</i> sp.†	12	2, 8, 12-15
4. Spiders (unspecified)	3, 12	8, 11-13
5. <i>Aeolothrips</i> sp.	12	9, 10
6. Syrphid larvae	12	9, 11
7. Parasitic Hymenoptera	12	11, 12, 14
8. <i>Empoasca fabae</i> (Harris)	3, 12	15
9. <i>Sericothrips variabilis</i> (Beach)	3, 12	15
10. Other herbivorous thrips	3, 12	15
11. Black alate aphids	3, 12	15
12. <i>Platypena scabra</i> (Fab.)	12	15
13. <i>Colias eurytheme</i> Boisduval	12	15
14. <i>Acrosternum hilare</i> (Say)	12	15
15. Soybean plant	3, 12	

* M. Mayse (*personal communication*, 2 November 1988) revised his (and P. Price's) published data. In their Fig. 11 (1978), add a cannibalism link to species 3 (*Nabis* sp. to *Nabis* sp.). Although their caption in Fig. 11 mentions two studies where consumers 2 and 3 reportedly eat 15 (Salas-Aguilav and Ehler 1977, Ridgway and Jones 1968), Mayse and Price did not "specifically observe such feeding in [their] study." Given that the authors included both observed and probable interactions in their time-specific webs, we elected to incorporate both links (2-15 and 3-15) in our reconstructions.

† Cannibalistic species.

TABLE A8. Cumulative food web for the Arctic tundra (Naumov 1972, from Sbodnikov 1958) during winter (W) and summer (S).

Species	Time in web (W and/or S)	Prey species
1. Marine mammals, fish and invert.	W, S	
2. Tundra vegetation	W, S	
3. Water & soil invertebrates, etc.	S	
4. Guillemots	S	1
5. Polar bear	W, S	1
6. Polar fox	W, S	1, 8-15
7. Gulls	W, S	1, 9-12, 14, 15
8. Northern reindeer	W, S	2
9. Lemmings	W, S	2
10. Ptarmigan	W, S	2
11. Sparrows	S	2
12. Geese, brants	S	2
13. White hare	W, S	2
14. Snipe	S	2, 3
15. Loons, eiders, ducks	S	1, 3
16. Tundra wolf	W, S	1, 8-10, 12, 13, 15
17. Ermine	W, S	9-11, 14
18. White owl	W, S	9-11, 13, 14
19. Falcon	S	9-12, 14, 15
20. Hawk	S	9-11, 14

TABLE A9. Cumulative food web of the dung arthropod community in a cow pasture near Ithaca, New York, reported by Valiela (1974) during days 1 and 5 of his 5-d study.* Only major taxa were included in his original food web graphs. Prey and time data for other "minor" species were determined using Figs. 1-3 and Table 1 of Valiela (1974). We include both established and presumed feeding links.

Species	Time in web (days 1 and/or 5)	Prey species
1. <i>Philonthus cruentatus</i> Gmelin	1, 5	3, 5-9, 17-23, 25, 27-29, 33-39, 42, 46
2. <i>Aleochara bipustulata</i> (L.)	1, 5	3, 5-9, 17-23, 25, 27-29, 33-39, 42, 46
3. <i>Aleochara</i> sp.	1, 5	6-9, 24, 46
4. <i>Hyponigrus obsidianus</i> Melsh.	1, 5	3, 5-9, 17-23, 25, 27-29, 33-39, 42, 46
5. <i>Oxytelus tetracarinus</i> Block	1, 5	6-9, 24, 46
6. <i>Macrochelus</i> sp.	1, 5	21-24, 27-29, 37-39, 46
7. <i>Parasitus</i> sp.	1, 5	21-24, 27-29, 37-39, 46
8. Uropodid sp.	1, 5	21-24, 27-29, 37-39, 46
9. Acarid sp.	1, 5	21-24, 27-29, 37-39, 46
10. <i>Aphodius haemorrhoidalis</i> (L.)	1, 5	46
11. <i>A. erraticus</i> (L.)	1, 5	46
12. <i>A. fimetarius</i> (L.)	1, 5	46
13. <i>A. stercorosus</i> Melsh.	1, 5	46
14. <i>A. prodiomus</i> (Brahm)	1, 5	46
15. <i>A. fossor</i> (L.)	1, 5	46
16. <i>Cothonaspis</i> sp.	1, 5	21-23, 27-29, 37-39
17. <i>Cercyon</i> sp. A	1, 5	46
18. <i>Cercyon</i> sp. B	1, 5	46
19. <i>Cercyon</i> sp. C	1, 5	46
20. <i>Cercyon</i> sp. F	1, 5	46
21. <i>Sarcophaga</i> sp. A	1, 5	46
22. <i>Ravinia l'herminieri</i> (Desv.)	1, 5	46
23. <i>Musca autumnalis</i> De Geer	1, 5	46
24. Collembola (unspecified)	1, 5	46
25. <i>Leptocera</i> adults	5	46
26. <i>Acrotrichis</i> sp. (<i>n. sericans</i>)	5	46
27. <i>Sepsis neocynipsea</i> M. & S. larvae	5	46
28. <i>Sepsis</i> sp. B	5	46
29. <i>Salpella sphondylia</i> (Schrank) larvae	5	46
30. <i>Aphodius</i> larvae	5	46
31. <i>Cercyon</i> larvae	5	46
32. <i>Oxytelina</i> larvae	5	46
33. <i>Platystethus americanus</i> Erichson	5	6-9, 24, 46
34. <i>Atheta sordida</i> Marsh	5	6-9, 24, 46
35. <i>Atheta</i> sp.	5	6-9, 24, 46
36. <i>Falagria dissecta</i> Erichson	5	6-9, 24, 46
37. <i>Leptocera</i> larvae	5	46
38. Diptera B66	5	46
39. Diptera C66	5	46
40. <i>S. bipostulatum</i> Fab. larvae	5	6-9, 24, 27-29, 37-39
41. <i>S. scarabaeoides</i> (L.) larvae	5	6-9, 24, 27-29, 37-39
42. Hydrophilid A65	1, 5	46
43. <i>Sphaeridum scarabaeoides</i> (L.)	1	46
44. <i>S. bipostulatum</i> Fab.	1	46
45. <i>S. lunatum</i> Fab.	1	46
46. Bovine dung	1, 5	

* Professor Ivan Valiela sent us unpublished detailed daily data for his 5-d dung arthropod web (*personal communication*, 19 December 1990). We plan to analyze these data in the near future.

TABLE A10. Cumulative food web for the acidic permanent pond on the Skipwith Common, North Yorkshire, United Kingdom, sampled from the open water by Warren (1989). Numbers in the column "Time in web" refer to the week(s) each species was recorded, starting from the week of 12–13 March 1986. Pond invertebrates were sampled on each of the following 5 dates: week 1, 12–13 March; week 10, 22–23 May; week 12, 7–8 June; week 23, 21–23 August; and week 29, 3–4 October. Warren found no fish or amphibians. For week 23 we combined Warren's observations of vegetated open water and unvegetated open water.

Species	Time in web (weeks 1, 10, 12, 23, and/or 29)	Prey species
1. <i>Polycelis tenuis</i> (Ijima)	23, 29	2, 23–27
2. Enchytraeidae	1, 10, 12, 23, 29	28
3. <i>Lumbriculus variegatus</i> (Muller)	29	28
4. Oribatei sp.	1, 10, 12, 23, 29	28
5. <i>Argyroneta aquatica</i> (Clerk)	29	4, 6, 7, 10, 13, 14, 16, 20–27
6. <i>Chydorus latus</i> Sars	1, 10, 12, 23, 29	28
7. <i>Acanthocyclops vernalis</i> (Fischer)*	1, 10, 12, 23, 29	2, 6, 23, 26
8. <i>Enallagma cyathigerum</i> (Charpentier)*	23, 29	2–4, 6, 7, 16, 22–27
9. <i>Sympetrum scoticum</i> (Donovan)	12, 23	2, 4, 6–8, 15–20, 22–27
10. <i>Callicorixa praeusta</i> (Fieber)	1, 10, 12, 23, 29	23–28
11. <i>Corixa punctata</i> (Illinger)	23, 29	28
12. <i>Hesperocorixa linnei</i> (Fieber)	12	28
13. <i>Hesperocorixa sahlbergi</i> (Fieber)	29	28
14. <i>Arctocoris germari</i> (Fieber)	1, 10, 12, 23, 29	23–28
15. <i>Sigaria semistriata</i> (Fieber)	23	28
16. Corixid nymphs	10, 12, 23, 29	28
17. <i>Hydroporus erythrocephalus</i> (L.)	23	2, 6, 7
18. <i>Agabus/Ilybius</i> larvae*	1, 10, 12, 23, 29	3, 8, 16, 19–27
19. <i>Sialis lutaria</i> (L.)*	1, 12, 23, 29	2–4, 6, 7, 16, 22–27
20. <i>Holocentropus picivornis</i> (Stephens)	12, 23, 29	2, 6, 7, 16, 22–27
21. <i>Limnephilus marmoratus</i> Curtis	1, 10, 23, 29	2, 4, 23–28
22. <i>Procladius sagittalis</i> (Kieffer)	1, 12, 23, 29	2, 4, 6, 7, 23, 25–27
23. <i>Corynoneura scutellata</i> Winnertz	1, 23, 29	28
24. <i>Chironomus dorsalis</i> Meigen	1, 10, 12, 23, 29	2, 28
25. <i>Glyptotendipes pallens</i> (Meigen)	1, 10, 12, 23, 29	28
26. <i>Tanytarsus bruchonius</i> Reiss & Fittkau	1, 10, 12, 23, 29	28
27. Other chironomids	12, 23, 29	28
28. Detritus	1, 10, 12, 23, 29	

* Cannibalistic species.

TABLE A11. Cumulative food web for the acidic permanent pond on the Skipwith Common, North Yorkshire, United Kingdom, sampled from the margins of the pond by Warren (1989). * Numbers in the column "Time in web" refer to the week(s) each species was recorded, starting from the week of 12–13 March 1986. Pond invertebrates were sampled on 5 dates: week 1, 12–13 March; week 10, 22–23 May; week 12, 7–8 June; week 23, 21–23 August; and week 29, 3–4 October. Warren found no fish or amphibians.

Species	Time in web (weeks 1, 10, 12, 23, and/or 29)	Prey species
1. <i>Polycelis tenuis</i> (Ijima)	1, 12, 23, 29	2, 3, 32–36
2. Enchytraeidae	1, 10, 12, 23, 29	37
3. <i>Lumbriculus variegatus</i> (Muller)	1, 29	37
4. <i>Oribatei</i> sp.	1, 10, 12, 23, 29	37
5. <i>Argyroneta aquatica</i> (Clerk)	10, 12, 23, 29	4, 6–8, 14, 19–21, 29–36
6. <i>Scaphaloberis mucronata</i> (Muller)	12, 23	37
7. <i>Chydorus latus</i> Sars	1, 10, 12, 23, 29	37
8. <i>Acanthocyclops vernalis</i> (Fischer)†	1, 10, 12, 23, 29	2, 7, 32, 35
9. <i>Enallagma cyathigerum</i> (Charpentier)†	1, 12, 23, 29	2, 4, 6–8, 21, 31–36
10. <i>Lestes sponsa</i> (Hansemann)†	10, 12, 29	2, 4, 6–9, 21, 28, 29, 31–36
11. <i>Aeshna juncea</i> (L.)†	1, 10, 12, 29	2–10, 12, 20, 21, 26, 28–36
12. <i>Sympetrum scoticum</i> (Donovan)	12, 23, 29	2–4, 6–9, 21, 22, 26, 28, 29, 31–36
13. <i>Notonecta glauca</i> L.†	1, 23, 29	3, 6, 9, 10, 12, 14, 17–21, 26, 28–36
14. <i>Callicorixa praeusta</i> (Fieber)	1, 10, 12, 23, 29	32–37
15. <i>Corixa dentipes</i> (Thomson)	1, 10, 23, 29	37
16. <i>Corixa punctata</i> (Illinger)	1, 10, 12, 23, 29	37
17. <i>Hesperocorixa linnei</i> (Fieber)	1, 12, 29	37
18. <i>Hesperocorixa sahlbergi</i> (Fieber)	1, 23, 29	37
19. <i>Arctocoris germari</i> (Fieber)	1, 12, 23, 29	32–37
20. <i>Sigaria semistriata</i> (Fieber)	1, 10, 29	37
21. <i>Corixidae</i> nymphs	10, 12, 23, 29	37
22. <i>Hydroporus erythrocephalus</i> (L.)	23	2, 6, 7
23. <i>Agabus sturmii</i> (Gyllenhal)	23, 29	2, 4, 6–9
24. <i>Agabus bipustulatus</i> (L.)	23, 29	2, 4, 6–9
25. <i>Ilybius fuliginosus</i> (Fab.)	23, 29	2, 4, 6–9
26. <i>Agabus/Ilybius</i> larvae†	1, 10, 12, 23, 29	3, 6, 9, 10
27. <i>Dytiscus marginalis</i> L.†	12, 23	5, 7, 9, 10, 12
28. <i>Sialis lutaria</i> (L.)†	1, 23, 29	2–4, 6–8, 21, 31–36
29. <i>Holocentropus picicornis</i> (Stephens)	1, 10, 12, 23, 29	2, 6–8, 21, 31–36
30. <i>Limnephilus marmoratus</i> Curtis	1, 10, 12, 23, 29	2, 4, 32–37
31. <i>Procladius sagittalis</i> (Kieffer)	1, 10, 12, 23, 29	2–4, 6–8, 32, 34–36
32. <i>Corynoneura scutellata</i> Winnertz	1, 12, 23, 29	37
33. <i>Chironomus dorsalis</i> Meigen	1, 10, 23, 29	2, 37
34. <i>Glyptotendipes pallens</i> (Meigen)	1, 10, 12, 23, 29	37
35. <i>Tanytarsus bruchonius</i> Reiss & Fittkau	1, 10, 12, 23, 29	37
36. Other chironomids	12, 23, 29	37
37. Detritus	1, 10, 12, 23, 29	

* P. Warren (*personal communication*, 4 April 1990) corrected several errors in the published data. To the predation matrix of Warren (1989: Table 2), add the entries "2b" (following Warren's code) to column 19 in rows 32–36. In his Fig. 3b (margin), consumer 11 eats prey 2, 10 eats 29, 5 eats 14, 20 and 29. His Table 2 shows 5 eating 14 and 20 but not his Fig. 3, so we assumed these links are present.

† Cannibalistic species.