(Reprinted from Nature, Vol. 270, No. 5633, pp. 165–167, November 10, 1977)

Ratio of prey to predators in community food webs

WHETHER the diversity of resources limits the diversity of consumers, and specifically, whether the number of kinds of prey limits the number of kinds of predators, has been of continuing interest in theoretical ecology and wildlife management[1–3]. Food webs from the ecological literature were collected in machine readable form to study this question empirically. We report here that in community food webs, the ratio of the number of kinds of prey to the number of kinds of predators seems to be constant, near 3/4. This invariance has not been noticed in earlier studies of individual cases.

Before analysis, food webs were characterised as one of three types—community, sink and source. Community food webs describe all kinds of organisms (possibly restricted to some location, size or taxa) in a habitat, without reference to the eating relations among them. Sink food webs describe all the prey taken by a set of one or more selected predators, plus all the prey taken by the prey of those predators, and so on. Source food webs describe all the predators on a set of one or more selected prey organisms, plus all the predators on those predators, and so on. Sink and source food webs, hypothetical or schematic constructions, and avowedly incomplete, partial or tentative food webs were excluded from further study. Fourteen community food webs were thus selected. The complete data and individual cases will be discussed elsewhere[4]. When the report of a food web contained ambiguous or uncertain information about a feeding relation, the web was included in two versions, one based only on the unambiguous information and the other incorporating the additional uncertain or probable eating relations. The analysis presented here based on all versions, makes no claim that the data points are statistically independent and attaches no probability values to the statistics calculated.

The food webs describe the diets or predators not of individual organisms but of kinds of organisms. A 'kind of organism' may be a stage in the life cycle or a size class within a single species, or a collection of functionally or taxonomically related species, according to the practice of the original report. The numbers in the following analyses refer to these ecologically defined kinds of organisms, not necessarily to any conventional taxonomic unit. A predator is defined as a kind of organism that consumes at least one kind of organism included in the food web. A prey is defined as a kind of organism that is consumed by at least one kind of organism in the food web. Some kinds of organisms may be both predators and prey.

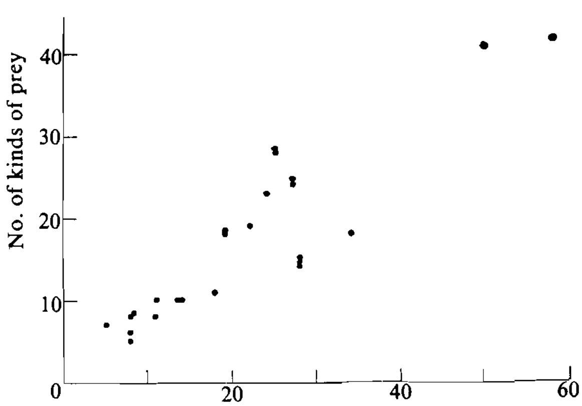

Fig. 1 The number of kinds of prey and the number of kinds of predators in community food web versions.

In community food webs, the number m of prey is very nearly proportional to the number n of predators (Fig. 1). A least squares regression of m against n gives

$$m=1.79+0.71\,n \qquad (1)$$

The sample standard deviation of the regression coefficient is 0.07 and the linear correlation coefficient between m and n is 0.90. The standard error of estimate, or sample standard deviation from regression, is 4.62. As is obvious from Fig. 1, the regression may be well approximated by a straight line through the origin. The least squares regression is

$$m=0.77\,n \qquad (2)$$

The proportionality between the number of prey and the number of predators in Fig. 1 is based on 24 versions of 14 food webs reported over a period of decades. When the food webs were collected and encoded it was not known that such a simplicity would emerge. It therefore seems likely that this invariance in the proportions of predators and prey represents a fact about nature, rather than an artefact of collusion or convention.

Given that the proportion of prey to predators is a scale-invariant feature of community food webs, the proportion can be predicted quantitatively from other facts. For a given food web with m prey and n predators, let A be the number of predator–prey couples. (If X eats Y and Y eats X, the couples (X,Y) and (Y,X) are counted as distinct. If X eats X, (X,X) also counts as a couple. In the conventional graphical representation of a food web, A is the number of directed arrows from prey to predator.) Then within any food web

$$\begin{aligned}A&=(\text{average prey per predator})\times n\\&=(\text{average predators per prey})\times m\end{aligned} \qquad (3)$$

The grand mean over all 24 community food web versions, weighting each food web equally, of the average prey per predator is 2.418; the grand mean of the average predators per prey is 3.199. If these means apply to each food web, then substitution into equation (3) predicts

$$m/n=2.418/3.199=0.756 \qquad (4)$$

which differs trivially from the least squares regression in equation (2).

The simplicity of the argument from the proportionality between m and n to equation (4) may raise a suspicion that its success depends on an arithmetical fact rather than on the observed invariance of proportions of predators and

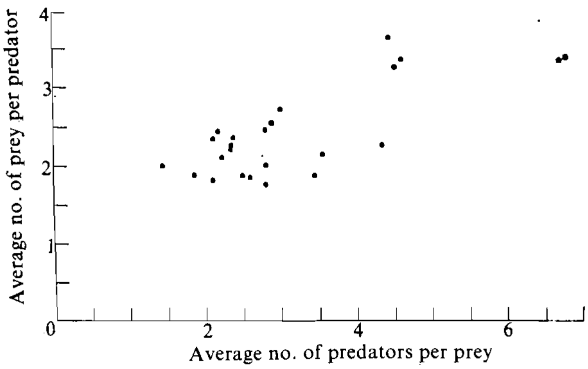

Fig. 2 The average number of kinds of prey per kind of predator and the average number of kinds of predators per kind of prey in community food web versions.

prey in nature. A numerical example disproves this suspicion. Suppose a sample of community food webs consisted of two food webs. Suppose the first food web matrix had $m_1=8$ prey, $n_1=6$ predators, and $A_1=19.2$ predator–prey couples (neglecting the requirement that A_1 be integer for the sake of argument). Then its (average predators per prey)$_1$ is 2.4 and its (average prey per predator)$_1$ is 3.2. Suppose the second food web matrix had $m_2=4$, $n_2=10$, and $A_2=16$. Then its (average predators per prey)$_2=4.0$ and (average prey per predator)$_2=1.6$. Then the grand mean over both food webs of the average predators per prey is 3.2 and the grand mean of the average prey per predator is 2.4, which are close enough to the observed. But the straight line through the pairs (n, m) satisfies $m=14-n$. Only because nature assures a constant proportion of prey to predators do the grand mean of the average predators per prey and the grand mean of the average prey per predator apply to all food webs.

If the ratio of prey to predators in community food webs is a constant of the order of 3/4, then dividing equation (3) by n leads to the prediction that a regression (Fig. 2) of average prey per predator against average predators per prey should be a straight line through the origin with slope 3/4. The regression coefficient of a straight line through the origin is 0.69, not far from 3/4.

In conclusion, in community food webs, the number of kinds of prey, as operationally defined by field ecologists, approximates 3/4 the number of kinds of predators. This results from the study only of an ensemble of food webs, rather than of individual cases.

This work was supported in part by US NSF grants GB-31049 and BMS74-13276.

JOEL E. COHEN

The Rockefeller University,
1230 York Avenue,
New York, New York 10021

Received 15 August; accepted 2 September 1977.

1. Haigh, J. & Maynard Smith, J. *Theor. Pop. Biol.* 3, 290–299 (1972).
2. Levin, S. A. & Paine, R. T. *Proc. natn. Acad. Sci. U.S.A.* 71, 2744–2747 (1974).
3. Sullivan, A. L. & Shaffer, M. L. *Science* **189**, 13–17 (1975).
4. Cohen, J. E. *Food Webs and Niche Space*, (Princeton University Press, Princeton, in the press).

Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset