# Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory

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## GARY A. POLIS

Department of Biology, Vanderbilt University, Box 93 Station B, Nashville, Tennessee 37235

*Abstract.*—Food webs in the real world are much more complex than food-web literature would have us believe. This is illustrated by the web of the sand community in the Coachella Valley desert. The biota include 174 species of vascular plants, 138 species of vertebrates, more than 55 species of arachnids, and an unknown (but great) number of microorganisms, insects (2,000–3,000 estimated species), acari, and nematodes. Trophic relations are presented in a series of nested subwebs and delineations of the community. Complexity arises from the large number of interactive species, the frequency of omnivory, age structure, looping, the lack of compartmentalization, and the complexity of the arthropod and soil faunas. Web features found in the Coachella also characterize other communities and should produce equivalently complex webs. If anything, diversity and complexity in most nondesert habitats are greater than those in deserts. Patterns from the Coachella web are compared with theoretical predictions and "empirical generalizations" derived from catalogs of published webs. The Coachella web differs greatly: chains are longer, omnivory and loops are not rare, connectivity is greater (species interact with many more predators and prey), top predators are rare or nonexistent, and prey-to-predator ratios are greater than 1.0. The evidence argues that actual community food webs are extraordinarily more complex than those webs cataloged by theorists. I argue that most cataloged webs are oversimplified caricatures of actual communities. That cataloged webs depict so few species, absurdly low ratios of predators on prey and prey eaten by predators, so few links, so little omnivory, a veritable absence of looping, and such a high proportion of top predators argues strongly that they poorly represent real biological communities. Consequently, the practice of abstracting empirical regularities from such catalogs yields an inaccurate and artifactual view of trophic interactions within communities. Contrary to strong assertions by many theorists, patterns from food webs of real communities generally do not support predictions arising from dynamic and graphic models of food-web structure.

Feeding relationships in communities are delineated in three ways. The first is the classic food web, a schematic description of trophic connections. The second quantifies energy or mass flow. Finally, interaction or functional webs experimentally identify strong links (Paine 1980; Menge and Sutherland 1987). Superficially, little work is needed to construct food webs; consequently, they most frequently represent communities. A rough, qualitative knowledge of "who eats whom" is all that is necessary to produce a simple food web, whereas experimental manipulations or quantitative measurements are necessary to construct webs of interaction or energy flow.

Several approaches analyze food webs (DeAngelis et al. 1983; May 1986; Lawton 1989; Schoener 1989). One uses models based on stability analysis. The re-

sults are complex and beyond the scope of this article. However, they basically show that model systems decrease in stability with more species, more links (connectance), or greater linkage strength. The dynamic constraints needed to maintain stability are hypothesized as important in shaping the properties of webs. Stable webs are relatively simple, short (with few trophic levels), and compartmentalized and exhibit little omnivory or looping (Pimm 1982).

A second approach analyzes real food webs to determine regularities in their properties. Analyzed webs were compiled by Cohen (1978), Cohen et al. (1986, 1990), Briand (1983), and Schoenly et al. (1991). Cohen et al. (1986) published a catalog of 113 webs, and Schoenly et al. compiled 95 insect-oriented webs. Theorists (Pimm and Cohen) argue that empirically derived patterns are consistent with and validate predictions of the dynamic models above (dynamic models: Pimm 1982, Pimm and Rice 1987; cascade model: Cohen et al. 1990). "Indeed, there is a close tie between the theoretical and observational studies: real food webs have a statistical predominance of those features that, in models, increase the chance that those models will be stable. The first is that trophic interactions, though highly complex, are reasonably patterned—they demonstrate a large catalogue of assembly rules" (Pimm and Rice 1987, p. 304). Some empirical patterns and assembly rules are presented in Appendix A.

In this article, the food web of a desert community is analyzed explicitly to evaluate the patterns in Appendix A. Observed patterns are quite different from those assembled from published webs. I argue that most cataloged webs are overly simplified and poorly represent actual communities. Consequently, the practice of abstracting empirical regularities yields an inaccurate and artifactual view of trophic interactions within communities.

GENERAL PROBLEMS IN THE ANALYSIS OF EMPIRICAL FOOD WEBS

Four substantial problems beset the catalogs of webs and make them totally inadequate for the types of analyses that have been conducted (also see Glasser 1983; May 1983a; Taylor 1984; Paine 1988; Sprules and Bowerman 1988; Lawton 1989; Winemiller 1990).

1. *Inadequate representation of species diversity.*—The *major* problem is that the numbers of species in cataloged communities are far less than those in real communities. Most authors of these webs simply ignored unfamiliar species, concentrated on taxa in their expertise, and/or aggregated or "lumped" unfamiliar species into higher categories. Lumping is a severe problem. Cohen (1978) labeled lumped categories "kinds of organisms." "'Kinds' are equivalent classes with respect to trophic relations" (Cohen 1978, p. 7). Briand (1983, p. 253) clarifies and expands: "A 'kind of organism' (interchangeable henceforth with the term 'species') may be an individual species, or a stage in the life cycle of a size class within a single species, or it may be a collection of functionally or taxonomically related species." "Kinds" are also called "trophic species" (Briand and Cohen 1984) and "species" (Cohen and Newman 1985). Kinds include "basic food," "benthos," "other carnivores" (matrix 1 in Briand 1983); "algae," "plankton," "birds" (matrix 9); "zooplankton," "ice invertebrates," "fish" (matrix 21); and

"trees and bushes," "insects," "spiders," "soil insects and mites," and "para-
sites" (matrix 27). Only 28.7% of the total kinds in all Briand's webs are real
species; nine matrices have no real species. The "kinds" simplification was criti-
cized by Glasser (1983), May (1983*a*), Taylor (1984), Paine (1988), Lawton (1989),
Lockwood et al. (1990), Winemiller (1990), and Cohen (1978) himself in a self-
critique (but see Sugihara et al. 1989).

Lumping is not uniform: plants, arthropods, parasites, and organisms that live
in the soil or benthos are most frequently grouped. Invertebrates are analyzed in
much less detail than vertebrates (Pimm 1982), thus obscuring food-web complex-
ity (Taylor 1984; Paine 1988). The incomplete presentation of these taxa is a
serious flaw. In particular, arthropods are central to the structure of terrestrial
communities. The ~800,000 identified species of insects represent ~89% of all
animal species (5–50 million insect species are estimated to exist; May 1988). Soil
organisms are usually ignored or lumped in spite of their importance as major
pathways of energy flow in terrestrial communities (Cousins 1980; Odum and
Biever 1984; Rich 1984). The tactics of ignoring and lumping species produce
the depauperate webs compiled by Cohen and Briand. This is obvious from an
inspection of Cohen et al.'s (1990) 113-web catalog. The number of "kinds"
ranged from 3 to 48 with the average web "community" having 16.9 kinds. Real
communities have more species.

This is illustrated by enumerating the species from the sandy deserts of the
Coachella Valley (hereafter CV; Riverside County, Calif.): 174 species of vascular
plants, 138 species of vertebrates, more than 55 species of arachnids, and a large
but unknown number of lower plants, nematodes, acari, and insects (Polis 1991*a*).
Insects are estimated at 2,000 to more than 3,000 species; I have identified 123
families. A still-incomplete survey in the adjacent Deep Canyon Desert Preserve
identified 24 orders, 308 families, and more than 2,540 species (Frommer 1986).

2. *Inadequate dietary information.*—Published analyses of diets or lists of ene-
mies (predators, parasites, and/or parasitoids) suggest that most species eat and
are eaten by from $10^1$ to $10^3$ other species (see below). The inadequate incorpora-
tion of these trophic links is another major weakness of cataloged webs. The
number of prey items recorded is usually a function of the amount of time and
effort devoted to observation. A "yield/effort" curve (Cohen 1978) is illustrated
by analyzing the diet of the scorpion *Paruroctonus mesaensis* (fig. 1). The number
of prey species continues to increase with observation time. The 100th prey
species was recorded on the 181st survey night; an asymptote was never reached
in 5 yr and more than 2,000 person hours of field time. This suggests that the
amount of effort and time needed to determine the complete diet of just the
numerically dominant species is astronomical. It is unlikely that such an effort
was made for most species in the cataloged webs. Thus a food web containing
all species still would be an inadequate description of community trophic relations
unless diets were known with more confidence.

Such inadequacy is manifested in cataloged webs. For example, they show a
high proportion (28.5%, Briand and Cohen 1984; 46.5%, Schoenly et al. 1991) of
top predators (consumers without predators). It is unlikely that even 1%, let alone
almost one-half, of all animals do not suffer predators sometime during their lives
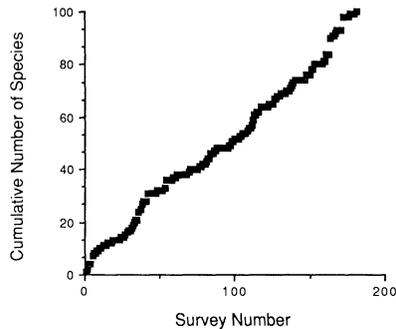
FIG. 1.—Yield effort curve for first 100 species of prey captured by the scorpion *Parurocto-nus mesaensis* in the Coachella Valley.

(see below). These high figures partially result from grossly incomplete data: for example, in Cohen et al.'s (1986) catalog, 57 chains were of length one, that is, 57 herbivores were with no recorded predators! Such top predators include spiders, mites, midges, mosquitos, bees, weevils, fish larvae, blackbirds, shrews, and moles.

3. *Age structure.*—Age-related changes in food and predators are not well incorporated into web analysis. Populations are composed of age/size classes, each exhibiting significant differences in resource use, predators, and competitors (Polis 1984, 1988a; Werner and Gilliam 1984; Polis and McCormick 1986a). Age classes often eat different foods, thereby expanding diet ("life-history omnivory"; Pimm and Rice 1987). "Ontogenetic diet shifts" characterize species that undergo metamorphosis. The juveniles of at least 27 families of CV holometabolic insects eat radically different foods (live arthropods) from adults (plants). For species that grow slowly through a "wide size range," diet changes more gradually as prey size increases with predator size (e.g., arachnids, reptiles; Polis 1988a). In fact, differences in body sizes and resource use among age classes are often equivalent to or greater than differences among most "biological species" (Polis 1984). This magnitude of change is typical of wide-size-range predators (most invertebrates, hemimetabolic insects, larva of holometabolic insects, arachnids, fish, and reptiles; Polis 1984).

Predators also change during growth. Juveniles are eaten by species too small to capture adults. Such developmental "escapes" are common to all communities. For example, snakes eat eggs and newborn (but not adults) of carnivorous birds and desert tortoises. Alternately, adults are eaten by predators that do not eat small juveniles. Thus some predators (e.g., owls, kit foxes) in the CV eat only adult scorpions (Polis et al. 1981).

In summary, age/size differences in predators, prey, and competitors are the norm in terrestrial as well as aquatic habitats (contrary to Pimm and Rice's [1987] assertions) and may be major determinants of population dynamics and community structure. Unfortunately, the richness that age structure contributes has been largely ignored (but see Pimm and Rice 1987). Usually only adults are considered or the diets of all age classes are combined. Age is recognized in only 22 of 875

kinds in Cohen's (1978) catalog and in 3 of 422 in Briand's (1983). Age structure is often difficult to incorporate into studies; nevertheless it is paramount to community dynamics.

4. *Looping*.—Looping is a feeding interaction whereby A eats B and B eats C but either B (in mutual predation) or C (in a three-species loop) eats A. Cannibalism is a "self-loop" (A eats A; Gallopin 1972). Food-web theorists dismiss loops as "unreasonable structures" (Pimm 1982, p. 70; see also Gallopin 1972; Cohen 1978; May 1983*a;* Cohen et al. 1990). Pimm summarizes from the catalog of webs: "I know of no cases, in the real world, with loops" (p. 67). He has modified this view to include loops in aquatic age-structured species (Pimm and Rice 1987) but still maintains that loops are rare in terrestrial systems.

Looping is widespread. Cannibalism is reported in more than 1,300 species and is a key factor in the dynamics of many populations (Polis 1981; see also Elgar and Crespi, in press). Cannibalistic loops are frequent in the CV. Ontogenetic reversal of predation among age-structured species is the most common form of mutual predation: A juveniles are eaten by B but A adults eat B (and/or B juveniles) (Polis et al. 1989). This occurs among CV insects, spiders, scorpions, and solpugids and among predaceous lizards, snakes, and birds. For example, gopher snakes (*Pituophis*) eat eggs and young of burrowing owls whereas adult burrowing owls eat young gopher snakes.

Mutual predation can occur independently of age structure (Polis et al. 1989; Schoener 1989; Winemiller 1990). Two examples from the CV are black widow spiders and CV ants. Black widow spiders (*Latrodectus hesperus*) catch three species of scorpions by using web silk to pull them up off the ground; black widows traveling on the ground are captured by these same scorpions (Polis and McCormick 1986*b*). Second, CV ants (*Messor pergandei, Pogonomyrmex californicus, Myrmecocystus flaviceps*) regularly eat each other (Ryti and Case 1988). Killing and predation of winged reproductives (after swarming) and workers (during territorial battles) are a regular interaction among many social insects (see Polis et al. 1989).

THE COACHELLA VALLEY

The Coachella Valley is located in Riverside County, California (166°37'W, 33°54'N; area = ~780 km²). Winters are mild; summers, dry and hot. It is a low-elevation rain shadow desert with average annual rainfall at Deep Canyon of 116 mm. The sand dune/intergrading sand flat habitat was chosen for analysis. This community is well studied because of the presence of the University of California Deep Canyon Desert Preserve. Beginning in 1969, Mayhew (1983) surveyed the vertebrates for the Deep Canyon Transect Study. This work established a list of 138 reptiles, birds, and mammals on sandy soils. Some species are not included in the web; for example, mountain lions and badgers are now absent. Further, only the 56 birds (out of 97 residents) that actually nest in the area are considered. Additional data on CV vertebrates were obtained from Weathers (1983) and Ryan (1968). Invertebrates are less well known. Much of the knowledge of them results from my long-term research (since 1973) over 17 yr and more

than 4,000 h of fieldwork including more than 4,300 trap days for arthropods. Taxonomic lists are obtained from this fieldwork and from catalogs of CV arachnids (Polis and McCormick 1986b) and insects (Frommer 1986). Plants were surveyed by Zabrinskie (1979).

Food and predators were determined from the literature and my work. Since 1979, I have read ~820 papers to assemble data for the CV web. Data from the CV were used with priority; however, I was forced to supplement this information with that from other regions, some quite near (e.g., the Palen Dunes) and some much farther away (e.g., the Chihuahuan Desert). I could not find the diets (from desert areas) of 18 birds and one rodent. Finally, interviews with scientists conducting research in the CV provided taxonomic and dietary data. Because of space limitations, I include only the most important references. Additional references and the identities and diets of vertebrate species and arthropod families are given in Polis (1991a).

A series of representative subwebs depicts trophic relations in the CV sand community. Subwebs proceed from plants and detritus to various secondary consumers. Subwebs are connected so that organisms in one web consume (or are consumed by) organisms in the next. Webs are incomplete because there are far too many species to include and adequate diet data are unavailable for many species. I thus concentrate on well-studied, focal species, the trophic interactions of which are relatively well known. Webs include only species that live in the CV and only interactions for which evidence exists. Similar complexity is expected for other, less known species. Thus, these webs understate actual complexity.

Consumers are classified in terms of resource specialization (i.e., number of species eaten within one group, e.g., plants) or trophic specialization (i.e., number of different types eaten, e.g., plants, detritus, arthropods) (Levine 1980). Species vary from resource specialists that eat a few species of the same resource type to trophic generalists (omnivores) that feed on several food types. Closed-loop omnivory is a special case of omnivory in which A eats both B and C but B also eats C (Sprules and Bowerman 1988).

RESULTS

*Plant-Herbivore Trophic Relations*

Herbivory describes feeding interactions involving several plant products: leaves, seeds, fruit, wood, sap, nectar, roots, and tubers. Desert herbivores include microbes, nematodes, arthropods, and vertebrates. I cannot detail the herbivores of the hundreds of CV plants. Rather, I discuss broad groups with the hope of conveying the complexity in the plant-herbivore link. A wide variety of arthropods eat desert plants (Orians et al. 1977; Powell and Hogue 1979; Crawford 1981; Wisdom 1991). At least 74 families of CV arthropods are herbivorous sometime in their lives. Plants that grow in the CV are attacked by many species of insect: more than 60 eat creosote (*Larrea tridentata;* Schultz et al. 1977), more than 200 on mesquite (*Prosopis glandulosa*), and more than 89 on ragweed (*Am-*

*brosia dumosa*) (Wisdom 1991). Both resource specialists and generalists live in the CV. Specialists include the grasshopper *Bootettix punctatus* (on creosote; Mispagel 1978). Insects on cactus usually specialize, and generalists do not attack cactus (Mann 1969). (Damage caused by feeding on cactus facilitates several specialist and generalist fungi.) Resource generalists are more common in deserts than are specialists (Orians et al. 1977; Crawford 1981, 1986). Generalists in the CV include the harvester ant *Messor pergandei* (97 species of CV seed; Gordon 1978) and the camel cricket *Macrobaenetes valgum* (16 plant species; G. A. Polis, unpublished data).

Most herbivorous arthropods are trophic specialists on plants all their lives: for example, hemimetabolic (Orthoptera, Hemiptera, Homoptera, Thysanoptera) and some holometabolic insects (e.g., curculionid, chrysomelid, scarabid, and buprestid beetles). However, many holometabolic insects have larvae that are parasitic or predaceous on arthropods but whose adults feed on plants (Ferguson 1962; Andrews et al. 1979; Powell and Hogue 1979; Wasbauer and Kimsey 1985). Trophically flexible generalists include CV harvester ants (more than 40 categories of foods including seeds, flowers, stems, spiders, and insects from at least six orders including four ant species; Ryti and Case 1988) and camel crickets (15% plant detritus, 41% animal detritus, and <1% conspecifics).

Most CV mammals (16 of 18 species) eat plant tissue (the two bats did not). Plants (fruit) formed 0.2%–4.1% of the diet of the largest mammal, the coyote (Johnson and Hansen 1979). This is the smallest plant component for any of the 16 mammals. Over 50% of the scats of the desert kit fox contained plant material. The two rabbits and the gopher are the only trophic specialists; however, they are resource generalists eating many species. Omnivorous antelope ground squirrels fed on a seasonally changing diet (10%–60% foliage, 20%–50% seeds, 62%–95% total plants by volume; W. Bradley 1968). Rodents (*Dipodomys, Peromyscus, Perognathus*) fed on seeds and plant parts (and arthropod prey). In total, 15 mammals eat seeds (only bats and the gopher do not). Nine regularly consumed more than 50% seeds in their diet. No CV mammals specialize on particular plants. For example, pocket mice *Perognathus formosus* feed on 27 plant species; antelope ground squirrels, 24 species. With the exception of the gopher and the two rabbits, all plant-eating mammals are trophic generalists that include arthropods in their diet, for example, 1%–17% for *Dipodomys merriami* and 2%–35% for antelope ground squirrels (this species also eats vertebrates; see below).

Many (34 of 56 species) birds in the sand community feed on plant parts (seeds, nectar, flowers, and fruit). Frugivorous birds are common (e.g., cactus wren, phainopepla, verdin, and doves). Some birds eat fruit as a minor component of an omnivorous diet (e.g., roadrunner, Scott's oriole, western tanager, western bluebird, warbling vireo, Bewick's wren). Granivory is also common: 22 of 56 CV birds were reported to eat seeds (13 are primarily granivorous). Many insectivorous desert birds eat significant quantities of seed when insects are scarce (Brown et al. 1979; Brown 1986; Wiens 1991). No herbivorous birds are resource specialists. In fact, trophic specialists are rare; of 34 plant-eating birds, only five are not recorded to eat arthropods.

Two species of CV reptiles are primarily herbivorous: desert tortoise and desert

iguana. Both are resource generalists eating a wide variety of plants (17–40 species for the tortoise) and plant parts. Only the tortoise is a trophic specialist. The diet of the desert iguana contains 1%–5% arthropods. Five of the nine other lizards (none of 10 snakes) consume a minor portion of plants.

### Detritus, Soil Biota, and Belowground Herbivory

Detritus is a broad term applied to nonliving organic matter from living organisms. It is a universal component of food webs simply because all organisms die, plant parts senesce, and animals defecate. It may originate from plants (e.g., wood, leaves, seeds, flowers, and roots [rhizodeposition]) or animals (feces, urine, secretions, molted skin or fur, and dead animals).

Most primary productivity flows directly or indirectly through the detrital component of food webs. Herbivores process 1%–50% of net primary productivity; the rest enters the detrital system (Macfayden 1963; Odum and Biever 1984). This is particularly so in deserts, where the main energy flow often proceeds directly from autotrophs to detritivores (Seely and Louw 1980; Wallwork 1982; Crawford 1991; Freckman and Zak 1991). The plant-herbivore-carnivore link forms 12%–33% of the fate of plant production in deserts; the remainder goes through the soil/detritus chain. Nevertheless, Cousins (1980) is one of the few to incorporate detritus explicitly into food-web analysis (see also Odum and Biever 1984). He disputes placing autotrophs alone at the basal position of webs; rather, herbivory and detritivory should be considered equally important links in a "trophic continuum." Energy, produced by autotrophs and consumed during secondary production, is recycled and made available to other consumers by detritivores.

A diverse biota lives within desert soils (Crawford 1981, 1991; Wallwork 1982; Freckman and Zak 1991). Microbes (fungi, yeast, bacteria, protozoa), nematodes, mites, termites, some ants, Collembola, Thysanura, cockroaches, tenebrionid larvae, millipedes, and isopods are some of the more common of the many detritivores that live within CV soils. Although species in these taxa degrade organic material, many include facultative or obligate herbivores on belowground plant parts (Crawford 1981, 1986). Over 50% of net primary production is commonly allocated to belowground plant parts (Andersen 1987). For example, in Russian deserts, 65% of the plant biomass is belowground (Rodin and Bazilevich 1964). Species from seven orders of insects, mites, nematodes, and some rodents have adopted belowground herbivory as their primary feeding mode (Andersen 1987).

Soil organisms are quite abundant in deserts. Nematode biomass of 1–20 g/m$^2$ normally occurs (Freckman and Zak 1991). Detritivores form 37%–93% (mean = 73%) of all individual macroarthropods in four deserts analyzed by Crawford (1991). Termites are particularly abundant; their biomass is often an order of magnitude higher than that of any other desert animal (MacKay 1991; Polis and Yamashita 1991). Wallwork (1982) emphasized their importance in desert webs: termites fix nitrogen, eat large quantities of detritus, recycle nutrients within their colonies via trophallaxis and cannibalism, and ultimately release nutrients to predators.

A rich web based on detritus and underground plant parts exists within desert soils (see, e.g., Whitford 1986). Nematodes occupy several trophic roles (Freck-

man and Zak 1991): herbivores, plant parasites, microbial feeders, fungivores, omnivores, omnivore predators, parasites. In the Mojave, there are four trophic groups of Prostigmata soil mites: phytophages (1 family), fungivores and detritivores (3), parasites (1), and predators (8) (Franco et al. 1979; see also Santos et al. 1981). Predatory mites in litter are as common as nonpredators in nearby Joshua Tree Monument (Wallwork 1982). These mites eat nematodes, Collembola, and other mites. The large number and diversity of predatory mites led Edney et al. (1974) to conclude that two or more predator trophic levels exist in the decomposer web. Wallwork (1982) and Santos et al. (1981) suggested that decomposer pathways in desert soils were regulated by mites that prey on nematodes that feed on microorganisms.

Soil interactions become even more complex with the inclusion of macroarthropods. Most detritivorous arthropods not only eat detritus, but also feed on microorganisms (bacteria, fungus, protozoa) feeding within the detritus (Janzen 1977). For example, in the CV, the burrowing cockroach *Arenievaga* feeds below ground on living and decaying roots and ensheathed mycorrhizae. Further, most detritivores (e.g., cockroaches, tenebrionids, millipedes) host cellulolytic microbes that degrade plant detritus (Crawford 1991). Although such symbionts form a separate energetic "trophic level," they usually are not included in web analysis. Finally, several desert insects consume detritus directly or are predaceous on microarthropods and nematodes (e.g., in the CV, larvae of asilid, bombyliid, and theriviid flies, and staphylinid and clerid beetles; Edney et al. 1974; Powell and Hogue 1979).

Soil interactions are not separate from the rest of the community. Surface and subsurface herbivores are involved in competition and facilitation (Seastedt et al. 1988). Most important, energy flows in both directions via the trophic continuum. Many surface dwellers in deserts either spend part of their lives in the soil (as larvae, e.g., tenebrionids) or feed on arthropods that live permanently or temporarily below ground (see Ghilarov 1964). For example, 46% of *Paruroctonus mesaensis* prey live in soils as larvae. *Arenivaga* form 23% by weight of this scorpion's diet. Termites (10 CV species) and tenebrionids (16 species) are important conduits of energy flow from below ground when they are eaten by a diverse group of arthropod and vertebrate predators (Wallwork 1982; 35 species of known surface predators in the CV). Such predation by surface dwellers exports much of the energy recycled by detritivores and links the soil subweb to that above ground. Thus, even if herbivores and detritivores operate in distinct microhabitats, energy flowing further into the community merges into the bodies of predators common to both consumers (Odum and Biever 1984).

No study has analyzed trophic interactions within detritus and soil in the CV. The studies above were conducted in deserts (Mojave, Chihuahua) geographically adjacent to the CV. I combined information from these studies (esp. Whitford 1986; Freckman and Zak 1991) with my data to construct a soil/detritus subweb (fig. 2) using CV taxa. Note the complexity (even with extensive lumping), loops, frequent omnivory (often at nonadjacent levels), closed-loop omnivory, chains of 4–5 links, and links between belowground consumers and aboveground predators.
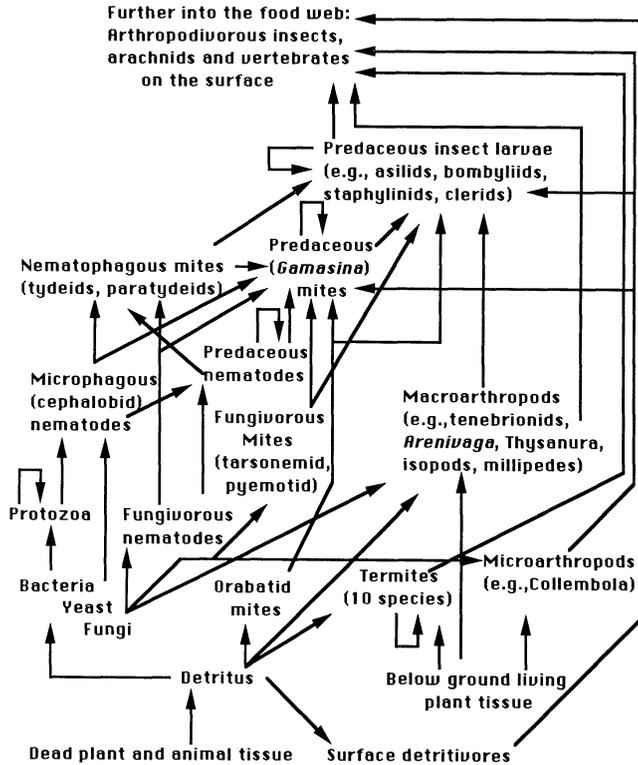
FIG. 2.—Trophic interactions within sandy soils in the Coachella Valley. The identities of a few of the important detritivorous species are as follows: Isopoda (*Venizillo arizonicus*), Collembola (Entomobryididae), Thysanura (*Leucolepisa arenaria, Mirolepisma deserticola*), Gryllacrididae (*Macrobaenetes valgum*), Blattidae (*Arenivaga investigata*), Isoptera (five *Amitermes* spp.; five other species), Tenebrionidae (16 species). Note that not all trophic links are represented (e.g., for tenebrionids and termites). An arrow returning to a taxon indicates cannibalism.

## Carrion Feeders

The decomposition of carrion results from the cumulative action of microorganisms, necrophagous insects, and some vertebrates. A rich carrion fauna occurs in deserts (McKinnerney 1978; Schoenly and Reid 1983; Crawford 1991). Complex interactions involve from 28 to more than 500 species. McKinnerney's analysis of carrion from two rabbits that occur in the CV identifies 63 arthropod and four vertebrate consumers. Some specialize on particular tissue; others do not. Trophic specialists and generalists occur. Species composition and diversity change through time. Necrophagous insects, generalist and specialist predators, and omnivores are common. Vertebrates not only eat carrion but eggs and larvae of insects. Carrion feeders also consume microorganisms within the carrion (Janzen 1977). Further, many carrion species are well-known cannibals (Polis 1981). Interactions within carrion do not constitute a distinct compartment: much of the energy from carrion is exported to the rest of the community. Most organisms

Further into
the food web

Diguetia          Clerid beetles
spiders           (e.g., *Phyllobaneus*)

Facultative hyperparasitoids
(2 Species)

17 species of          Primary parasitoids   Predators
parasitoids            (7 species)           (2 species)

*Rileya* parasitoid

Cecidomyid gall formers    Inquilines in gall
(8 species)                (7 species)

Other herbivorous
arthropods

*Larrea* and 4         *Atriplex* salt bush
other species
of shrubs

*Larrea* (creosote)
food web
(>60 species of
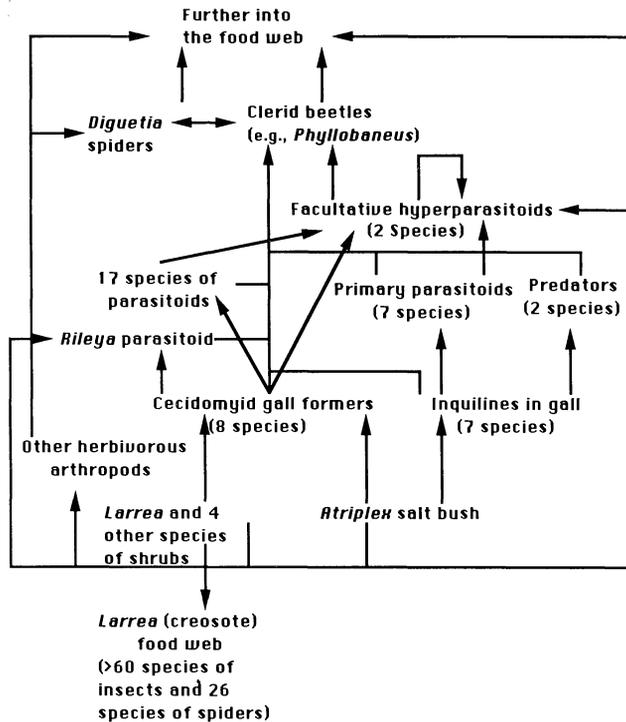insects and 26
species of spiders)

FIG. 3.—Trophic interactions within galls on saltbush *Atriplex canescens* within the Coachella Valley. In total, 67 species interact within galls formed by Cecidomyidae (midge) larvae. Many of these species are also involved in the subweb centering on creosote (*Larrea divaricata;* see Schultz et al. 1977). Note that the interactions of some species are not fully represented (e.g., *Diguetia, Phyllobaneus*). Modified from Hawkins and Goeden (1984).

associated with carrion are opportunistic: spiders, solpugids, Opiliones, ants, asilids, staphylinid beetles, reduviids, and the vertebrates not only eat insects associated with carrion (or carrion itself) but also prey on other species (McKinnerney 1978). In turn, all these species are eaten by other predators.

### Arthropod Parasitoids

Parasitoids from several families of flies, wasps, and beetles are a diverse component of webs representing more than 10% of all animal species (Askew 1971). They lay eggs in or on arthropod hosts; larvae feed on and cause the death of the host (in contrast to parasites in general). Adults almost always feed on other foods (usually of plant origin). Parasitoids' trophic relations are generally quite complex (Askew 1971; Price 1975; Pimm 1982; Hawkins and Goeden 1984; Polis and Yamashita 1991). Hawkins and Lawton (1987) estimate that each species of insect herbivore is host to 5–10 species of parasitoids.

A few studies detail parasitoid-host relationships in the CV. Hawkins and Goeden (1984) studied insects associated with saltbush (*Atriplex*) galls. The system is complex with 67 species (40 common ones), at least five trophic links, and
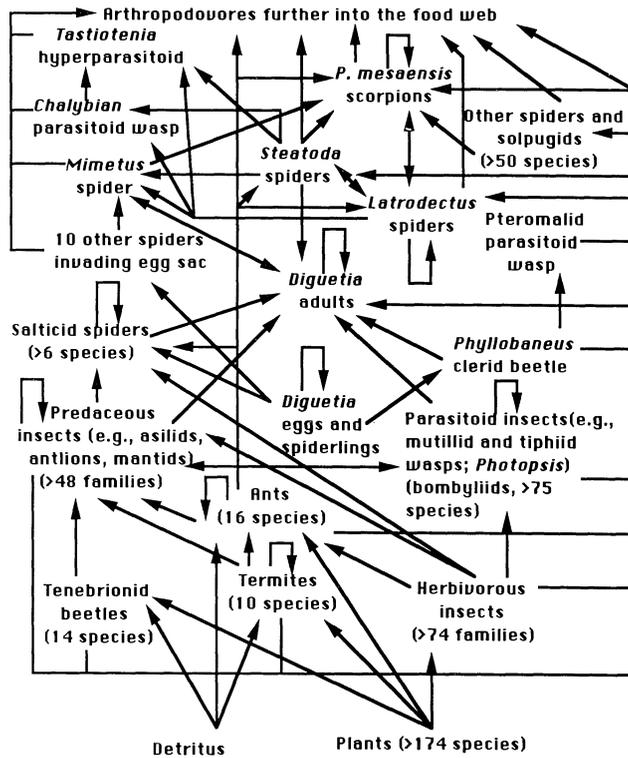
FIG. 4.—Trophic interactions above the soil surface involving a few of the predaceous arthropods living within the Coachella Valley. This subweb is focused around the spiders *Diguetia mohavea* and *Latrodectus hesperus*. Note that no vertebrates are represented.

extensive omnivory. Gall-forming midges (3 species), parasitoid Hymenoptera (26), predators (4), and inquilines (7) interact within galls (fig. 3). Midge larvae are either resource specialists on *Atriplex* or generalists on other plants. Most parasitoids are primary, attacking only midges or inquilines; seven also feed on gall tissue. Two facultative hyperparasitoids feed on gall tissue, midges, and primary and hyperparasitoids. A clerid beetle (*Phyllobaenus*) is in 10% of galls and feeds on at least 17 species from all trophic groups (and spiders; fig. 4).

The trophic relations of *Photopsis* (an abundant mutillid wasp in CV sands) are diagrammed in figure 5 (from Ferguson 1962 and my data). Females oviposit into larval cells, and *Photopsis* larvae consume the entire host. They parasitize several species of hymenopteran larva and are hyperparasitoid on parasitoids of these larva (i.e., other Hymenoptera; stylopid, meloiid, and rhipiphorid beetles; and bombyliid flies). Some hyperparasitized wasps (e.g., sphecids) also may parasitize spiders (this is likely but not established). Up to 37% are destroyed when *Photopsis* larvae themselves are parasitized by some of the same parasitoids (e.g., sphecids) that fall host to *Photopsis*. This is an example of looping via mutual parasitism and tertiary parasitism. Some *Photopsis* larvae are also host to bombyliid (e.g., *Bembix*) and stylopid parasitoids. Further, *Photopsis* larvae also are
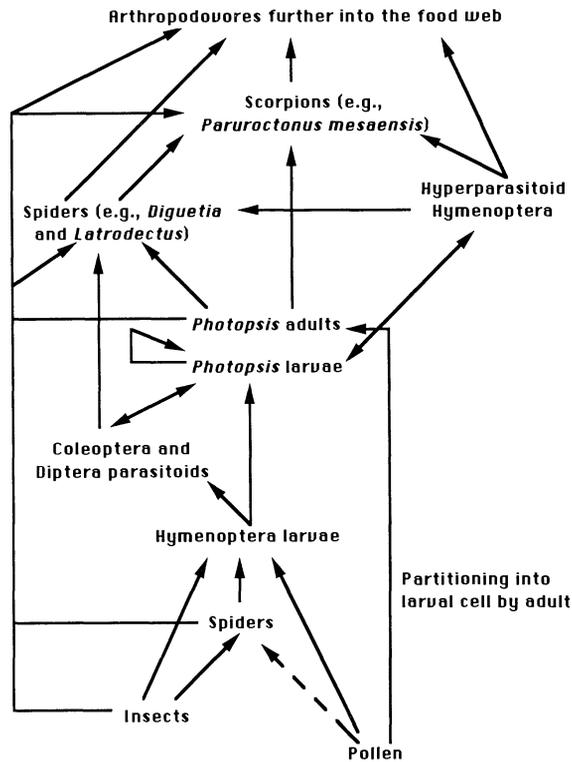
FIG. 5.—Trophic interactions involving parasitoid mutillid wasps in the genus *Photopsis* within the Coachella Valley. Note that the interactions of some species are not fully represented (e.g., scorpions, spiders). A double-headed arrow indicates looping via mutual predation.

cannibalized (and self-regulated? [Ferguson 1962]). Adults eat not only nectar, pollen, and flowers but also ground-nesting Hymenoptera. Adults are frequent prey to many arthropods (e.g., scorpions and spiders; see figs. 4 and 6).

These parasitoid subwebs are characterized by long chains and frequent omnivory, closed-loop omnivory, and looping (via cannibalism, mutual predation, and three-species loops). Further, key species export energy from this subweb when they are predators or prey in the rest of the community.

Overall, more than 20 families of insects are parasitoids of CV insects. Many prefer host species; others, however, are more generalized (see figs. 3 and 5). They sometimes cause high mortality (Mispagel 1978). Several dipteran (tachinid, bombyliid, sarcophagid) and hymenopteran (tiphiid, ichneumonid, mutillid, sphecid, and chalcidoid wasps) parasitoids are common in the CV. These develop on eggs and immature stages of Orthoptera, Neuroptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera. Velvet mite larvae (*Dinothrombium pandorae*) are ectoparasites of CV grasshoppers (Tevis and Newell 1962).

Spiders host many parasitoids (pompilid, sphecid, and ichneumonid wasps; many Diptera). Adult wasps partition nests with captured spiders; developing
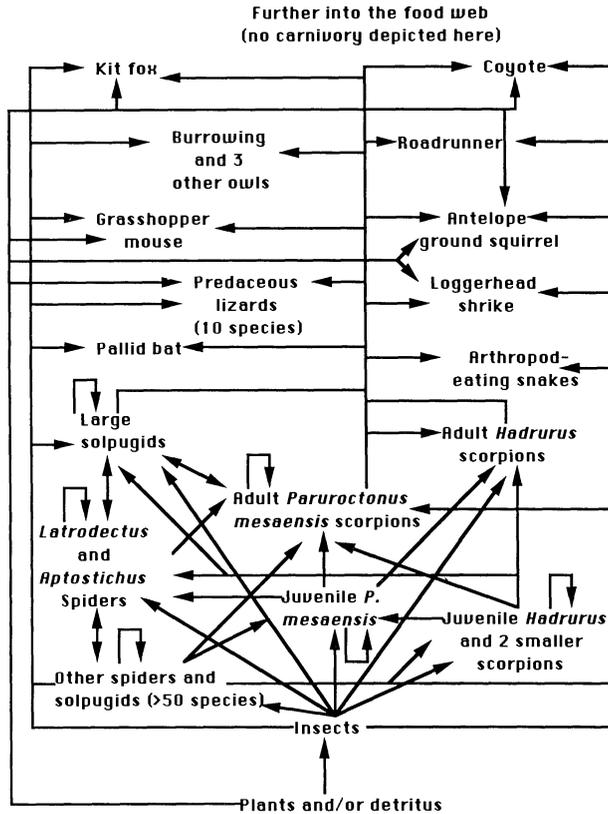
FIG. 6.—Trophic interactions centered around the prey and predators of the scorpion *Paruroctonus mesaensis*. Note that the interactions of some species are not fully represented (e.g., "spiders" and "insects") and carnivory on vertebrates is not depicted (see figs. 5 and 7).

larvae eat the moribund spiders. Adults usually eat nectar. Wasps vary from resource specialists on particular families to generalists on several families. Many pompilids (more than 11 species) occur in the CV (Wasbauer and Kimsey 1985). Abundant *Aporus hirsutus* and the less common *Psorthaspis planata* feed trapdoor spiders (*Aptostichus*, Ctenizidae) to their larvae; adults drink sugar secretions from aphids and nectar from more than 10 plant species. Some CV pompilids are hyperparasitoids (e.g., *Evagetes mohave*). Spiders are also beset by a diversity of egg parasitoids/predators (Polis and Yamashita 1991). Further, kleptoparasitic insects (e.g., Drosophiloidea flies) and spiders parasitize spiders by robbing captured prey (G. A. Polis, personal observation).

### Parasites

Parasites are a diverse and species-rich group that feed on almost all taxa. They can influence greatly population dynamics and community structure (May 1983b) and form another step in the flow of energy (some ectoparasites form yet another

"gratis" level when they themselves host parasites). Many feed on several hosts during their complex life cycle. However, parasites are neither well represented in food webs nor well studied in natural communities. Of animals living in the CV, only the parasites of the coyote, lizards, and scorpions were examined in any detail. Otherwise, few data exist on the hundreds of CV endo- and ectoparasites.

Telford (1970) identified parasites in 10 CV lizards. Lizards were infected by several protozoans (mean = 7.8 species; range = 3–10) including flagellates, ciliates, amoebas, sporozoans, and gregarines. Helminth parasites (mean = 1.4; range = 0–5) included nematodes, cestodes, and Acanthocephala. Each lizard also was infested with an unknown number of mite species.

Coyote parasites include mange mites, ticks (seasonal), lice (rare), and *Pulex* fleas (on all individuals) (Gier et al. 1978). Adult fleas feed on blood; flea larvae feed on organic debris. Endoparasites, specifically the tapeworm *Taenia pistiformes*, occur in 60%–95% of all coyotes. The prime intermediate host of *Taenia* is the cottontail rabbit.

It is likely that most (all?) of the free-living animals in the CV harbor parasites. For example, 23.4% of 1,525 birds (112 species) from deserts and other areas in the southwestern United States had blood parasites (Woods and Herman 1943; Welty [1962] lists the diverse parasite fauna of birds). Inspection of CV spiders and insects usually reveals mite infestation. Many genera of CV spiders were reported with nematode parasites. Coachella Valley scorpions support nematodes and eight (pterygosomid) mite species (G. A. Polis, unpublished data).

### Arthropod Predators

Arthropods are one of the most important conduits of energy flow in desert webs. Most consumed primary productivity in deserts is utilized by arthropods rather than by vertebrates (Seely and Louw 1980). These arthropods, in turn, are eaten by a host of predators, the vast majority of which are other arthropods (Crawford 1981). Many predaceous arthropods are dense and may play important community roles (Polis and Yamashita 1991); in the CV these include species of scorpions, solpugids, spiders, mantids, ant lions, robberflies, small carabid beetles, and facultatively predaceous ants.

A great variety of arthropods are predaceous sometime during their lives. In the CV, mites (8 families), arachnids (more than 23), and insects (more than 21) are predators as juveniles and adults. The complex life cycle of holometabolic insects often results in different feeding habits between stages. At least 27 families of Diptera (e.g., Tachinidae), Hymenoptera (e.g., Tiphiidae), and Coleoptera (e.g., Cleridae, Meloidae) are trophic generalists: they are predaceous as larvae and herbivorous as adults. For example, *Pherocera* (Therevidae) fly larvae are predators on beetle, fly, and moth larvae (and are cannibals) in sandy CV soils; adults drink nectar. Some parasitic Hymenoptera (e.g., sphecids, pompilids) function as predators: adults eat pollen and nectar but capture prey to feed larvae. Finally, some taxa (e.g., ants, camel crickets) are occasionally but regularly predaceous. For example, after heavy rains in the CV, the diet of *M. pergandei* included 80% *Amitermes wheeleri* termites; normally, arthropods form 2%–10% of this ant's diet (Gordon 1978).

TABLE 1

DIET CLASSIFICATION OF SOME REPRESENTATIVE PREDATORS ON ARTHROPODS

| TAXON | PERCENTAGE OF ARTHROPOD TAXA IN DIET | | |
| --- | --- | --- | --- |
| | Predaceous and Parasitoid | Herbivorous and Detritivorous | $n$ |
| Arachnids:* | | | |
| Hadrurus arizonensis | 53 | 47 | 15 |
| Paruroctonus luteolus | 60 | 40 | 10 |
| Paruroctonus mesaensis | 47 | 53 | 126 |
| Vaejovis confusus | 50 | 50 | 12 |
| Diguetia mohavea | 45 | 55 | 71 |
| Latrodectus hesperus | 54 | 46 | 35 |
| Arachnid average ± SD | 51.5 ± 5.4 | 48.5 ± 5.4 | 47.3 |
| Lizards: | | | |
| Callisaurus draconoides | 45 | 55 | 22 |
| Cnemidophorus tigris | 46 | 54 | 15 |
| Gambelia wislizenii | 33 | 67 | 15 |
| Phrynosoma platyrhinos | 28 | 72 | 18 |
| Uta stansburiana | 39 | 61 | 28 |
| Birds: | | | |
| Blue-gray gnatcatcher | 36 | 64 | 69 |
| Burrowing owl | 36 | 64 | 14 |
| Loggerhead shrike | 35 | 65 | 17 |
| Roadrunner | 35 | 65 | 23 |
| Mammals: | | | |
| Ammospermophilus leucurus | 71 | 29 | 7 |
| Antrozus pallidus | 31 | 69 | 16 |
| Onychomys torridus | 40 | 60 | 15 |
| Pipistrellus hesperis | 32 | 68 | 22 |
| Vulpes macrotus | 67 | 33 | 6 |
| Vertebrate average ± SD | 41 ± 12.9 | 59 ± 12.9 | 20.5 |

NOTE.—A taxon is the designated unit in which the diet was classified by the author. It varies from species to families and orders.

* The first four arachnids are scorpions; the last two are spiders.

Most are resource generalists (Polis and Yamashita 1991); for example, *P. mesaensis* is recorded to eat more than 125 prey species, *Digueta mohavea* more than 70 species, and *Latrodectus hesperus,* 35 species. In fact, some scorpions and spiders are neither true trophic specialists nor obligate predators: both scavenge dead arthropods and some spiderlings are aerial plankton feeders, eating pollen and fungal spores trapped by their web (Polis and Yamashita 1991). Facultative predators are trophic generalists eating plants, detritus, dead arthropods, and live prey. A few specialize. Adult velvet mites, *D. pandorae,* feed almost exclusively on termites (Tevis and Newell 1962). *Mimetus* spiders prey primarily on other spiders.

Trophic interactions are complex. Generalized diets are established by size relationships: predators catch what they can subdue. Consequently, smaller and/ or younger arthropods are potential prey and predators eat from all trophic levels. For example, the diet of six CV arthropods averages 51.5% other predaceous arthropods (table 1). Predator-predator feedings are particularly common in deserts because predators form a high proportion of all arthropods (Crawford 1991; Polis and Yamashita 1991). Clearly, a web representing all CV predaceous arthro-

pods would be difficult to depict. Thus, I present subwebs (figs. 4 and 6) centered on three common species that I have studied extensively: the scorpion *P. mesaensis* (see earlier references) and the spiders *D. mohavea* and *L. hesperus* (Nuessly and Goeden 1984; Polis and McCormick 1986a, 1986b; G. A. Polis and K. H. Sculteure, unpublished manuscript).

Spiderling *D. mohavea* develop in sacs protected by the mother until her death. Eggs and spiderlings are then eaten by invaders (spiders [9 families, more than 14 species], solpugids, mites, mantispids, chrysopids, and the clerid beetle *Phyllobaenus* from fig. 3). These stages of most spiders are attacked by similar invaders (Polis and Yamashita 1991). Sibling cannibalism is also frequent (Polis 1981) and occurs among *D. mohavea* (and *L. hesperus*) spiderlings. At least three trophic levels occur in the *D. mohavea* retreat: the clerid likely eats other egg predators and is itself host to a pteromalid wasp parasitoid. Adult *Diguetia* eat more than 70 species, including 14 families of predatory insects (e.g., *Photopsis* and *Phyllobaenus*), and eight spider species, including the same species of invading *Habronatus* salticids and the araneophagous *Mimetus*. One-third of all *D. mohavea* webs include salticid prey. Adult *D. mohavea* are fed upon by *Mimetus*, *P. mesaensis*, birds, and a parasitoid pompilid. *Diguetia* is involved in at least four cases of mutual predation.

Predators form 54% of *L. hesperus*'s diet (table 1). *Latrodectus hesperus* is prey of at least eight predators including other *L. hesperus* and three predators that it eats (mutual predators = *Steatoda grossa*, *Steatoda fulva*, *P. mesaensis*). The sphecid (*Chalybian californicum*) specializes on *Latrodectus* and other theridiid spiders (e.g., *Steatoda*) (Wasbauer and Kimsey 1985). *Tastiotenia festiva* (Pompilidae) is a hyperparasitoid eating both cached theridiid spiders and developing wasps.

The biomass (g/ha) of *P. mesaensis* is the greatest of any CV predator (including vertebrates). Diet shifts during growth partially explain trophic interactions with more than 125 prey species, including 47% other predators (table 1), and mutual predation with at least 10 species (three scorpions, five solpugids, two spiders—young *P. mesaensis* are eaten by the same species eaten by adults).

Note the complexity of these webs: looping via mutual predation and cannibalism is frequent; (closed-loop) omnivory is the norm; omnivorous predators feed on herbivores, detritivores, predators, and predators of predators. Consequently, chain lengths are long even excluding parasitoids and loops (e.g., detritus–termite–*Messor* ants–ant lion–*Latrodectus*–*Steatoda*–*Mimetus*–*P. mesaensis*–Eremobatid solpugids–*Hadrurus* scorpion–[vertebrate subweb]). I strongly suspect that the depicted interactions are representative of the hundreds of other arthropod predators in the CV. Omnivory (due to age structure, opportunism, and generally catholic diets) combined with a high diversity of insect and arachnid predators necessarily creates trophic complexity. Complexity increases even further when we consider vertebrate predators of these arthropods.

### Arthropodivorous Vertebrates

Arthropodivory is the consumption of arthropods. A less familiar word than insectivory, it conveys that predators eat all types of arthropods (insects, arach-

TABLE 2

FEEDING CATEGORIES OF THE VERTEBRATES RESIDENT IN THE COACHELLA VALLEY

| | VERTEBRATE CLASS | | | |
| --- | --- | --- | --- | --- |
| FEEDING CATEGORY | Reptiles ($n$ = 21) | Birds ($n$ = 56) | Mammals ($n$ = 18) | All Vertebrates ($n$ = 95) |
| Granivory: | | | | |
| Primary | 0 (0) | 14 (25) | 8 (44) | 22 (23) |
| Secondary | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Total | 0 (0) | 14 (25) | 8 (44) | 22 (23) |
| Herbivory: | | | | |
| Primary | 2 (10) | 5 (9) | 5 (28) | 11 (12) |
| Secondary | 5 (24) | 15 (27) | 1 (6) | 21 (22) |
| Total | 7 (33) | 20 (34) | 6 (33) | 32 (34) |
| Arthropodivory: | | | | |
| Primary | 11 (52) | 34 (61) | 9 (50) | 55 (58) |
| Secondary | 4 (19) | 15 (27) | 5 (28) | 24 (25) |
| Total | 15 (71) | 49 (88) | 14 (78) | 79 (83) |
| Carnivory: | | | | |
| Primary | 9 (43) | 12 (21) | 3 (17) | 24 (25) |
| Secondary | 2 (10) | 2 (4) | 1 (6) | 5 (5) |
| Total | 11 (52) | 14 (25) | 4 (22) | 29 (31) |

NOTE.—Species are classified as belonging primarily (food is a major component of the diet) or secondarily (food < 10% of total diet) to a feeding category. Some omnivorous species (2 reptiles, 9 birds, 7 mammals) belong to two (each > 33% of diet) or three (each >20% of diet) primary categories. The numbers in each column indicate the number and percentage (in parentheses) of species in the primary (e.g., 11 herbivorous species) or secondary (e.g., 21) feeding category and the total in this category (e.g., 32).

nids, myriapods, and terrestrial Crustacea). Most vertebrates (83% of 95 species) in the CV eat arthropods (table 2). Over half (58%) primarily eat arthropods, including 52% of the reptiles, 61% of the birds, and 50% of the mammals. Most (80%) of the 25 primary carnivores also feed on arthropods. Two-thirds (24 of 36) of the primarily herbivorous/granivorous vertebrates eat arthropods, at times in large quantities (e.g., 88%–97% of the seasonal diet of the sage sparrow in the Great Basin Desert). In total, 71% of all reptile species, 88% of birds, and 78% of mammals primarily or secondarily eat insects or arachnids (only 17 species are not reported to eat arthropods).

These vertebrates are resource generalists eating all trophic categories of arthropods (herbivores, detritivores, predators, parasitoids). For example, of 36 arthropodivorous birds whose diet is detailed sufficiently, 58% eat spiders in addition to insects. Seven of 10 lizards eat spiders and four eat scorpions. Spiders are eaten by three of 14 arthropod-eating mammals; scorpions, by five. Predaceous arthropods average 41% of the diet of the vertebrates in table 1. Further, these vertebrates tend to be trophic generalists. Most (28 of 55 species = 51%) primary arthropodivores eat plants (59% of 79 vertebrates that eat arthropods also eat plants). Of these 79, 32% are also carnivorous. A few arthropodivorous vertebrates tend to specialize. Ants form 89% by frequency of the prey of the horned lizard *Phrynosoma platyrhinos*. However, these lizards eat 17 other categories of prey (including spiders and solpugids) and 20%–50% of the diet of some
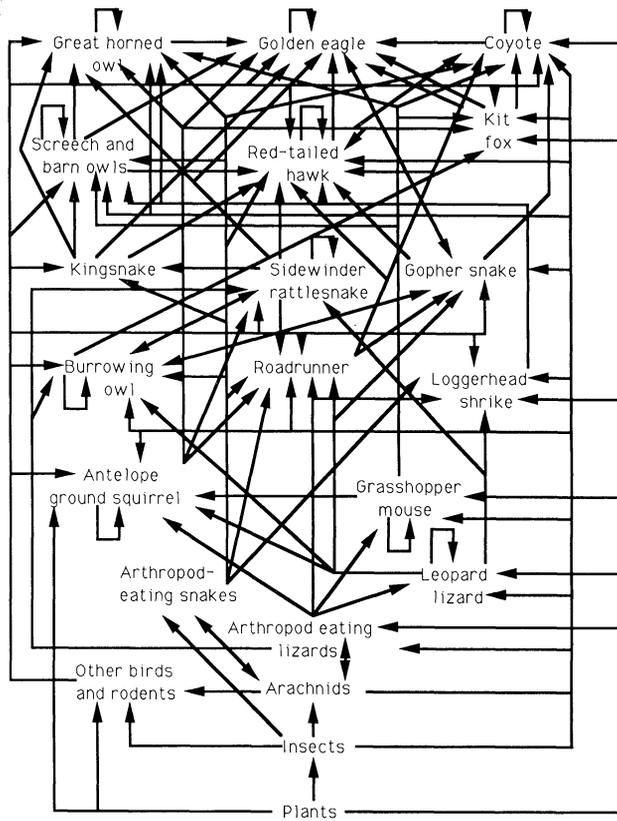
FIG. 7.—Trophic interactions involving a few of 96 vertebrates resident in the Coachella Valley. Note that the bottom of this subweb is simplified from the proceding five subwebs (figs. 2–6).

individuals is beetles. The worm snake (*Leptotyphlops humilis*) mainly eats termites and ants. No other CV vertebrates specialize on certain arthropods.

The omnivory exhibited by arthropodivorous vertebrates is illustrated in the web focused on predators of *P. mesaensis* (fig. 6). All 16 reptiles, birds, and mammals recorded to eat *P. mesaensis* eat (predaceous, detritivorous, herbivorous) insects; 44% eat plant material. Many (81%) are also carnivores (see fig. 7; three of 11 arthropods eating *P. mesaensis* also eat vertebrates).

### Carnivorous Vertebrates

Carnivores kill and eat vertebrates. Of the 95 vertebrates, 24 are primarily carnivorous and five others eat vertebrates occasionally (table 2). Reptiles are the most carnivorous (9 primary, 2 secondary of 21 species = 52%; 8 of 10 snakes are primarily carnivores). The proportion of carnivores is about the same for birds (12, 2 of 56 species = 25%) and mammals (3, 1 of 18 species = 22%).

All carnivores are resource generalists preying on many vertebrates. Most (79% = 19 of 24 primary carnivores) are trophic generalists that eat arthropods (71%)

and/or plants (33%). For example, coyotes eat mammals (12 of 19 species in the CV: rabbits, rodents, gophers, antelope ground squirrels, and even kit foxes and other coyotes), birds (including eggs and nestlings; e.g., roadrunners, doves, quails), snakes (e.g., gopher and kingsnakes), lizards (e.g., horned lizards), and young tortoises as well as scorpions, insects, and fruit (see fig. 7; Johnson and Hansen 1979; G. A. Polis, unpublished data). Coyotes actively forage on nonvertebrate prey; for example, they excavate entire ant nests in the CV (Ryti and Case 1986). Great horned owls consistently eat arthropods (14.7% of diet; e.g., spiders, centipedes, Orthoptera) in addition to rodents, squirrels, lizards, snakes, and other horned owls (Ohlendorf 1971; Johnegard 1988). Many carnivores (33%) feed on carrion in addition to live prey: sidewinder rattlesnake, raven, golden eagle, horned owl, red-tailed hawk, coyote, kit fox, and antelope ground squirrel. Such scavenging means that these primary carnivores also include in their diets both microorganisms (Janzen 1977) and the rich arthropod fauna that use decaying carcasses (e.g., the horned owl).

Figure 7 is a subweb focusing on some carnivores in the CV. Note the frequency of omnivory, closed-loop omnivory, cannibalism (10 of 16 species in fig. 7), and mutual predation. In each of the three cases of mutual predation A adults eat B, but the eggs or nestling-stage individuals of A are eaten by B. For example, many snakes are nest predators (e.g., in the CV, whip snake, sidewinder, rosy boa, gopher snake). These snakes eat eggs and nestlings of species (e.g., burrowing owls) whose adults are predators upon the same snakes (e.g., gopher snakes, sidewinders). Finally, note that only the golden eagle approaches the status of top predator (i.e., a species without predators). However, even the golden eagle may not be a true top predator: at other locations, gopher snakes eat golden eagle eggs, and parasitic thrichomoniasis and sibling fratricide/cannibalism cause nestling mortality (30% and 8%, respectively; Olendoroff 1976; Palmer 1988). Thus, here is a community and food web with potentially no top predators.

DISCUSSION

Sandy areas in the Coachella Valley are the habitat for about 175 species of vascular plants, 100 vertebrates, and thousands of arthropods, parasites, and soil organisms. These species form a community connected trophically into a single food web. Although only a few components of the CV web were presented, it is possible to summarize several general trends.

1. Each subweb is complex because of the large number of interactive species, age structure, and high omnivory. A web representing all species would increase complexity even more.

2. Age structure is central to complexity. Growth necessitates and/or allows changes in diet (life-history omnivory), either gradually or radically (e.g., predaceous larvae, herbivorous adults). Predators also change with size.

3. Different microhabitats and times are connected trophically. At first inspection, distinct compartments appear (e.g., diurnal vs. nocturnal, surface vs. subsurface). However, extensive crossover exists. Foraging times change from day to night as a function of temperature; nocturnal species eat diurnal prey (e.g.,

scorpions on robberflies). Plants and detritus are eaten during all periods by species that live above and below the surface. Arthropods feeding below ground export energy when they become surface-dwelling adults (e.g., tenebrionids). "Different-channel omnivores" link compartments by feeding from different sub-webs or "energy channels" (Moore et al. 1988). Consumers eat food types rather than specialize on trophic levels (Polis et al. 1989). Such connections decompartmentalize webs and increase complexity.

The CV is not unique in its diversity or properties of its food web. Other deserts are also characterized by thousands of species (Polis 1991b). The same suite of plants, herbivores, detritivores, arthropodivores, parasitoids, parasites, and carnivores is present in all deserts. In particular, the universal existence of diverse assemblages of predaceous arthropods (Polis and Yamashita 1991) and soil organisms (Freckman and Zak 1991) must contribute to a trophic complexity similar to that of the CV. Further, omnivory is normal among desert consumers (Noy-Meir 1974; Orians et al. 1977; Seely and Louw 1980; Brown 1986).

R. Bradley (1983) also illustrates the complexity in deserts with a source web focused on predators of camel crickets in sandy areas of the Chihuahuan desert. These predators (scorpions, solpugids, burrowing owls, grasshopper mice, and pallid bats) are quite omnivorous (only 2 of 27 species pairs are noninteractive, i.e., not linked as predator or prey). Closed-loop omnivory occurs for every predator. Looping is common: six cases of mutual predation occur; six of eight species are cannibalistic. Finally, at least 18 three-species loops exist.

### Comparison with Published "Empirical Generalizations"

Theorists have produced a series of generalizations derived from catalogs of published webs (see App. A). These generalizations are entering accepted ecological literature (see May 1986, 1988; Lawton and Warren 1988; Lawton 1989; Schoener 1989). The food web of the CV offers little support for these patterns.

Web patterns from the CV are now compared with those from published catalogs of webs. An argument could be made that CV web statistics should not be calculated. Even with its complexity, this web is vastly incomplete and literally scores of other subwebs could be presented. Statistics would represent only the level of complexity I arbitrarily present rather than true web parameters. However, to facilitate comparisons, I present a highly simplified web/matrix of the CV community (App. B). The thousands of species are heavily lumped into 30 "kinds of organisms" forming 22,220 chains. Table 3 compares 19 web statistics from the CV with those from published catalogs of webs (Pimm 1982; Briand 1983; Cohen et al. 1986; Schoener 1989; Schoenly et al. 1991). In the discussion below, I use the statistics from the simplified web and those from the more complete web depiction presented throughout the text.

1. The number of interactive species in the CV web is two orders of magnitude greater than the average number (17.8, Briand 1983; 16.7, Cohen et al. 1986; 24.3, Schoenly et al. 1991) from webs analyzed by theorists. In fact, Briand and Cohen's most species-rich web contains only 48 species, less diverse than any of the following CV taxa: plants, nematodes, mites, arachnids, bees, beetles, bombyliid flies, and birds.

TABLE 3

Comparison of Statistics from the Coachella Valley Food Web
with Means of the Statistics from Cataloged Webs

|  | Cohen et al. and Briand | Schoenly et al. | Coachella* |
|---|---|---|---|
| Total number of "kinds" or species (S) | 16.7 | 24.3 | 30 |
| Total number of links per web (L) | 31 | 43.1 | 289 |
| Number of links per species (L/S) | 1.99 | 2.2 | 9.6 |
| Number of prey per predator | 2.5 | 2.35 | 10.7 |
| Number of predators per prey | 3.2 | 2.88 | 9.6 |
| Total prey taxa/total predator taxa | .88 | .64 | 1.11 |
| Minimum chain length | 2.22 | 1 | 3 |
| Maximum chain length | 5.19 | 7 | 12†(18) |
| Mean chain length | 2.71, 2.86 | 2.89 | 7.34† |
| Connectance (C = L/S[S − 1]/2) |  | .25 | .49† |
| Species × connectance (SC) | 2–6 | 4.3 | 14.7† |
| Basal species (%) | 19 | 16 | 10 |
| Intermediate species (%) | 52.5 | 38 | 90 |
| Top predators (%) | 28.5 | 46.5 | 0 |
| Primarily or secondarily herbivorous (%) |  | 14.6 | 60 |
| Primarily or secondarily saprovorous (%) | 21 | 35.5 | 37 |
| Omnivorous (%) | 27 | 22 | 78 |
| Consumers with "self-loop" (%) | <1.0 | <1.0 | 74 |
| Consumers with mutual predation loop (%) | ≪1.0 | ≪1.0 | 53 |

Sources.—Briand 1983; Cohen et al. 1986. See also Schoener 1989; Schoenly et al. 1991.

* The Coachella statistics are derived from the extremely simplified and highly lumped food-web matrix presented in App. B.

† Mutual links (loops) were not used to calculate the statistic.

2. Coachella Valley chain lengths average more links than 2.86 (Briand 1983), 2.71 (Cohen et al. 1986), or 2.89 (Schoenly et al. 1991). Even excluding looping and parasites, lengths of 6 to more than 11 are common. Both J. E. Cohen (personal communication) and I interpret short chain length as an artifact of totally inadequate descriptions of real communities. Short average lengths are derived from catalogs biased toward less complex, vertebrate-centered webs. Chains are lengthened in the CV primarily during trophic interactions among the soil biota, the arthropods, and intermediate level predators. Webs including invertebrates are typically more complex than those centering on vertebrates (see 10 below). Shorter chains exist (e.g., plant–rabbit–eagle), but these are much less frequent simply because vertebrates form a relatively small proportion of all species when arthropods and soil biota are not ignored. For example, chains containing plants, insect herbivores, and insect parasitoids are estimated to contain over half of all known metazoans (Hawkins and Lawton 1987). The average length of all chains in the simplified CV web is 7.3; its maximum chain length is 18 (12 with no loops).

3. Omnivory is frequent in the CV web but statistically "rare" in cataloged webs (Pimm 1982; Yodzis 1984). In cataloged webs, 22% (Schoenly's catalog) to 27% (Briand and Cohen's catalog) of all "kinds" are omnivorous; 78% in the simplified CV web are omnivorous. Adequate diet data, not lumping arthropods, and the inclusion of age structure partially explain the ubiquity of omnivory in the CV. It is possible that long chains in the CV exist because energy to top

consumers comes from many (lower) trophic levels in addition to adjacent upper levels (see also Sprules and Bowerman 1988).

4. Loops are "unreasonable" to modelers and purported to be "very rare in terrestrial" webs (Pimm 1982; Pimm and Rice 1987; Cohen et al. 1990). Looping also violates the assumption that body-size relations arrange species along a cascade or hierarchy, such that a species preys on only those species below it and is preyed on only by those above it ("upper triangular web structure"; Warren and Lawton 1987; Lawton 1989; Cohen et al. 1990). However, looping is neither rare nor abnormal in the CV. Most frequently, loops are a product of age structure: cannibalism and mutual predation usually result when large individuals eat smaller or younger individuals. Other factors also produce mutual predation (e.g., group predation by ants). In the simplified community matrix, 74% of the consumers show self-loops; 44% are involved in loops with another "kind."

5. Coachella Valley species interact with many more species than those in cataloged webs. Cohen (1978) and Schoenly et al. (1991) calculated the number of predators on each prey (mean = 3.2 and 2.88, respectively) and the number of prey per predator (2.5 and 2.35). Overall, cataloged species interact directly with 3.2–4.6 other species (Cohen et al. 1985). Parameters from the CV are one to two orders of magnitude greater. Higher values exist first because most CV consumers eat many species (e.g., see table 1; diets range from 15 to more than 125 items; a few arthropod herbivores and some parasites are exceptions). Second, most individual species are eaten by tens to hundreds (e.g., mesquite) of species. Such discrepancies occur because cataloged webs lump several species into "kinds" and diet data are grossly inadequate. However, even the highly lumped CV web shows that each "kind" is eaten by about 10 predators and each consumer eats about 10 prey (table 3).

6. Top predators are rare or nonexistent in the CV. Coyotes, kit foxes, horned owls, and golden eagles (the largest predators in the CV) suffer the fewest predators, but each is the reported prey of other species. This finding stands in marked contrast with cataloged webs: 28.5% (Briand and Cohen 1984; Cohen et al. 1990) to 46.5% (Schoenly et al. 1991) of kinds were top predators. This great discrepancy is undoubtedly due to the inadequacy of diet information in cataloged webs and/or to the fact that these webs only focus on a limited subset of a trophically linked community.

7. Coachella Valley data pose great difficulty to the observation that prey/predator ratios are greater than 1.0 (0.88, Briand and Cohen 1984; 0.64, Schoenly et al. 1991); that is, the number of organisms heading rows (prey) in web matrices is less than the number heading columns (predators). It is easy to show that the ratio in the CV and other real communities should be greater than 1.0. Because all heterotrophs must obtain food, every animal should head a column. Rows (prey) include plants, detritus, and all animals except those with no predators (i.e., top predators). Let $x$ be the number of animal species that are intermediate predators (i.e., both predator and prey). Then the total number of prey is $x$ + the number of plant species (174 in the CV) + the number of categories of detritus and carrion; the number of predators is $x$ + the number of top predators (0 or 1 in the CV). If more species of plants exist than top predators, then the prey/

predator ratio will always be greater than 1.0. Few real (no?) communities have more top predators than autotrophs. The appearance that top predators are more frequent is an artifact (see 6 above). It appears that lumping obliterates the actual ratio primarily because more species of plants are lumped than (easily recognized) animals that are top predators. The CV community web exhibits a prey/predator ratio of 1.11. Glasser (1983), Paine (1988), and Lockwood et al. (1990) also criticize prey/predator ratios.

8. Factors 1–7 make the CV web much more complex than cataloged webs. For example, the number of trophic links varies from 31 (Cohen et al. 1986) to 43 (Schoenly et al. 1991); only 2 of Cohen et al.'s (1986) 113 webs had more than 100 links. The average CV *subweb* (figs. 2–7) has 54.7 links; the carnivore subweb alone, 107; and the simplified community web, 289.

9. The CV web questions the utility of the concept of "trophic level." A trophic level is defined as a set of organisms with a common number of chain links between them and primary producers. The nearly universal presence of omnivory and age structure makes this concept nonoperational. What trophic level are consumers that ontogenetically, seasonally, or opportunistically eat all trophic levels of arthropods in addition to plant material and (for carnivores) vertebrates? Looping further blurs the concept. If A eats B but B eats A, is B on the first, third, or (after another loop) fifth trophic level (ad infinitum)? I am not alone in criticism of this concept (see Gallopin 1972; Cousins 1980, 1987; Levine 1980; Lawton 1989).

10. Patterns 4 and 5 in Appendix A are confirmed by the CV web. First, separate compartments did not exist within one habitat. Second, arthropod-dominated systems are more complex than those dominated by vertebrates. However, few communities are not dominated (in number of individuals or species) by arthropods (Hawkins and Lawton 1987; May 1988). So not lumping arthropods, the most species-rich taxon on this planet, should increase the complexity of any web, including those cataloged by theorists.

Overall, a general lack of agreement exists between patterns from the CV and those from catalogs of published webs. Is the CV web unique or are cataloged webs so simplified that they have lost realism? That cataloged webs depict so few species, such low ratios of predators on prey and prey eaten by predators, so few links, so little omnivory, a veritable absence of looping, and such a high proportion of top predators argues strongly that they do not adequately describe real biological communities. Taylor (1984), Paine (1988), Lawton (1989), and Winemiller (1990) reach a similar conclusion.

This conclusion carries important implications. First, controversies over such issues as the causes of short chain length and omnivory, complexity versus stability of ecosystems, and the role of dynamics versus energetics in shaping web patterns (see DeAngelis et al. 1983; Yodzis 1984; Lawton 1989) are based on patterns abstracted from cataloged webs. If catalogs are an inadequate data base, these controversies may be nonissues and theorists are trying to explain phenomena that do not exist. This is a real possibility (see Lawton and Warren 1988; Paine 1988; Lawton 1989; Winemiller 1990). Second, characteristics of the CV web (complexity, omnivory, long chain lengths, looping, absence of compart-

ments) considerably reduce stability in dynamic models of food webs (see Pimm 1982; Pimm and Rice 1987). These simplified models apparently tell us little about the structure of food webs in nature.

### Self-Critique and Prospectus

Several issues need to be addressed.

1. Should all trophic links be included, or are some too weak or unusual to list (May 1983a, 1986; Paine 1988; Lawton 1989; Schoener 1989)? I included all links in the CV web. This decision was based on four factors. First, it is arbitrary and impossible to evaluate which links are and which are not important. Most CV consumers eat 20 to more than 50 items. Which should be included, which excluded? Some consumers (esp. in deserts) likely exist because they are sufficiently flexible to include a number of infrequent links that sum into an important source of energy, at least during some periods. For example, the seasonal switch by granivorous birds to arthropods provides protein and water for nestlings and may allow permanent residence for some desert birds (Welty 1962; Brown 1986).

Second, dynamics and trophic linkage are not necessarily correlated (Paine 1988; Lawton 1989). A 1% frequency of a rare species in the diet of a common species may produce high mortality; conversely, a rare species eating only one common species may scarcely affect dynamics. Further, short but intensive predation events may contribute little to the diet of a predator but may be central to prey dynamics (e.g., Wilbur et al. 1983; Polis and McCormick 1987).

Third, each link enriches the description of the community (the original purpose of food webs). We must not blur the distinction between food webs and interaction/functional webs. Food webs (such as the CV web) are based on observations of trophic relationships while interaction webs summarize the subset of all interactions that are "strong." This insight argues that all trophic links should be included because this is a food web, not an interaction web. No justification exists for excluding links from a food web. Fourth, the exclusion of certain links produces systematic bias against complexity.

2. Are desert food webs (a)typical of other webs? Deserts may differ in two main ways from other systems. First, deserts are relatively simple ecosystems characterized by low productivity and low species richness (Noy-Meir 1974; Seely and Louw 1980; Louw and Seely 1982; Whitford 1986; Polis 1991b). Should such depauperate communities translate into relatively simple webs? If so, the complexity of the CV web is much less than that of more species-rich systems.

Second, is omnivory more common in deserts than in other habitats? It is impossible to answer this question with rigor. I can only indicate that features that promote omnivory (and web complexity) in the CV are present in all systems: age structure, life-history omnivory, predators that ignore the feeding history of prey (different-channel omnivory), opportunistic feeding, and consumers that eat food in which other consumers live (e.g., scavengers, frugivores, granivores, detritivores; Polis et al. 1989). High omnivory is not restricted to deserts. Price (1975) and Cousins (1987) argue that it is normal throughout the animal kingdom. Omnivory characterizes feeding in aquatic and marine habitats (Menge and Sutherland 1987). These authors and Walter (1987) maintain that omnivory is also

common in terrestrial communities. Walter and Moore et al. (1988) provide strong evidence that omnivory is one of the most frequent and dynamically important trophic links among soil and detrital webs. Sprules and Bowerman (1988) analyzed zooplankton in 515 lakes and concluded that omnivory is common. (They also note long chains, looping, cannibalism, and mutual predation.)

Regardless of whether deserts are unique, desert food webs are still of general importance. Deserts occupy at least one-quarter of the earth's land surface (Crawford 1981; Polis 1991*b*), and patterns observed in the CV thus should describe a good fraction of the terrestrial communities on this planet.

3. Not all diet data for Coachella Valley species came from the Coachella. How this affects the web is uncertain. However, the overall conclusion of great complexity should not be influenced unduly by errors arising from use of these studies.

4. The sections of this article that critique "food-web theory" tend to be nihilistic. A more satisfying article would further suggest how we can replace or revise these theories. Because of space limitations, I cannot focus on future directions other than to offer the general caveat that we cannot overlook complexity and reality in our attempts to comprehend nature. However, this article suggests that a host of important issues need to be resolved. Foremost, we need criteria to recognize which links are "sufficiently important" to include in descriptions and analyses of communities. We must establish more uniformly the spatial limits and species membership of a community and not analyze webs as different as those found in catalogs (Arctic seas to toad carrion; Briand 1983; Sugihara et al. 1989). We need to assess what easily studied subwebs (e.g., phytotelmata, plant galls, carrion) tell us about the structure of community webs and how isolated or connected these subwebs are with respect to the rest of the community. We must determine how omnivory affects the recognition of important links and how the ubiquity of omnivory affects web structure. Finally, we must incorporate age structure, changes over time and space, and recycling via the detrital loop into web analyses.

## CONCLUSIONS

It appears that much "food-web theory" is not very descriptive or predictive of nature. The catalogs of webs used to abstract empirical generalizations were derived from grossly incomplete representations of communities in terms of both diversity and trophic connections. Consequently, theorists have constructed an oversimplified and invalid view of community structure. The inherent complexity of natural communities makes web construction by empiricists and analysis by theorists difficult.

So what good are food-web representations and analyses? At a minimum, they are descriptors of communities and trophic interactions. As a future goal, they may tell us how communities function and are assembled. In an ideal world, hypotheses and generalizations made by theorists could be viewed as a stage in the evolution of understanding food webs; they are definitely not finished products (J. E. Cohen, and S. L. Pimm, personal communication). Theory is designed

to provoke concept-focused fieldwork that hopefully promotes the next iteration of descriptive models and generalizations that will, in turn, encourage more empirical work, all the while approaching more accurate predictions and descriptions of reality. However, a strong implication of my analysis is that many existing hypotheses and generalizations are simply wrong. For example, much theory (see Pimm 1982; DeAngelis et al. 1983; May 1983a; Lawton and Warren 1988) would hold that the Coachella Valley food web should be completely unstable. To advance our understanding, an adequate data base of community food webs must be assembled, experiments must be conducted, and new questions asked. This will take time. Only then will a useful, heuristic theoretical framework be constructed. Meanwhile, we should reevaluate where we now stand: it appears that much food-web theory is in critical need of revision and new direction.

## APPENDIX A

### A Partial Summary of "Features Observed in Real Food Webs"

These "empirical generalizations" were derived by food-web theorists from the catalog of published webs assembled by Cohen (1978), Briand (1983), and Schoenly et al. (1991; see text). All quoted phrases are from chapter 10 in Pimm 1982 (see esp. table 10.1). Roman numerals in parentheses refer to pattern number in Pimm's table 10.1.
1. Chain lengths are limited to "typically three or four" (2.86–3.71) trophic levels (iii)
    (Pimm 1982; Briand 1983; Cohen et al. 1986; Schoener 1989; Schoenly et al. 1991).
2. Omnivores are statistically "rare" (iv)
    (Pimm 1982; Yodzis 1984).
3. Omnivores feed on adjacent trophic levels (v)
    (Pimm 1982).
4. Insects and their parasitoids are exceptions to patterns 2 and 3 (vi)
    (Pimm 1982; Hawkins and Lawton 1987).
5. Webs are usually compartmentalized between but not within habitats (viii)
    (Pimm 1982).
6. Loops are rare or nonexistent and do not conform to "biological reality" (i)
    (Gallopin 1972; Cohen 1978; Pimm 1982; Pimm and Rice 1987; Lawton and Warren 1988; Cohen et al. 1990).
7. The ratio of prey species to predator species is greater than 1.0 (0.64–0.88) (x)
    (Cohen 1978; Briand and Cohen 1984; Schoenly et al. 1991).
8. The proportion of species of top predators to all species in a community averages 0.29–0.46
    (Briand and Cohen 1984; Schoenly et al. 1991).
9. Species interact directly (as predator or prey) with only 2–6 other species
    (Cohen 1978; Cohen et al. 1985; Schoenly et al. 1991).

# APPENDIX B

## TABLE B1

Summary Food-Web Matrix for the Coachella Valley Sand Community

| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | / | / |  | / |  | / | / |  |  |  | / | / | / | / | / | / | / | / | / | / | / |  | / | / |  | / |  |
| 2 | / | / |  | / | / | / |  |  |  |  | / |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 3 | / | / |  | / |  |  |  |  |  |  | / |  |  |  |  |  |  |  |  | / |  |  |  | / | / | / | / |
| 4 | / | / | / | / | / | / | / |  |  |  | / |  |  |  |  |  |  |  |  | / |  |  |  | / | / | / | / |
| 5 |  |  | / |  | / |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 6 |  |  | / |  | / |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 7 |  |  | / | / |  |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 8 |  |  |  |  | / |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 9 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 10 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 11 |  |  |  |  |  |  |  | / | / | / | / | / | / | / | / |  | / |  | / | / | / | / | / | / |  | / | / |
| 12 |  |  |  |  |  |  |  | / | / | / | / | / | / | / | / |  | / |  | / | / | / | / | / | / |  | / | / |
| 13 |  |  |  |  |  |  |  | / | / | / | / |  |  | / | / |  |  |  | / | / | / | / | / | / | / | / | / |
| 14 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 15 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / |  | / |  | / | / | / | / | / | / | / | / | / |
| 16 |  |  |  |  |  |  |  | / | / | / | / | / | / | / | / | / | / |  | / | / | / | / | / | / | / | / | / |
| 17 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / | / |  |  |  |  |  |  |  |  |  |  |  |
| 18 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / | / |  |  |  |  |  |  |  |  |  |  |  |
| 19 |  |  |  |  |  |  |  | / | / | / | / | / | / |  | / | / |  |  |  |  |  |  |  |  |  |  |  |
| 20 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  |  | / | / | / | / |
| 21 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  |  | / | / | / | / |
| 22 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  |  |  | / | / | / | / |
| 23 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  |  | / | / | / |  |
| 24 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  | / | / |  |  |  | / | / | / | / |
| 25 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / |  |  |  | / | / |  | / | / | / | / | / | / |
| 26 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | / | / |  | / | / | / | / | / | / |

TABLE B1 (*Continued*)

| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | | | | | | | | | | | | | | | | | | | / | / | | | | / | / | / | / |
| 28 | | | | | | | | | | | | | | | | | | | | | | | | / | / | | / |
| 29 | | | | | | | | | | | | | | | | | | | | | | | | | | / | / |
| 30 | | | | | | | | | | | | | | | | | | | | | | | | / | | | / |

NOTE.—The thousands of species were lumped extensively to 30 "kinds of organisms" in order to facilitate comparison with webs contained in the various catalogs. Entries along the diagonal indicate a "self-loop" within that kind of organism. Entries below the diagonal are loops caused by mutual predation. Some statistics from this matrix are summarized in table 3. The kinds of organisms are as follows: 1, plants/plant products; 2, detritus; 3, carrion; 4, soil microbes; 5, soil microarthropods and nematodes; 6, soil micropredators; 7, soil macroarthropods; 8, soil macroarthropod predators; 9, surface arthropod detritivores; 10, surface arthropod herbivores; 11, small arthropod predators; 12, medium arthropod predators; 13, large arthropod predators; 14, facultative arthropod predators; 15, life-history arthropod omnivore; 16, spider parasitoids; 17, primary parasitoids; 18, hyperparasitoids; 19, facultative hyperparasitoids; 20, herbivorous mammals and reptiles; 21, primarily herbivorous mammals and birds; 22, small omnivorous mammals and birds; 23, predaceous mammals and birds; 24, arthropodivorous snakes; 25, primarily arthropodivorous lizards; 26, primarily carnivorous lizards; 27, primarily carnivorous snakes; 28, large, primarily predaceous birds; 29, large, primarily predaceous mammals; and 30, golden eagle.

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