6

Species Interactions and Community Structure

Questions concerning the nature and importance of species interactions have become increasingly controversial. In the mid-1960s it was thought that interspecific competition was the major organizing factor in many communities. Through the pioneering work of the late Robert MacArthur and his students, many aspects of the structure and dynamics of bird communities seemed best explained by competitive interactions, which could be described in a general way by the Lotka-Volterra competition equations. This work, or at least its generality, has been challenged on three levels. First, there is the question of how important species interactions are in general and whether the interactions are competitive, parasitic, predatory, or mutualistic. For example, Connell (1975) noted that a significant fraction of, but by no means all, communities are physically rather than biotically controlled. In addition, there has been a tendency in the last few years to concentrate on single-species demography. While interactions between species can still be considered in the guise of age-specific fecundity and mortality effects, the emphasis is away from a coevolutionary perspective and toward a individualistic concept of communities.

Second, the question of which type of interaction is most important in structuring a particular community is very much open. Many ecologists have pointed out that the birds studied by MacArthur and his students were at or near the top of the food chain. There is no *a priori* reason to expect that competition will also be important lower in the food chain. Thus Connell argues that predation is a more widespread and important interaction. Furthermore, some of the best examples of competition, such as character displacement in the Galápagos avifauna, are probably not examples of competition at all (Strong, Szyska, and Simberloff 1979). Until very recently the debate revolved around the relative importance of competition and predation. However, Risch and Boucher (1976) and Price (1980) have forcefully argued that whole classes of interactions have been ignored. Risch and Boucher, among others, have argued that mutualistic interactions may be the key to understanding community structure, while Price argues the same for parasitism.

Third, there has been widespread disillusionment with the utility of simple mathematical models to describe species interactions. In part, this disillusionment stems from the very real difficulties in measuring interaction coefficients and from the failure of almost all suggested shortcuts to measuring interaction coefficients. But in part it comes from the failure of the models to predict observed patterns (Neill 1974).

These three questions will be considered throughout this chapter in various ways. The first section reviews what is known about the relative importance of different interactions in cave communities. The second section considers in some depth the beetle–cricket egg interaction, and the third section reviews in detail the interactions in cave stream communities in the southern Appalachians, the most thoroughly studied case. The concluding section suggests that most questions about species interactions are ill posed and argues for the central importance of models.

Which Interactions Are Important?

As Price (1980) points out, the role of parasites in the structure and dynamics of most communities has been greatly underestimated. Even the inventory of parasites of cave organisms is very incomplete (Vandel 1964), and there are almost no data on the percentage of the host population infected or the effect of the parasite on the host. Even the meager data available suggest that parasites may be important in some communities. Keith (1975) found that almost all *Pseudanophthalmus tenuis* beetles in Murray Spring Cave in Indiana were infected with the fungal parasite *Laboulbenia subterranea,* with an average of up to fifteen infestations per beetle. The effect on the beetles of these symbionts on the integument is not known, and in fact they may be commensals rather than parasites. Extremes of specialization, even for parasites, occur in caves. One of the most spectacular examples are the Temnocephala, parasitic platyhelminth worms intermediate in morphology between turbellarians and trematodes, which parasitize European cave shrimp. Matjašič (1958) reported that seven species and several genera of Temnocephala are found only on the cave shrimp *Trogocaris schmidti,* with each species specializing on a particular region of the body. For example, *Subtelsonia perianalis* is found around the anus of *T. schmidti.*

A similar level of ignorance obtains for mutualistic interactions. No free-living mutualists have been reported from caves, but ectosymbionts that are probably mutualistic or commensal are known. Hobbs (1973, 1975) studied the entocytherid ostracods that live on the exoskeletons of cave crayfish. They feed on microorganisms and on detritus that accumulates on the host exoskeleton and are unable to complete their life cycle away from their host. Crayfish probably derive some advantage from the cleaning activity of the ostracods, but the main effect of the interaction is benefit to the ostracods. Hobbs compared the ostracod symbionts of the cave-limited *Orconectes inermis* to those of the facultative cave dweller *Cambarus laevis.* Almost all the ostracods on *O. inermis* were *Sagittocythere barri,* which is rarely found on other species in Hobbs' study area. In contrast, *C. laevis* commonly harbored three species. Infestation and reinfestation occur when the hosts copulate, when ostracod eggs become attached to newly hatched crayfish carried under the abdomen and, following a molt, when the exuviae are eaten by the crayfish. Levels of infestation are lower in the cave-limited species, but this is complicated by the strong effect of crayfish size on the number of ostracod infestations (Table 6–1). Since the cave-limited species are smaller, fewer ostracods per crayfish are expected. Regression analysis indicates that a larger minimum size is required for infestation of the cave-limited species than of the facultative cave dwellers, but that the rate of infestation increases more rapidly with size in troglobitic species. This may be a consequence of the specialization of *S. barri* on *Orconectes inermis,* but the adaptive significance, if any, is not clear.

Christiansen and Bullion (1978) attempted to assess the importance of competition and predation for terrestrial cave fauna in the Haute-Garonne and Ariège regions of France. Their basic procedure was to visually census for 100 minutes the populations of about fifty terrestrial

Table 6–1 Numbers of entocytherid ostracods inhabiting various crayfish, and the relationship ($y = a + bx$) between crayfish carapace length (x) and number of ostracod infestations (y); b is the slope and a is the intercept of the regression equation. Minimum size is the smallest crayfish expected to harbor ostracods, based on the regression analysis. (Data from Hobbs 1973, 1975.)

Species	Habitat	Ecological range	$\bar{y}$ (± 95% confidence interval)	a	b	Minimum size (mm)
Orconectes inermis inermis	Cave	Cave-limited	18.8 ± 3.6	−28	1.95	15
Orconectes inermis testii	Cave	Cave-limited	20.2 ± 13.6	−45	2.80	16
Cambarus laevis	Cave	Facultative cave-dweller	26.5 ± 3.7	6.2	0.60	0
Cambarus bartonii	Surface	Occasionally in caves	119 ± 17.5	—	—	—

species and to estimate various environmental parameters, such as dry speleothems, calcareous clay, guano, and standing crop of organic debris, for fifty-eight caves. Some classification of caves was made, distinguishing underground rivers, vertical sinks, and so on, as well as the aphotic and entrance zones. Each environmental parameter was rated on a scale of 1 to 6. They then attempted to determine what affected the abundance of various species by stepwise multiple regression techniques. Their study was almost exclusively a between-cave comparison and did not detect all interactions, such as competition resulting in microhabitat separation within a cave. Christiansen and Bullion themselves pointed out some statistical weaknesses and noted that some climatic variables were not measured, but their study did provide insights into the importance of species interactions. There were examples of apparent competitive exclusion between troglobitic omnivore and troglophilic carnivore beetles but not among troglobitic carnivores or troglophilic omnivores. That is, competitive exclusion occurred but was infrequent.

Collembola species were analyzed more completely. Table 6–2 summarizes the results for three cave-limited Collembola: *Tomocerus problematicus, Pseudosinella theodoridesi,* and *P. virei.* Most of the major negative correlates are other species rather than physical factors, and most are probably competitors rather than predators. Possible competitors include other Collembola, millipeds, and bathyscine

Table 6–2 Summary of major factors affecting the abundance of *Tomocerus problematicus, Pseudosinella theodoridesi,* and *P. virei* in caves in southern France. (Data from Christiansen and Bullion 1978.)

	Correlates		
Rank	*T. problematicus*	*P. theodoridesi*	*P. virei*
Negative			
1	Other Entomobryidae[1]	Other Entomobryidae[1]	*P. superduodecima*
2	*T. minor*	Dry speleothems	Cave length
3	Millipedes	*P. impediens*	Carabid beetles
4	*P. impediens*	Bathyscine beetles	*P. impediens*
5	*P. virei*	*T. minor*	Mites
Positive			
1	Noncalcareous clay	Altitude	Guano
2	Diplurans	Organic debris	Breakdown
3	Calcareous clay	Diplurans	Organic debris
4	Altitude	Calcareous clay	Wet speleothems
5	Standing water	Opilionids	Sand and silt

1. *Pseudosinella sexoculata, P. alba, Heteromurus nitidus,* and *Lepidocyrtus* spp.

beetles. The only certain predator effect listed is that of carabid beetles on *Pseudosinella virei.* Therefore, predation appears to be much less important than competition in determining community structure. Among the positive correlates listed in Table 6–2, almost all are environmental and resource parameters, but Diplura are positively correlated with both *T. problematicus* and *C. theodoridesi.*

One correlation not included in the table is a very strong positive correlation between *T. problematicus* and *P. theodoridesi.* Christiansen and Bullion felt that this indicated joint correlation with other variables rather than a mutualistic interaction, but they did not attempt to confirm that. Instead, they deleted the abundance of one species in the stepwise regression analysis of the other species. The authors may be correct in assuming that the correlation between *T. problematicus* and *P. theodoridesi* is spurious, but they also share the bias of most ecologists, at least until very recently, that mutualisms outside the tropics are rare. It is at least possible that the two species are mutualists. In the laboratory, successful establishment of culture jars is often facilitated by the presence of a reproducing population of another species (Culver 1974), indicating that mutualistic effects do occur.

In contrast to Christiansen and Bullion's study, Kane's (1974) study of terrestrial cave communities in Mammoth Cave National Park gives some hints that predation may be much more important than competition. To attract organisms, Kane set out leaf litter in m^2 quadrats. In Little Beauty Cave, between 36 and 40 percent of the species attracted, depending on the quadrat, were predators, and between 9 and 15 percent of the individuals were predators. In the Natural Bridge area of Mammoth Cave, between 38 and 39 percent of the species and between 8 and 48 percent of the individuals were predators. The large and relatively constant ratio of predator species to prey species is, at the least, consistent with Kane's hypothesis that predation largely controls community structure.

There is also evidence for competition among predators. Van Zant, Poulson, and Kane (1978) claimed that character displacement occurred when two small beetle predators, *Pseudanophthalmus menetriesii* and *P. pubescens* occurred together. In caves where both were found, *P. pubescens* was between 4.7 and 4.8 mm long, and *P. menetriesii* was between 4.4 and 4.5 mm long. In the one cave where only *P. menetriesii* was present, it was 4.6 mm long. The authors speculate that this difference is due to differences in sizes of prey taken. Both species feed on small invertebrates such as Collembola. Barr and Crowley (1981), however, suggest that the size differences of *P. menetriesii* are clinal and unrelated to competition.

There are no similar studies of aquatic cave communities available, but a few comments can be made. In several major cave regions, such as the Appalachians, detritivores such as isopods and amphipods are at the top of the food chain. The question of whether competition or predation is more important among the macroscopic fauna is often trivial because this fauna has no predators. The absence of large predators in a particular area is most likely caused by historical factors (see chapter 7). In many caves with fish predators, macroscopic detritivores are very rare or absent because the streams are mud-bottomed, a generally unfavorable amphipod and isopod habitat. One example of an aquatic community with macroscopic predators and competitors will be considered in the section on Appalachian cave stream communities.

The Beetle–Cricket Interaction

One terrestrial predator-prey relationship that has received particular attention is the interaction between carabids and cave cricket eggs (Fig. 6–1). Over 75 percent of the diet of *N. tellkampfi* is eggs and

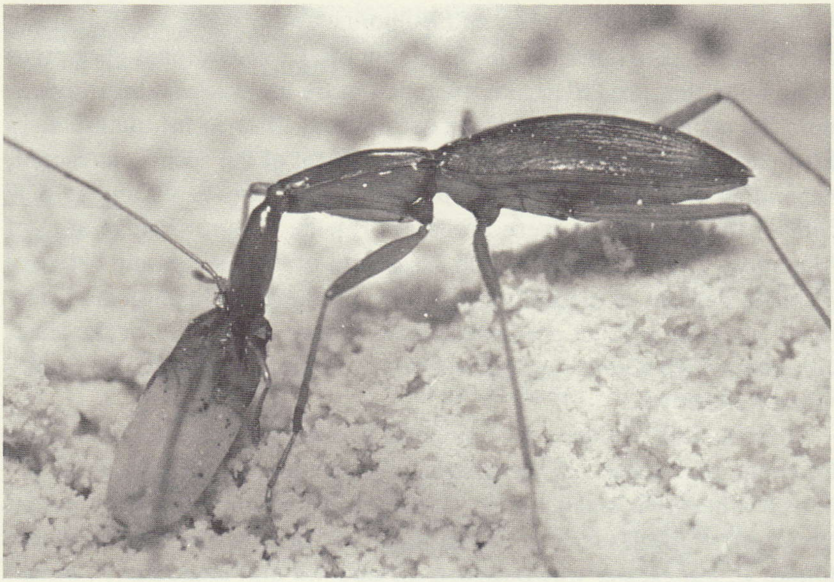

Figure 6–1 *Rhadine subterranea* eating cricket egg. (Photo courtesy of Dr. Robert W. Mitchell, Department of Biology, Texas Tech University, Lubbock, Texas.)

nymphs of *H. subterraneus* (Norton, Kane, and Poulson 1975), with eggs the preferred food (Kane and Poulson 1976). Like most other cave crickets, *Hadenoecus subterraneus* is an omnivore and obtains nearly all its food outside the cave. Although no long-term studies have been done, there can be little doubt that this predator–prey pair have a major effect on each other's population sizes. In an ingenious experiment in which *N. tellkampfi* beetles were excluded by a low barrier that did not prevent the crickets from ovipositing, Kane and Poulson (1976) found that *Hadenoecus* egg densities in beetle-free enclosures were about ten times higher than in the surrounding area. *N. tellkampfi* ate between 72 percent and 97 percent of the eggs oviposited in the surrounding area.

Hubbell and Norton (1978) found one morphological difference in preyed-upon and non-preyed-upon populations: ovipositor lengths were significantly longer in preyed-upon populations. Apparently eggs buried deeper in the sand are more difficult for beetles to locate. The crickets show a peak in egg laying in early spring that coincides with or slightly precedes the resumption of epigean feeding (Hubbell and

Norton 1978). This seasonality of egg laying produces a seasonality in the life cycle of the beetle, with a sharp increase in the emergence of teneral *Neaphaenops* about three months after the peak of cricket egg laying (Fig. 6–2).

Because these beetles are almost certainly the major cause of cricket mortality, and crickets are the major source of food for the beetles, the dynamics of the interaction are particularly interesting. It is a sad commentary on the gap between theoretical and field ecology that in spite of extensive work on this interaction, there are no data available to make any but the most general application of predator–prey models. The following paragraphs are speculations and suggestions for a closer connection between theory and field work.

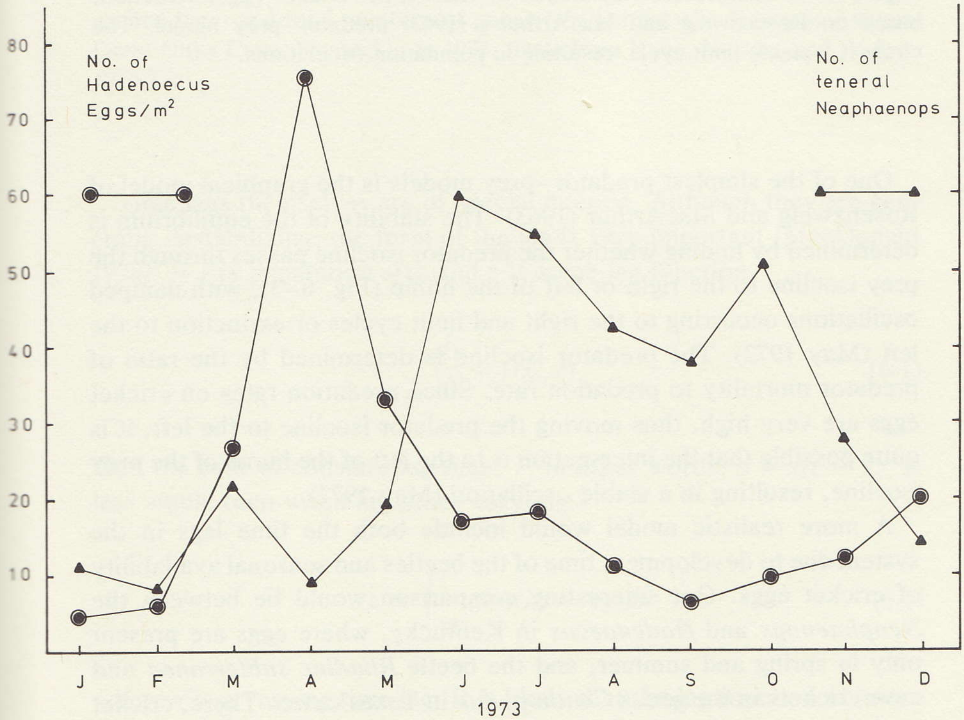

Figure 6–2 Seasonal changes in number of eggs per m² of the cave cricket *Hadenoecus subterraneus* and a visual census of newly emerging adults (tenerals) of the beetle *Neaphaenops tellkampfi* in Edwards Avenue, Great Onyx Cave, Kentucky. (Date from Kane, Norton, and Poulson 1975 and Norton, Kane, and Poulson 1975.)

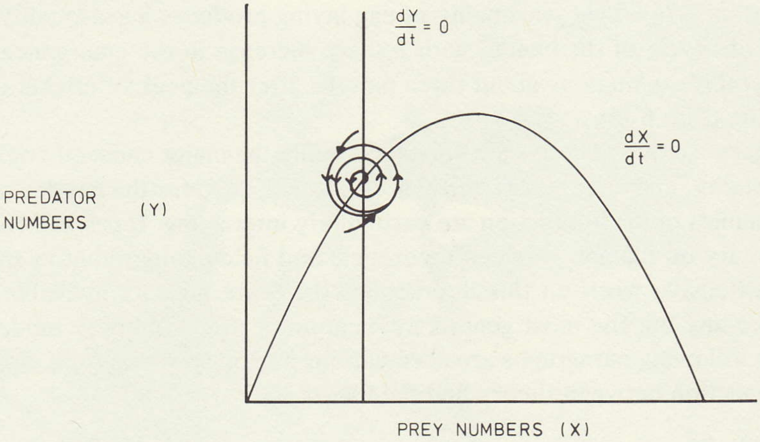

Figure 6–3 Conjectured dynamics of the beetle–cricket egg interaction, based on Rosenzweig and MacArthur's (1963) predator–prey model. The circle is a stable limit cycle, resulting in population oscillations.

One of the simplest predator–prey models is the graphical model of Rosenzweig and MacArthur (1963). The stability of the equilibrium is determined by finding whether the predator isocline passes through the prey isocline to the right or left of the hump (Fig. 6–3), with damped oscillations occurring to the right and limit cycles or extinction to the left (May 1972). The predator isocline is determined by the ratio of predator mortality to predation rate. Since predation rates on cricket eggs are very high, thus moving the predator isocline to the left, it is quite possible that the intersection is to the left of the hump of the prey isocline, resulting in a stable oscillation (May 1972).

A more realistic model would include both the time lags in the system due to development time of the beetles and seasonal availability of cricket eggs. One interesting comparison would be between the *Neaphaenops* and *Hadenoecus* in Kentucky, where eggs are present only in spring and summer, and the beetle *Rhadine subterranea* and cave crickets in the genus *Ceuthophilus* in Texas caves. There, cricket eggs are available throughout the year because both a summer egg-laying and a winter egg-laying species are present—*C. cunicularis* and *C. secretus* (Mitchell 1968). One would expect greater seasonal and long-term fluctuations in population sizes of both species in the Kentucky system.

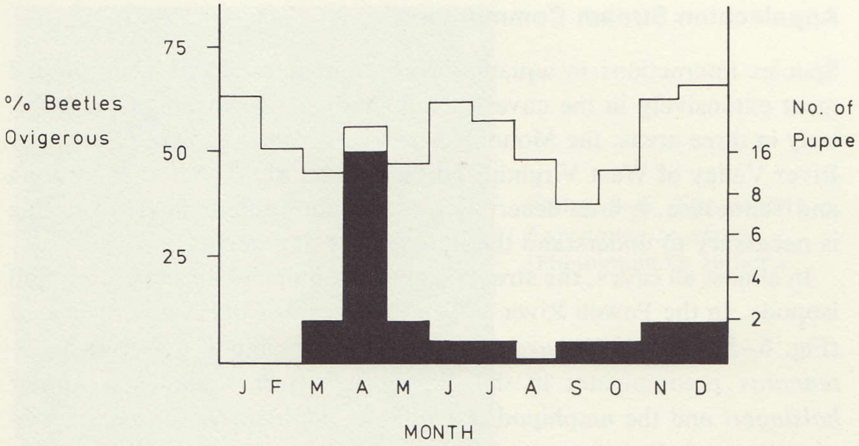

Figure 6–4 Monthly percentages of ovigerous *Neaphaenops tellkampfi* (unshaded bars) and total numbers of pupae (shaded bars) in Edwards Avenue, Great Onyx Cave, Kentucky, in 1973. (Data from Kane, Norton, and Poulson 1975.)

Time lags themselves are of special interest. Although they are generally destabilizing, the form of the lag is very important (MacDonald 1978). If x is population size and z is some lag function

$$\frac{dx}{dt} = f(x, z) \tag{6-1}$$

then the case of constant lag time, T, in other words, $z = x(t - T)$, is less stable then when lag times vary, as:

$$z = \int_{-\infty}^{t} x(\tau)G(t - \tau)\, d\tau \tag{6-2}$$

where τ is a varying time lag. It is likely that the lag function G (more properly the memory function) varies for different life history stages of *N. tellkampfi.* Most striking are the differences between monthly percentages of ovigerous beetles, which are mostly uniform throughout the year, and number of pupae, which show a sharp increase in the spring (Fig. 6–4).

Appalachian Stream Communities

Species interactions in aquatic cave communities have been studied most extensively in the caves of the southern Appalachians, particularly in three areas: the Monongahela River Valley and the Greenbrier River Valley of West Virginia and the Powell River Valley of Virginia and Tennessee. A brief description of the fauna and its physical setting is necessary to understand the interactions that occur.

In almost all caves, the stream fauna is dominated by amphipods and isopods. In the Powell River Valley the isopods *Caecidotea recurvata* (Fig. 6–5) and *Lirceus usdagalun* and the amphipod *Crangonyx antennatus* predominate; in the Greenbrier River Valley *Caecidotea holsingeri* and the amphipods *Gammarus minus, Stygobromus emarginatus,* and *Stygobromus spinatus* predominate; and in the Monongahela River Valley *Caecidotea cannula* and *C. holsingeri* predominate. There are few other macroscopic detritivores in the stream. Very occasionally, other amphipod and isopod species, for example, *Caecidotea richardsonae,* are in the Powell River Valley, but these almost always replace another species, in this case *C. recurvata.* In a few Greenbrier River Valley caves, the crayfish *Cambarus nerterius* is common, but these caves have large, mud-bottomed streams instead of the small, gravel-bottomed streams where amphipods and isopods occur. Snails in the genus *Fontigens* occur sporadically in all three drainages.

Considerable information is available about the evolutionary history of the major amphipod and isopod genera. In a recent revision of *Stygobromus,* Holsinger makes a strong case that there was a freshwater invasion from marine waters during the late Paleozoic or early Mesozoic and that the subsequent invasion of caves occurred from interstitial rather than epigean habitats. Although the evolutionary history of *Caecidotea* is less well studied, and their nomenclatural history is intricate, there are parallels with *Stygobromus* (Steeves 1969) that suggest a similar history, if not so ancient. *Crangonyx* is a more recent cave inhabitant than *Stygobromus,* although how recent is unknown (Holsinger 1969). The genus is also found in streams and springs and may have invaded caves directly from streams or via interstitial habitats. *Lirceus usdagalun* probably invaded caves from springs or streams, but its relationships to other *Lirceus* species are obscure (Holsinger and Bowman 1973). Finally, *Gammarus minus* is common in springs and spring runs as well as caves, so it is clearly a recent cave invader from surface waters.

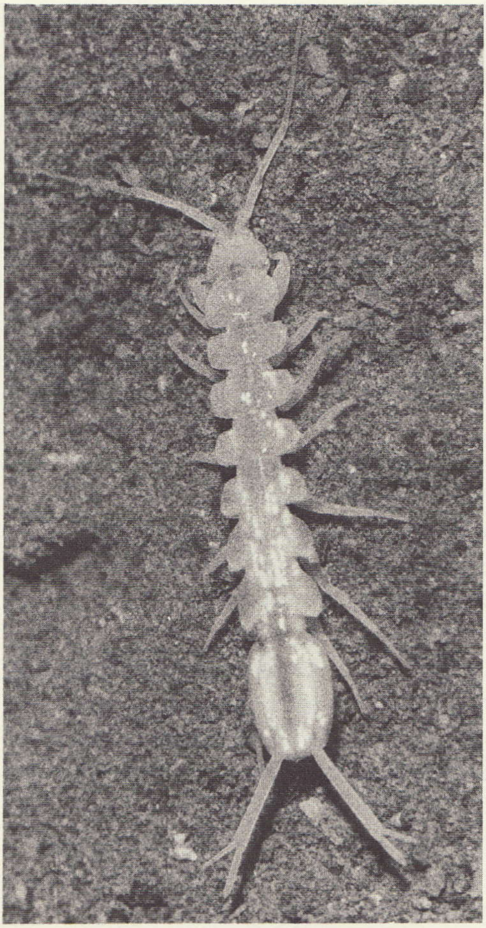

Figure 6–5 The isopod *Caecidotea recurvata*. (Photograph by author.)

Aquatic predators are generally uncommon. Planarians are locally common but probably feed mostly on injured or moribund individuals. The only predators of note are larvae of the salamander *Gyrinophilus porphyriticus,* which are especially important in many Powell River Valley caves.

In common with gravel-bottom streams on the surface, nearly all cave streams in the southern Appalachians alternate between deeps (pools) and shallows (riffles). The riffles are much shorter than the pools and repeat at a more or less regular interval of five to seven stream widths (Leopold, Wolman, and Miller 1964). The formation and maintenance of riffles is a fascinating topic in its own right, but there are two points of biological interest. First, larger rocks lie on top of smaller rocks, and second, individual rocks move from riffle to riffle, especially during spring floods, but the position of riffles stays the same.

The majority of amphipods and isopods are found in riffles rather than in pools. For example, in Benedict's Cave in Greenbrier County, West Virginia, the population density in riffles was more than five times that of pools. There are several explanations for the greater densities in riffles. First, there is more dissolved oxygen in the water; second, riffles act as detritus traps and so more food is available; and third, salamander predators, when present, are concentrated in pools, where their lateral line system functions more efficiently for detecting distant prey.

The riffles themselves present problems to isopods and amphipods. The evolutionary history of many of the species has been in slow-moving interstitial water, and they are especially vulnerable to currents. Many individuals cannot maintain their position in the current of a cave stream even if they are clinging to the top of a rock. The major exception to this vulnerability seems to be *Lirceus usdagalun,* which is the only species that is at all common on the tops of rocks, and then only in very slow-moving streams. In the absence of predators, dislodgement is the major source of mortality. Dislodged animals frequently suffer appendage damage in laboratory streams, and many amphipods and isopods collected in natural streams have appendage damage. Since the gravels themselves move, at least during floods, immediate mortality is important as well. The field evidence is consistent with this. In Benedict's Cave, for example, the low point of the *Gammarus minus* population corresponded to early spring flooding, and population size did not reach preflood levels for four months, indicating a real population drop rather than a movement into areas inaccessible to sampling (Culver 1971a).

The Basis of Competition In most of the caves, amphipods and isopods use the undersides of rocks and gravels primarily as refuges from the brunt of the current, but they are also places to feed and to hide from salamanders. Although there are almost always many more rocks than there are animals, the percentage of amphipods washed out by the current, at least in laboratory streams, is density dependent, indicating that competition is a factor (Fig. 6–6). The most parsimonious explanation of this is that washouts are primarily the result of encounters between individuals. The volume of water on the underside of

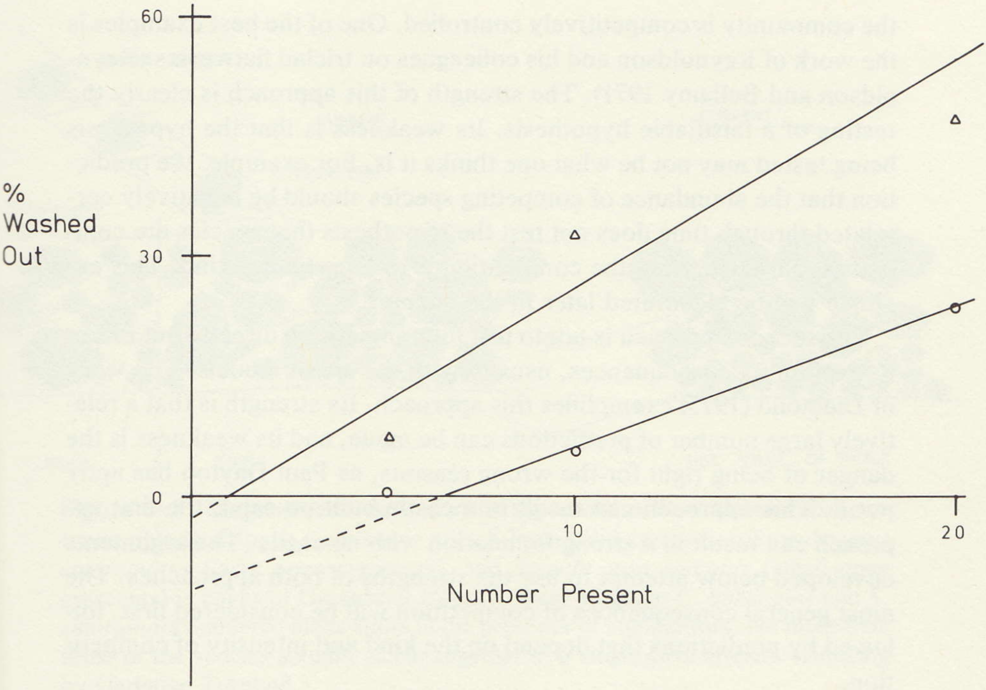

Figure 6–6 Percentage of *Gammarus minus* washed out of an artificial stream in 24 hours in relation to the number originally present. In the experiment represented by the upper curve, paper "detritus" was present, and in the experiment shown by the lower curve, leaf detritus was present. The rise in both curves indicates density dependence. (From Culver 1971a.)

a rock out of the brunt of the current is actually quite small (Ambühl 1959), and there is considerable movement or dislodgement of animals among rocks in the same riffle. The hypothesis of density dependence of the washout rate is augmented by the avoidance behavior displayed by most individuals toward others of the same and of different species (Culver 1970a). For example, in experiments in a mud-bottomed finger bowl with one rock, a single *Caecidotea holsingeri* strongly preferred the rock when alone, but was excluded from it when either *Stygobromus emarginatus* or *Gammarus minus* was present (Culver 1970a).

The studies described above have identified a mechanism of competition, but the question remains of how important it is in nature. There have been two somewhat overlapping approaches to studying competition. The first is to carefully document that competition is occurring and to design experiments that can directly falsify the hypothesis that *the community is competitively controlled. One of the best examples is* the work of Reynoldson and his colleagues on triclad flatworms (Reynoldson and Bellamy 1971). The strength of this approach is clearly the testing of a falsifiable hypothesis. Its weakness is that the hypothesis being tested may not be what one thinks it is. For example, the prediction that the abundance of competing species should be negatively correlated through time does not test the hypothesis that species are competing, but rather that the competition is of a particular kind. This example will be elaborated later in the chapter.

The second approach is not to test for competition directly but rather to explore its consequences, usually with the aid of models. The work of Diamond (1975) exemplifies this approach. Its strength is that a relatively large number of predictions can be made, and its weakness is the danger of being right for the wrong reasons, as Paul Dayton has aptly put it. This approach can result in a castle built on sand; the first approach can result in a strong foundation with no castle. The arguments developed below attempt to use the strengths of both approaches. The most general consequences of competition will be considered first, followed by predictions that depend on the kind and intensity of competition.

Niche Separation One of the most universal results of competition is niche separation. Particularly interesting are populations that show a niche difference in allopatry and sympatry. A qualitative view of niche shifts in the Greenbrier Valley stream fauna is shown in Figure 6–7. Two species, *Gammarus minus* and *Stygobromus spinatus,* do not show any significant niche shift when in the same cave stream (syntopy). *Stygobromus spinatus* is found deep in riffles and does not usually encounter any other species, so it is not surprising that it does not undergo any niche shift. *Gammarus minus* occurs near the top of riffles, where it overlaps with *Stygobromus emarginatus* and *Caecidotea holsingeri.* In syntopy with *G. minus,* these two species are excluded from riffles. *Caecidotea holsingeri* is limited to pools, and *S. emarginatus* is limited to tiny trickles of water feeding into the stream. All four species feed on dead leaves and their microflora, and there is no evidence of shifts in food eaten when in syntopy (Culver 1970a).

Estes (1978) has made a more detailed study of the microhabitat niche of *Lirceus usdagalun* in two caves in the Powell Valley. In Gallohan Cave No. 1, there are significant populations of *Caecidotea recurvata* and *Crangonyx antennatus,* in addition to *L. usdagalun.* In the area of Thompson Cedar Cave sampled by Estes, *C. recurvatus* and *C.*

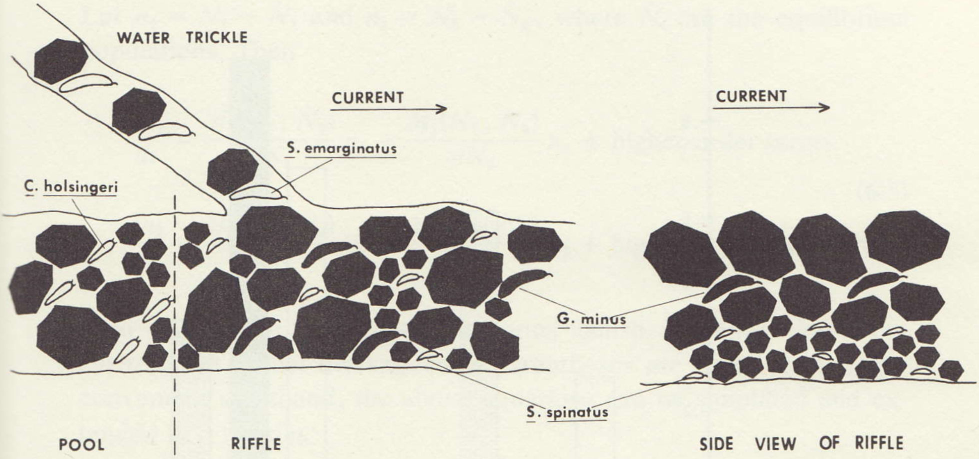

Figure 6–7 Diagrammatic view of niche separation of *Caecidotea holsingeri* (open oblong shapes), *Gammarus minus* (large solid crescents), *Stygobromus emarginatus* (large open crescents), and *Stygobromus spinatus* (small open crescents) in caves of Greenbrier County, West Virginia. *C. holsingeri* and *S. emarginatus* undergo niche shifts in the presence of competitors. No more than three of the species actually occur together in a single cave stream. (Drawing by Christine Turnbull.)

antennatus are almost completely absent, but *L. usdagalun* is common. Estes sampled six microhabitats and two velocity:depth profiles (with 0.67 used as an arbitrary dividing line between the two). Estes compared densities for each microhabitat at each velocity:depth profile and found a significant reduction in the density of *L. usdagalun* in Gallohan Cave No. 1 on bedrock in slow current, among small rocks in slow current, and among gravels in slow current. This difference is almost certainly due to the presence of competitors in these three areas. The niche breadth (*B*) of *L. usdagalun,* calculated using

$$B = 1 \Big/ \sum_i p_i^2 \tag{6-3}$$

where p_i is its frequency in microhabitat-velocity type *i*, is greater in the absence of competitors ($B = 7.8$) than in the presence of competitors ($B = 5.7$), as expected. It is clear that current velocity plays a major role in niche separation. With each microhabitat–velocity:depth type weighted equally to facilitate comparison, there is a shift of *L. usdagalun* toward faster currents when competitors are present. In the

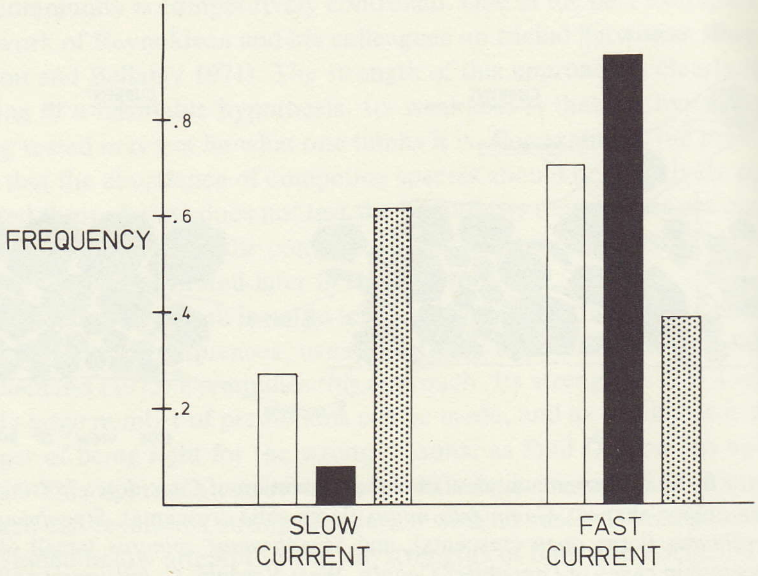

Figure 6–8 Relative frequencies of *Lirceus usdagalun* and its competitors in microhabitats of slow and fast current. The open bars represent the frequencies of *L. usdagalun* in the absence of competitors; the solid bars are the frequencies of *L. usdagalun* with competitors present; the shaded bars are frequencies of competitors (*Caecidotea recurvata* and *Crangonyx antennatus*). (Data modified from Estes 1978.)

absence of competitors, approximately 70 percent of the population occurs in fast currents, but over 90 percent occurs in fast currents when competitors are present (Fig. 6–8). Estes suggests that the success of *L. usdagalun* in Thompson Cedar Cave is due at least in part to the higher current velocities in that cave.

Population Size Changes Due to Competition Simply stated, the summed abundances of competing species should vary less through time than the abundances of any individual species. This prediction makes general sense where the total food or habitat available remains constant, and the prediction can be developed more formally as follows (Culver 1981). Consider two competitors whose abundances are N_1 and N_2:

$$\frac{dN_1}{dt} = f_1(N_1, N_2), \frac{dN_2}{dt} = f_2(N_1, N_2) \qquad (6\text{-}4)$$

Let $n_1 = N_1 - \hat{N}_1$ and $n_2 = N_2 - \hat{N}_2$, where $\hat{N}_i$ are the equilibrium populations. Then

$$\frac{dn_1}{dt} = \frac{\partial f_1(\hat{N}_1, \hat{N}_2)}{\partial N_1} n_1 + \frac{\partial f_1(N_1, N_2)}{\partial N_2} n_2 + \text{higher-order terms}$$

$$\frac{dn_2}{dt} = \frac{\partial f_2(\hat{N}_1, \hat{N}_2)}{\partial N_1} n_1 + \frac{\partial f_2(N_1, N_2)}{\partial N_2} n_2 + \text{higher-order terms} \tag{6-5}$$

Near equilibrium the higher-order terms vanish. If competition is occurring, the partial derivatives in parentheses are negative. Using a convenient shorthand, the above equations can be simplified and extended to n species:

$$\dot{n} = An \tag{6-6}$$

where $\dot{n}$ is a column vector with elements dn_i/dt and A is a matrix of partial derivatives as in equation 6-5.

$$Av = \lambda v \tag{6-7}$$

where λ is a scalar eigenvalue and v is the associated eigenvector. (For an explanation of eigenvalues and eigenvectors in an ecological context, see Roughgarden 1979.) The real parts of the eigenvalues measure the community's rate of return to (or departure from) equilibrium following a perturbation. Associated with each eigenvalue is an eigenvector, which is a linear combination of the deviations of population sizes from equilibrium. The rate of return following a particular perturbation depends on the magnitude of the eigenvalue associated with the eigenvector that most closely approximates the perturbation. The Perron-Frobenius Theorem (Gantmacher 1959) demonstrates that the eigenvector associated with the largest eigenvalue has all positive elements. A perturbation that changes the abundance of all species in the same direction will damp out more quickly than any other perturbation. Thus total abundance should vary less through time than the abundance of an individual species.

This competition hypothesis can be tested by comparing the variance of total abundance, which is controlled by the largest eigenvalue, to the sum of the individual species variances, which are controlled by smaller eigenvalues. In three of the four caves studied in the Powell Valley, the variance of total abundance is less than the sum of the variances of abundances of individual species (Table 6–3). The variance ratios range from 2.39 in Gallohan Cave No. 2 to 0.98 in Gallohan No. 1. None are statistically significant. If these variance ratios are typical for communities of competitors, there will rarely be sufficient data to demonstrate statistical significance.

All in all, the fit of the data to the prediction is poor. In part this may be because of small sample sizes, but it also seems likely that some other process is involved. Either competition is not occurring, or the null hypothesis of no correlation in the absence of competition is incorrect. The hypothesis above was generated for the situation in which equilibrium is fixed and the population sizes are subject to random perturbation about this equilibrium. But the equilibrium itself may vary because of changes in current or food availability. If carrying capacities (*K*'s of the standard competition equations) of species are positively correlated through time, then the variance in total abundance may exceed the sum of the variances of individual species' abundances. For example, if the carrying capacities of two competitors are both low in winter and high in summer, then species abundances might be positively correlated even though they are competing.

Correlation of abundances of pairs of species through time provides much stronger evidence for competition, but the predictions depend on the intensity of competition, so discussion of these data will be deferred until after the measurement of competition is discussed. It should be noted in passing that all *partial* correlations of competitor abundances should be negative (if carrying capacities are not too strongly correlated), and eight of ten such partial correlations are negative for the amphipod-isopod systems, three significantly so.

Table 6–3 The ratio of the sum of the variances of individual species abundances ($\Sigma\ V_i$) to the variance of total abundance (V_T). If species are competing, this ratio should be greater than unity. The number of samples required for statistical significance ($p > 0.95$), if the ratio observed is the true variance ratio, is listed in the column labeled N*. (Data from Culver 1981.)

Cave	No. species	No. time samples	$\Sigma V_i/V_T$	N*
Gallohan No. 2	3	4	2.39	12
Court Street	3	7	1.77	25
Spangler	2	4	1.12	> 100
Gallohan No. 1	3	5	0.98	> 100

Measurement of Competition Coefficients Any model of competition among these amphipods and isopods must take into account the physical structure of the stream. A riffle is a patchy environment from the point of view of an amphipod or isopod. It consists of a set of habitable patches (the undersides of rocks) separated by uninhabitable areas where the animals face the brunt of the current. Competition is for places to avoid the brunt of the current (or for feeding sites), and such places are in short supply whenever two individuals meet. The continued movement or dislodgement of animals among rocks in a riffle results in competition even when both species are rare.

This view of a riffle as a series of tiny islands is supported not only by the laboratory stream studies mentioned earlier but also by field observations. In such a system one would expect to see turnover in the individuals occupying particular rocks and riffles because of continuing movement and dislodgement. Changes in species composition were frequently observed for individual rocks and whole riffles and occasionally for entire cave streams (Culver 1973a). The chance events of migration and extinction should result in some habitable patches being unoccupied, and it was observed that most rocks, some riffles, and occasionally whole streams were unoccupied.

The model used (Culver 1973a) allows the proportion of rocks occupied to be a balance between births and emigrations from other patches, on the one hand, and washouts, on the other. If p_i is the frequency of rocks occupied by species i, then

$$\frac{dp_i}{dt} = m_i p_i (1 - p_i) - e_{ii} p_i^2 - \sum_{j \neq i} e_{ij} p_i p_j \qquad (6\text{-}8)$$

The first term is the birth plus emigration rate, m_i, times the frequency of occupied spaces (p_i) times the frequency of unoccupied spaces ($1 - p_i$). The second term is the washout rate due to an intraspecific collision (e_{ii}) times the frequency of intraspecific collisions (p_i^2), and the remaining terms are the analogous effects of interspecific collisions on washout rate. Equations of this type have been criticized by Levin (1974) and Slatkin (1974) because the probability of contact between two species is in general not equal to the product of their separate frequencies, in other words, $p_i p_j$. But for this particular system the short time scales and high frequency of mixing greatly reduce this problem. Equation 6-8 can be rearranged in the form of standard competition equations as follows:

$$\frac{dp_i}{dt} = m_i p_i \frac{K_i - p_i - \sum_{j \neq i} \alpha_{ij} p_j}{K_i} \tag{6-9}$$

where $$K_i = \frac{m_i}{m_i + e_{ii}} \quad \text{and} \quad \alpha_{ij} = \frac{e_{ij}}{e_{ii} + m_i} \tag{6-10}$$

The washout rates, e_{ii} and e_{ij}, can be measured directly in the laboratory, using appropriate combinations of species and controlling for total density. The birth and emigration rates cannot be measured directly, but m_i must be small compared to e_{ii} because the frequency of rocks occupied by a species when alone ($p_i = m_i/m_i + e_{ii}$) is small. With the arbitrary assumption that $m_i = 0.01$, competition coefficients, α_{ij}, were determined for three Powell Valley species (Culver 1973a):

$$\begin{bmatrix} 1 & \alpha_{12} & \alpha_{13} \\ \alpha_{21} & 1 & \alpha_{23} \\ \alpha_{31} & \alpha_{32} & 1 \end{bmatrix} = \begin{bmatrix} 1 & 0.99 & 1.32 \\ 0.32 & 1 & 1.29 \\ 1.16 & 0.49 & 1 \end{bmatrix} \tag{6-11}$$

with *Crangonyx antennatus* as species 1, *Caecidotea recurvata* as species 2, and *Lirceus usdagalun* as species 3. Similarly, competition coefficients were found for two Greenbrier Valley species:

$$\begin{bmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{bmatrix} = \begin{bmatrix} 1 & 2.46 \\ 5.68 & 1 \end{bmatrix} \tag{6-12}$$

with *Caecidotea holsingeri* as species 1 and *Caecidotea scrupulosa* as species 2.

Predicted Microhabitat Separation The competition coefficients calculated by formula 6-10 are not in any sense niche overlaps. Rather, they purport to be measures of the intensity of competition and should be positively correlated with the amount of microhabitat separation. By far the largest α values are associated with *Caecidotea holsingeri* and *C. scrupulosa.* The latter is known from twelve caves in the southern part of the Greenbrier Valley (Monroe and Greenbrier counties), and *C. holsingeri* is known from sixteen caves in the same area. The two have been found in the same cave (General Davis Cave) only once, and even then they were not found at the same time or place in the cave. For the Powell Valley species, there is a match between intensity of competition and amount of microhabitat separation. The species pair that competes the least is *Caecidotea recurvata* and *Crangonyx antennatus,* and they are routinely found in the same riffle, with the smaller *C. antennatus* deeper in the gravels. The species pair that competes the most is *Lirceus usdagalun* and *C. antennatus,* and they never coexist in the same stream. The maximum amount of microhabitat overlap observed for these two species occurs where *C. antennatus* is limited to side pools off the main stream (Fig. 6–9). The pair with intermediate competition is *C. recurvata* and *L. usdagalun,* and they occur in different riffles of the same stream.

Stability Rules It is also possible to analyze the stability of the equilibrium of various species combinations using the competition coefficients. Since all three species co-occur in three caves (See Table 6–3), the calculated values of α_{ij} should result in a stable equilibrium, which they do. Following Lawlor (1980), one can ask whether the observed minimum eigenvalue of the observed matrix of competition coefficients is significantly different from minimum eigenvalues obtained from matrices with the same elements as the observed matrix but arranged at random. For the α-matrix, the minimum eigenvalue must be positive for stability. The mean minimum eigenvalue of 100 such randomly constructed matrices is -0.12, with a standard deviation of 0.20, indicating that most randomly arranged communities are unstable. The

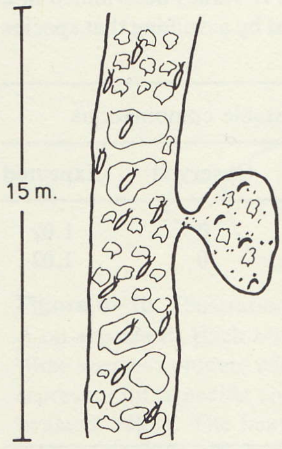

Figure 6–9 Schematized map of the distribution of *Lirceus usdagalun* (oblong symbols) and *Crangonyx antennatus* (crescent symbols) in Surgener Cave, Lee County, Virginia. The large irregular shapes represent large rocks (>10 cm) and the small irregular shapes represent small rocks in a riffle. The side pool is mud-bottomed with a few small rocks. In subsequent visits, *C. antennatus* had disappeared, and *L. usdagalun* was in the side pool. (From Culver 1973a; copyright 1973, the Ecological Society of America.)

minimum eigenvalue of the actual matrix is $+0.08$. The minimum value is larger than the average of the randomly constructed matrices but not significantly larger.

More generally, it is possible to use the calculated α values and estimates of the carrying capacities, K_i, to determine which combinations of species are stable and which species can invade which communities (Culver 1976). Two species pairs are predicted to be unstable when the pair is isolated from some third species: *L. usdagalun* with *Crangonyx antennatus*, and *L. usdagalun* with *Caecidotea recurvata*. Neither of these pairs has been found in isolation in any cave stream, the closest case being the one shown in Figure 6–9, which did not persist.

The absence of predicted unstable pairs can be made somewhat more quantitative. If there are such assembly rules, as Diamond (1975) termed them, then unstable communities should occur less frequently, on a statistical basis, than expected by chance. The actual analysis is complicated by the small range of *L. usdagalun*. Inclusion of cave streams that this species has never reached would obscure the analysis, so the following rather arbitrary convention was adopted: a cave stream was included if it was within one km of a known locality of *L. usdagalun*. Table 6–4 summarizes the results of the analysis. Because of the small number of caves, the results are only marginally significant, even though no caves had "forbidden" communities.

These results point up a recurring problem in cave ecology. The rela-

Table 6–4 Observed communities and subcommunities of *Caecidotea recurvata* (Cr), *Crangonyx antennàtus* (Ca), and *Lirceus usdagalun* (Lu) in cave-streams within the geographic range of all three. Stable and unstable combinations were determined by stability analysis of α and K values determined in a laboratory stream. Expected numbers were generated by assuming that species were distributed at random.

Stable combinations			Unstable combinations		
Species	Observed	Expected	Species	Observed	Expected
None	0	0.16	Lu-Cr	0	1.02
Lu	2	0.41	Lu-Ca	0	1.02
Cr	0	0.41			
Ca	0	0.41			
Cr-Ca	2	1.02			
Cr-Ca-Lu	3	2.55			

$\chi_1^2 = 2.80$, $p > 0.90$

tive simplicity of the systems makes possible more complete predictions than is usually the case. For example, in this situation there is a complete *a priori* set of assembly rules for the aquatic community. But the very simplicity of the community, and in this case the restricted ranges of the species, makes statistical testing difficult. There is much to be said on both sides of the argument (see Culver 1978 and Pimm 1978). My own point of view is that we lose much by taking the overly dogmatic view that the only interesting results are statistically significant, but the absence of firm statistical results makes any conclusions more in the way of suggestions than conclusions.

Qualitative data on distributions and on successful and failed invasions lend weight to the existence of assembly rules. Especially impressive is the species distribution pattern in the three physically distinct sections of the cave stream in Thompson-Cedar Cave. All three species occur in the downstream section, *C. recurvata* and *C. antennatus* occur in the upstream section, and *L. usdagalun* occurs alone in the middle section. Thus no predicted unstable communities occur even with the species in very close proximity. Also as predicted, neither *C. antennatus* nor *C. recurvata* has been able to successfully invade a stream dominated by *L. usdagalun*. Only one successful inva-

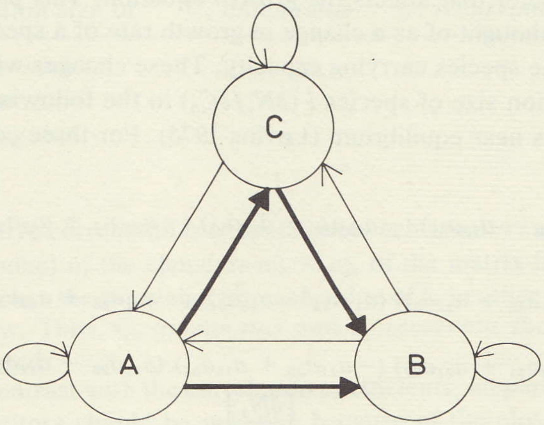

Figure 6–10 Illustration of the direct effect and the indirect effect of species A on species B. Each arrow indicates a competitive effect. In this example all three species compete with each other. The arrows from a species back to itself represent intraspecific competition. The heavy arrow from A to B is the direct negative effect. The heavy arrows from A to C and back to B represent the indirect positive effect of species A on species B.

sion has been recorded; as predicted, *L. usdagalun* successfully invaded a community with the other two species (Culver 1976).

Apparent Mutualisms and Indirect Effects Correlations and partial correlations of species through time provide further insights into the community. Levins (1975) and Levine (1976) have pointed out that when three or more competitors are present, there is the possibility that some pairs of competitors will be positively correlated and be "apparent mutualists," rather than negatively correlated as is expected intuitively. This can arise in the following way, as shown in Figure 6–10. When there are three competitors, species A has two effects on species B: first, a direct negative effect, and second, an indirect positive effect via species C. That is, species A has a negative effect on species C, which has a negative effect on species B, so the overall indirect effect of species A on species B is positive. The correlation between the two species (A and B) depends on the relative magnitude of these effects. Davidson (1980) has documented a very striking case of an apparent mutualism between competitors in a desert ant community.

The actual computations of indirect effects are rather lengthy (Levine 1976), so I will give only the bare essentials here. A change in the growth equations, $f_i = dN_i/dt$, can be written as $\partial f_i/\partial C_h$ where C_h is some parameter that affects the growth equation. This partial derivative can be thought of as a change in growth rate of a species due to a change in the species carrying capacity. These changes will in turn affect population size of species i $(\partial N_i/\partial C_h)$ in the following way if the population is near equilibrium (Levins 1975). For three competitors:

$$\frac{1}{|A|}\begin{bmatrix} (a_{22}a_{33} - a_{23}a_{32}) & (-a_{33}a_{12} + a_{32}a_{13}) & (-a_{22}a_{13} + a_{12}a_{23}) \\ (-a_{21}a_{33} + a_{23}a_{31}) & (a_{11}a_{33} - a_{13}a_{31}) & (-a_{11}a_{23} + a_{13}a_{21}) \\ (-a_{22}a_{31} + a_{21}a_{32}) & (-a_{11}a_{32} + a_{12}a_{31}) & (a_{11}a_{22} - a_{12}a_{21}) \end{bmatrix} \begin{bmatrix} \dfrac{-\partial f_1}{\partial C_h} \\ \dfrac{-\partial f_2}{\partial C_h} \\ \dfrac{-\partial f_3}{\partial C_h} \end{bmatrix} = \begin{bmatrix} \dfrac{\partial N_1}{\partial C_h} \\ \dfrac{\partial N_2}{\partial N_2} \\ \dfrac{\partial N_3}{\partial C_h} \end{bmatrix} \tag{6-13}$$

where a_{ij} is the effect of species j on species i, and $|A|$ is the determinant of the matrix of interaction coefficients, a_{ij}. For the standard competition equations,

$$a_{ij} = \frac{-r_i\hat{N}_i}{K_i}\,\alpha_{ij} \tag{6-14}$$

Each term of the matrix is the effect of a change in carrying capacity of species i on the population size of species j. Each off-diagonal term (a'_{ij}) is the difference between the direct and the indirect effect for species j on species i. Each diagonal term (a'_{ii}) is the determinant of the subcommunity formed by deleting species i.

Correlations can be predicted in the following way. A change in K_i (or any parameter affecting species i directly) results in changes in population sizes of all species; these are given in column i of equation 6-13. The expected correlation between two species because of changes in K_i can be found by comparing the signs of the two appropriate terms in column i. Using the above recipe, the elements of the matrix for the Lee County cave communities have the following signs:

Effect on population size of	Increase in K of *C. antennatus*	*C. recurvata*	*L. usdagalun*
C. antennatus	+	−	0
C. recurvata	+	−	−
L. usdagalun	−	+	+

A positive correlation is expected between species i and species j when the product of the elements $a'_{ik} \times a'_{jk}$ of the matrix in equation 6-13 is zero or has the same sign for each value of k, in other words, for the entire row. Thus, *C. antennatus* and *C. recurvata* should be positively correlated.

In contrast with the correlation coefficients, all partial correlations of competitors should be negative because of the close correspondence between the definitions of partial correlation and of competition coefficients. Both measure the effect of species j on species i with all other species held constant.

The set of predictions and the actual data (see Culver 1981) are given in Table 6–5. Of the nineteen predictions about the signs of cor-

Table 6–5 Comparison of observed and predicted correlations and partial correlations of species abundance through time. (Culver 1981.)

		Partial correlation			Correlation		
Cave	Species pair	Predicted	Observed	*p*	Predicted	Observed	*p*
Spangler	*C. recurvata* *C. antennatus*	−	−0.34[1]	N.S.	−	−0.34[1]	N.S.
Gallohan No. 2	*C. recurvata* *C. antennatus*	−	−0.99	>.99	+	+0.28	N.S.
	C. antennatus *L. usdagalun*	−	−0.99	>.99	−	−0.57	N.S.
	C. recurvata *L. usdagalun*	−	−0.99	>.99	−	−0.95	>.95
Gallohan No. 1	*C. recurvata* *C. antennatus*	−	+0.30	N.S.	+	+0.11	N.S.
	C. antennatus *L. usdagalun*	−	−0.82	N.S.	−	−0.82	>.95
	C. recurvata *L. usdagalun*	−	+0.05	N.S.	−	+0.07	N.S.
Court Street	*C. holsingeri* *S. emarginatus*	−	−0.36	N.S.	−	−0.38	N.S.
	C. holsingeri *S. spinatus*	−	−0.51	N.S.	−	−0.48	N.S.
	S. emarginatus *S. spinatus*	−	−0.01	N.S.	+	+0.19	N.S.

[1] Correlation and partial correlation are identical because there are only two species in the community.

relations and partial correlations, sixteen are in agreement with the signs of the calculated values. This level of agreement would be attained on a chance basis with a probability of only 0.002 (sign test). In addition, five of the correlations were statistically significant. Especially interesting is the complete agreement of observed and predicted correlations and partial correlations for Gallohan Cave No. 2. The time period of sampling in Gallohan No. 2 covers the period of the invasion of *L. usdagalun* (Dickson 1976), a time of intense competition but also a time when the populations are far from equilibrium. This suggests that the linear models used may hold when the situation is far from equilibrium.

The interaction between *Crangonyx antennatus* and *Caecidotea recurvata* epitomizes the importance of indirect effects in the organization of communities. When no other competitors are present (Spangler Cave) the two species are negatively correlated. When a third competitor is present (Gallohan Cave No. 1 and No. 2), the two species are positively correlated.

Effects of Predation In a few caves in the Powell Valley, larvae of the salamander *Gyrinophilus porphyriticus* are important predators of the amphipods and isopods. From the point of view of the behavioral ecologist, their feeding behavior is very simple (Culver 1973b) and even uninteresting. The larvae live in pools in the stream, and when hungry they rise up on their front legs and also usually their hind legs. When an amphipod or isopod comes within 2 to 4 cm of its snout, the larva will eat the prey with a rapid sucking action. The larvae apparently do not distinguish between prey species, but they are more successful in capturing isopods than amphipods, because amphipods sometimes escape by swimming off, while isopods do not. At least in the laboratory, the probability of successful predation by the larvae is quite high: over 75 of their feeding attempts on *Caecidotea recurvta* were successful. Peck (1973b) found similarly high successful predation rates in caves for the salamander *Haideotriton wallacei.* Individuals in riffles suffer little predation because almost all the larvae are in quieter waters, where water currents interfere little with their mechanoreception of prey movements. In McClure's Cave, the most intensively studied cave, actual predation rates on the two prey species, *C. recurvata* and *C. antennatus,* are very similar to the laboratory results. Although the probability of successful capture of *C. antennatus* is lower, the fraction of the population accessible to predation is higher, because it is partly excluded from riffles by *C. recurvata* (Culver 1975). The functional response (number of prey taken plotted against prey density) is linear over the naturally occurring range of prey densities. The absence of the usual nonlinearities in the functional response curve results from the negligible handling times of prey and the absence of any evidence of predator satiation.

In spite of nearly equal predation rates and a linear functional response curve, predation models have been of very limited use in answering two questions: first, how does predation affect the stability and size of prey populations? and second, why don't most cave invasions by cave salamanders result in successful establishment of a salamander population? The reasons for the limited utility of models is very different for the two questions. Analysis of a model of the two competitors (*C. antennatus* and *C. recurvata*) with equal predation rates on the two indicates that predation either stabilizes or destabilizes the system, depending on whether the intrinsic rate of increase of *C. antennatus* is greater or less than the intrinsic rate of increase of *C. recurvata* (Culver 1975). Neither of these parameters has been measured, and there is little likelihood they will be, given the very low rates of increase of most cave populations (chapter 3). In the case of field observations indicating that invasion rarely results in establishment, the predation model is actually misleading in a way that will be discussed below.

In McClure's Cave, predation results in an increase in the density of *C. antennatus* and a decrease in the density of *C. recurvata* in the immediate vicinity of salamander larvae (Fig. 6–11A). Since population densities of *C. antennatus* are low when the predator is absent, predation stabilizes the system in the sense that *C. antennatus* is less likely to become extinct because of random fluctuations in population size. In sharp contrast, in Sweet Potato Cave *C. recurvata* is absent in the vicinity of predators and *C. antennatus* is reduced in density (Fig. 6–11B). The differential effects of predation in the two caves results from the differences in the physical environment. In Sweet Potato

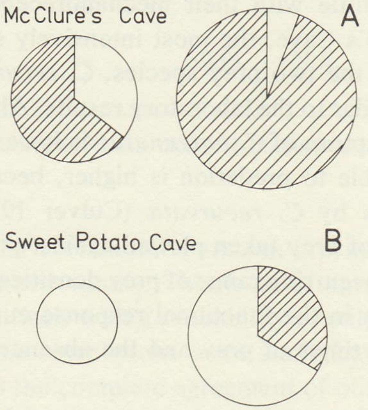

Figure 6–11 Effect of predation by larval *Gyrinophilus porphyriticus* on its prey in (*A*) McClure's Cave and (*B*) Sweet Potato Cave. The area of the circle indicates total prey abundance. The striped sector represents *Caecidotea recurvata;* the open sector represents *Crangonyx antennatus*. The circles on the left represent prey abundance in the presence of a predator; those on the right represent prey abundance in the absence of a predator.

Table 6–6 Fraction and density (per 0.09 m²) of the prey populations of McClure's Cave accessible to salamander predators when predators are nearby and when they are not. (From Culver 1975.)

Prey	*Gyrinophilus* larvae nearby	Fraction accessible to predator	Density accessible to predator
Crangonyx antennatus	Yes	0.29	0.30
	No	0.51	0.15
Caecidotea recurvata	Yes	0.10	0.13
	No	0.19	0.78

Cave the habitat is a series of mud-bottomed rimstone pools. There are no refugia for the prey in the form of riffles. Predation is high enough so that isopods are not present in the same pool with salamander larvae. In some pools *C. antennatus* persists with salamanders because amphipods are harder to capture and because they burrow in the mud (Holsinger and Dickson 1977). In contrast, in McClure's Cave only a fraction of each prey population is vulnerable to predation, because the salamanders do not occur in riffles or flowstone habitats.

In McClure's Cave a comparison of areas near and away from larvae showed that both the fraction and the density of the *C. recurvata* and the fraction of *C. antennatus* accessible to predators declined in the vicinity of a predator (Table 6–6). Consequently, colonizing salamanders encounter a relatively dense, accessible prey population, and initially the predation rate for each larva is higher than for an individual in a resident population, where the prey are relatively scarce and inaccessible.

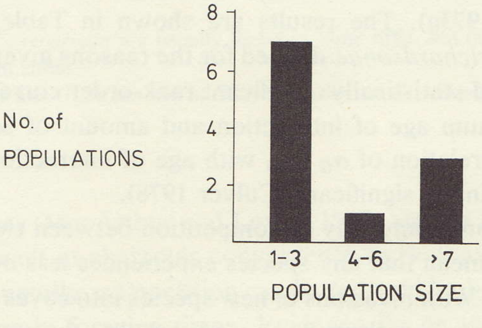

Figure 6–12 Frequency distribution of numbers of larval *Gyrinophilus porphyriticus* in caves in Lee County, Virginia, and Claiborne County, Tennessee. (From Culver 1975.)

Therefore, predation is not constant, as is assumed in the model. Biologically, we would expect most "populations" of predators to consist of a few individuals, since population growth would be difficult, and this is in fact the case (Fig. 6–12). Only three of eleven caves have populations of sufficient size to expect a persistent population.

Evolutionary Considerations There is some evidence that the intensity of competition between pairs of species declines with evolutionary time. The length of time each Appalachian isopod and amphipod has been in caves can be roughly determined by examining their distribution patterns and the amount of regressive evolution, which should increase with time (Culver 1976). The "cave age" of the species can be conveniently divided into four groups. The youngest species occur in cold-water habitats outside caves and show little signs of regressive evolution, retaining eyes and pigment. In the next group are species with very restricted ranges and with reduced eyes and pigmentation. Species in the third group have large geographic ranges, no pigment, and vestigial eyes. In the oldest group are species without eyes and pigment, with small ranges per species but with large species groups in which the species show clear morphological differences. Further justification of this scheme is given in Culver (1976).

With one exception, the length of time available for interaction between two species can be estimated by the cave age of the younger of the pair. The exception is a pair of old species (*Caecidotea recurvata* and *C. richardsonae*) whose ranges are barely overlapping and whose contact is much more recent than their cave age. Intensity of interaction is known directly for those species pairs whose α's were measured, and indirectly for a larger set of species on the basis of microhabitat separation, which is correlated with the intensity of competition (Culver 1973a). The results are shown in Table 6–7, with *C. recurvata–C. richardsonae* deleted for the reasons given above. There is a perfect and statistically significant rank-order correlation between average minimum age of interaction and amount of separation. The rank-order correlation of $\alpha_{ij} \cdot \alpha_{ji}$ with age of interaction is suggestive but only marginally significant (Culver 1978).

The reduction in intensity of competition between two species over time does not mean that any species experiences less overall competition with time. With invasions of new species into caves and migrations of other cave species, there is no evidence that the overall amount of competition experienced by a species diminishes.

To many field biologists, character displacement is the *sine qua non* of interspecific competition. Yet it has been repeatedly shown by theo-

Table 6–7 Intensity of competition and relative length of isolation in caves. (From Culver 1976, reprinted by permission of the University of Chicago Press, © 1976, the University of Chicago.)

Species pair	Valley	Relative age of interaction[a]
Species in different habitats of same riffle		
Gammarus minus-Stygobromus spinatus	Greenbrier	1
Stygobromus emarginatus-Stygobromus spinatus	Greenbrier	4
Stygobromus emarginatus-Caecidotea holsingeri	Greenbrier	4
Stygobromus spinatus-Caecidotea holsingeri	Greenbrier	4
Gammarus minus-Caecidotea holsingeri	Greenbrier	1
Crangonyx antennatus-Caecidotea recurvata[b] ($\alpha_{ij}\alpha_{ji} = 0.3$)	Powell	3
$\bar{X} = 2.8$		
Species in different riffles		
Crangonyx antennatus-Caecidotea recurvata[b]	Powell	3
Lirceus usdagalun-Caecidotea recurvata ($\alpha_{ij}\alpha_{ji} = 0.65$)	Powell	2
Caecidotea scrupulosa-Gammarus minus[c]	Greenbrier	1
Caecidotea scrupulosa-Crangonyx sp.	Greenbrier	1
$\bar{X} = 1.8$		
Species barely coexisting		
Caecidotea scrupulosa-Gammarus minus†	Greenbrier	1
Gammarus minus-Stygobromus emarginatus	Greenbrier	1
Crangonyx antennatus-Lirceus usdagalun ($\alpha_{ij}\alpha_{ji} = 1.5$)	Powell	2
$\bar{X} = 1.3$		
Complete exclusion		
Caecidotea scrupulosa-Caecidotea holsingeri ($\alpha_{ij}\alpha_{ji} = 13.4$)	Greenbrier	1
Crangonyx sp.-*Gammarus minus*	Greenbrier	1
$\bar{X} = 1.0$		

a. See text for explanation of relative age. The larger the number, the longer the time species has been isolated in caves.

b. *C. antennatus* and *C. recurvata* are usually found in same riffle, but in a few caves (*e.g.*, Cope Cave) they are in different riffles.

c. Either *C. scrupulosa* and *G. minus* are in different riffles, or *C. scrupulosa* is very rare.

retical ecologists (MacArthur and Levins 1967; Slatkin 1980) that competition can result in character convergence as well as character displacement. Generally, competition can be reduced by habitat selection or by difference in foraging times. Evidence for or against character displacement is not evidence for or against competition, but evidence for or against the particular kind of competition that leads to character displacement.

There are no documented cases of character displacement among aquatic cave invertebrates, but one apparent case of character displacement is worth considering. Two closely related species of isopods, *Caecidotea cannula* and *C. holsingeri,* occur in caves in

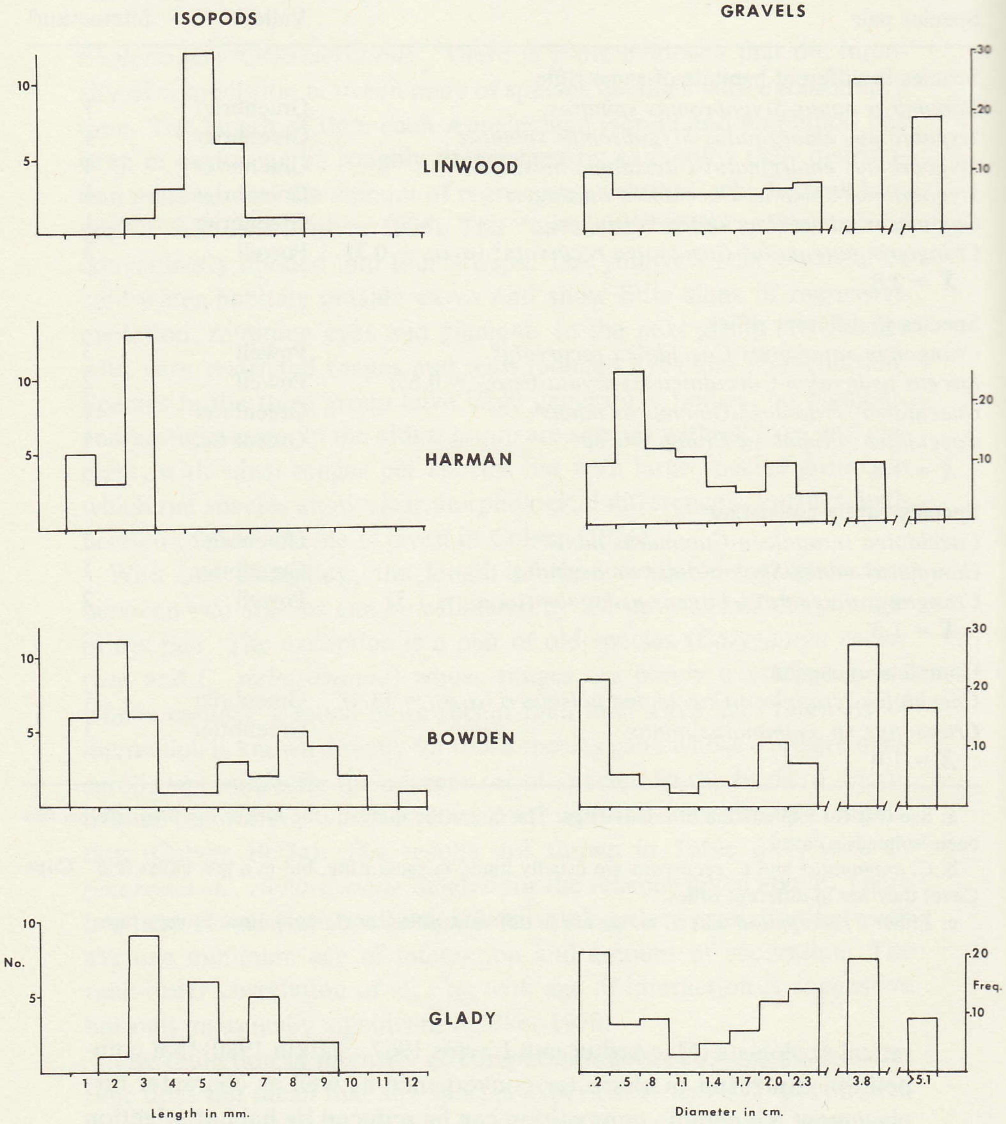

Figure 6–13 Gravel and isopod sizes for Linwood, Harman, Bowden, and Glady Caves, West Virginia. See Table 6–8 for a description of the distribution. (From Culver and Ehlinger 1980.)

Table 6–8 Qualitative characteristics of the isopod and gravel size distributions shown in Figure 6–13. Quartiles and medians are given for each distribution (length in mm for isopods, diameter in mm for gravels). Frequency (F) of large gravel (>12.3 mm) is also given. (From Culver and Ehlinger 1980.)

	Gravel					Isopods			
Cave	Q_1	M	Q_3	Qualitative features	F	Q_1	M	Q_3	Qualitative features
Linwood	5.6	11.9	19.1	Uniform for small gravel	0.44	5.0	5.4	6.2	Strongly unimodal, narrow size range, all intermediate in size
Harman	2.4	5.6	10.3	Unimodal, skewed to small sizes	0.12	1.6	3.1	3.6	Unimodal, narrow size range, all small in size
Bowden	2.4	11.9	19.1	Strongly bimodal	0.43	2.4	3.3	8.3	Bimodal, broad size range
Glady	2.4	8.7	19.1	Weakly bimodal	0.27	3.7	5.3	7.6	Unimodal, broad size range, skewed toward small size

northern West Virginia. In the Monongahela River drainage where both occur, *C. cannula* is twice the size of *C. holsingeri,* and in other drainage systems where *C. cannula* does not occur, *C. holsingeri* is larger, which led us to suspect character displacement (Holsinger, Baroody, and Culver 1975). We also suspected that the size of gravels in a cave stream had a strong effect on isopod size. Experiments in a laboratory stream indicated that both hypotheses were possible: isopods of different sizes competed less strongly than isopods of the same size, and large isopods could better maintain their position in a current with large gravels than with small gravels. The question is which factor is more important in the field. There is a strong correlation between the shape of the distribution of gravel sizes and the shape of the distribution of isopod sizes (Fig. 6–13, Table 6–8), indicating that isopod size is largely determined by gravel size in the stream rather than by the presence of competitors (Culver and Ehlinger 1980). The two mismatches of distributions provide no support for character displacement. In Glady Cave, gravel sizes are bimodally distributed, while isopod sizes are unimodal, but if character displacement were important, the differences in isopod size should be more rather than less pronounced. The mismatch in Linwood Cave results from the absence of *C. cannula* from the Elk River drainage rather than from competitive effects.

Summary: The Role of Models

The differential equation models used in the previous sections allowed a deeper probing into the structure and dynamics of cave stream communities than otherwise would have been possible. It was possible to proceed in a logical way toward an explanation of the varying amounts of microhabitat separation between species and to successfully predict stable and unstable species combinations. The models suggested some nonobvious patterns to search for, especially the relative constancy of total abundance and the possibility of indirect mutualisms. It was also clear when the models were inadequate. The predation model used was insufficient to explain some important features of the predator–prey system, most notably niche shifts of the prey and the relative ease of predator invasion compared to predator establishment.

Two factors stand in the way of making a very strong claim about the importance for noncave systems of the particular models used for caves. The first is the problem of statistical testing. Because of the very simplicity of a community that allows measuring pairwise interactions in the first place, the data base is relatively small. The most extreme case occurred in the attempt to test assembly rules. No unstable subcommunities were found, yet the results were only marginally significant. In some cases it was possible to generate a larger data base, but it is unlikely that cave ecologists in general will be able to generate the large data sets that it is currently in vogue to test. What data from cave communities can provide is a clear indication of whether a particular model seems to work in a relatively simple system.

The second objection raised about cave communities is that they are in some way so aberrant that the rules governing their structure and dynamics are either completely different from those for other communities or so trivial as to not constitute worthy objects of study. What is obviously missing from caves are green plants and thus plant–animal interactions. However, the study of other detritus-based communities, such as freshwater streams, has added greatly to our general ecological knowledge. Other interactions clearly are present in caves, including competition, predation, and symbiosis. Free-living mutualists may or may not be present, but that statement can be made for many temperate zone communities.

Even the relatively simple aquatic stream communities of Appalachian caves make clear some inadequacies in the current questions being asked about species interactions. It is difficult to state precisely what it means to weigh the relative importance of different species interactions. Consider the communities with predaceous *Gyrinophilus porphyriticus* larvae and its prey, *Caecidotea recurvata* and *Crangonyx antennatus*. The predator clearly alters the relative abundance of prey and can cause the extinction of *C. recurvata* in particular habitats, but the predator effect just as clearly depends on competition between the prey. Both interactions are important, and the interactions are complex enough that these complexities, which Levins (1975) termed network effects, have come to predominate in the community. Network effects are important not only for the predator–prey systems but also for three competitors, where indirect mutualisms were observed.

The potential of cave communities for studies of species interactions is by no means exhausted. In particular, terrestrial communities are generally more complicated than aquatic communities, and their potential is largely untapped. The terrestrial fauna of Mammoth Cave has attracted attention because of its complexity (see Barr 1967a), but even the supposedly simple terrestrial faunas of most caves is more complex than those of aquatic communities. Shelta Cave in Alabama has one of

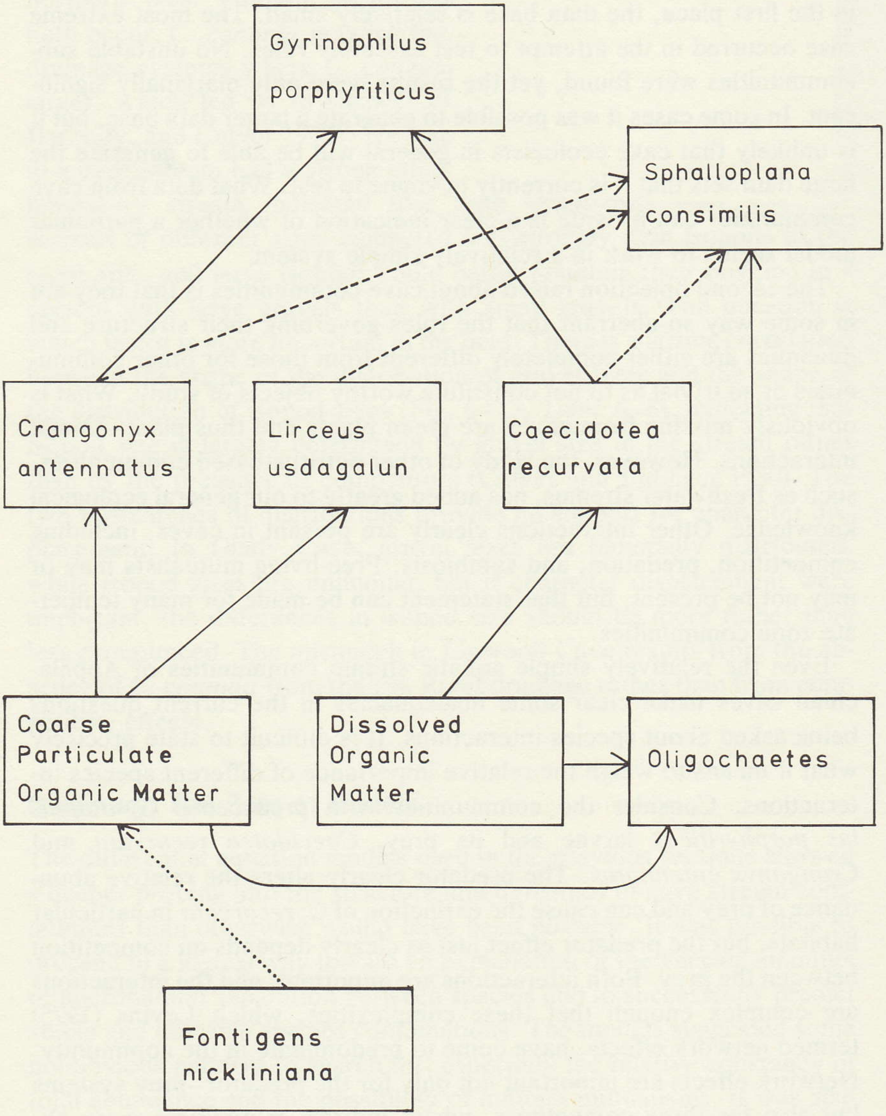

Figure 6-14 Food web for the aquatic fauna of Gallohan Cave No. 1, Lee County, Virginia. Dashed lines indicate feeding on dead and moribund individuals; dotted lines are conjectured feeding relationships.

Table 6–9 Visual census of terrestrial arthropods in a 100 m by 5 m strip of wet passage with organic debris in Gallohan Cave No. 1. Species marked with an asterisk are cave-limited (troglobites). (Data from T. Kane, unpublished.)

Class	Order	Species	No. individuals
Crustacea	Isopoda	*Amerigoniscus henroti**	2
Arachnida	Acarina	*Rhagidia* sp.*	1
	Araneae	*Nesticus carteri*	11
		*Phanetta subterranea**	3
	Pseudoscorpionida	*Kleptochthonius proximosetus**	2
Diplopoda	Chordeumida	*Pseudotremia nodosa**	47
		Pseudotremia valga	5
Insecta	Diplura	*Litocampa cookei**	1
	Collembola	*Pseudosinella orba**	12
		Tomocerus bidentatus	2
		Arrhopalites hirtus	4
	Coleoptera	*Pseudanophthalmus delicatus**	13

the richest aquatic faunas in North America, yet there are as many terrestrial troglobitic species, twelve, as aquatic troglobitic species (Cooper 1975). Gallohan Cave No. 1 in Lee County, Virginia, has an exceptionally rich aquatic fauna, the food web of which is shown in Figure 6–14. By contrast, the less thoroughly studied terrestrial fauna includes at least twelve species (Table 6–9), the feeding relationships of which are nearly a complete mystery.