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COMPETITION IN SPATIALLY HETEROGENEOUS SYSTEMS: AN ANALYSIS OF SIMPLE CAVE COMMUNITIES¹

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Abstract. A model of competition for aquatic cave invertebrates in the southern Appalachians in which competition affects washout rate in the cave stream is presented. The model accounts for the two major generalizations about microdistribution of cave isopods and amphipods in the Appalachians: species distribution is uncertain and only one species is found in a habitat patch. The model also predicts the amount of habitat overlap various species pairs have. Experiments to verify the model were conducted in an artificial stream.

The importance of competition in animal communities has been debated at least since the publication of Gause's classic, The Struggle for Existence, in 1934. Until recently, investigators claimed to have measured competition only in laboratory populations while field biologists largely devoted themselves to testing the competitive exclusion principle. In the last decade, an increasing number of ecologists claim to have measured competition in natural communities (Levins 1968, MacArthur 1968, Pianka 1969, Culver 1970b). Interest increased with the theoretical demonstration that competition sets a limit on the number of species in a community (MacArthur and Levins 1967, Levins 1968). Unfortunately, field work and experimental work has not kept pace with the rapidly growing theoretical developments (Cohen 1970, MacArthur 1970, Vandermeer 1970, Scudo 1971).

I will here consider general aspects of the interrelationship of aquatic cave crustaceans in three major karst valleys (Greenbrier, Powell, and Clinch) in the southern Appalachians, construct a model of competition based on these broad outlines of the species' biology, and test the model by considering details of the interactions and microdistribution of one species pair from the Greenbrier Valley in West Virginia and a species triad from the Powell Valley in Virginia. Thus, I can test whether my initial assumption of the importance of competition is justified.

The karst valleys of the Greenbrier, Powell, and Clinch rivers are long (120-240 km) and narrow (less than 35 km) and bounded by synclinal ridges of shale and sandstone which act at least as partial dispersal barriers to many cave-limited species (Holsinger 1969*a*). All three karst valleys have a large number of caves; for example, over 500 caves are known in the Greenbrier Valley (R. Baroody, personal communication). The karst area of the Greenbrier Valley begins near the origin of the river in Blister Swamp in Pocahontas County, continues through Greenbrier County, and ends in Monroe

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County, West Virginia, near the point where the Greenbrier River joins the New River. The karst area of the Powell River begins near Norton in Wise County, Virginia, and ends near La Follette, Tennessee. The karst area of the Clinch River Valley begins near Tazewell in Tazewell County, Virginia, continues through Russell and Scott counties, Virginia, down to near La Follette, Tennessee, where it joins the Powell River 240 km from its headwaters.

FIELD OBSERVATIONS

Perhaps the dominant aspect of the distribution of aquatic species in caves in these karst valleys is the uncertainty of distribution. By uncertainty I mean that any given species does not occur in all the caves, habitats, and microhabitats that appear to be optimal for its survival. Let us begin by considering species' presence or absence from caves. Frequencies of occurrence of all macroscopic crustaceans except for crayfish known to occur regularly in caves in the three karst valleys are given in Table 1. With the exception of Crangonyx antennatus in the Powell Valley, none of the species occur in all "suitable" caves and most occur in a small percentage of the suitable caves. Some of the percentages, e.g., Asellus scrupulosus and A. holsingeri in the Greenbrier Valley, may be reduced by competition. In addition to the uncertainty of occurrence of the species in all the valleys, there are differences in the degree of uncertainty between the valleys and between different parts of the same valley. For example, most of the species in the Powell Valley occur in most of the caves, but in the lower part of the Greenbrier Valley the occurrence of all species is sporadic. There is, at present, no explanation for these differences, but they probably are related to differences in karst development in the different areas (Curl 1966) and differences in hydrology (Culver 1970a).

This general unpredictability of species' presence or absence in a cave is strong presumptive evidence that local immigrations and extinctions are an important determinant of frequency of occurrence (Culver 1971a). Even stronger evidence is that temporal

Valley	Sub-valley	Species	Frequency	Number of caves investigated
Greenbrier	North of Droop	Gammarus minus	0.78	9
	Mountain	Asellus holsingeri	0.44	9
		Stygonectes spinatus	0.22	9
		Stygonectes emarginatus	0.22	9
Greenbrier	Greenbrier River to	Gammarus minus	0.57	30
	Droop Mountain	Asellus holsingeri	0.27	30
		Stygonectes spinatus	0.33	30
		Stygonectes emarginatus	0.23	30
		Asellus scrupulosus	0.07	30
		Apocrangonyx sp. n.*	0.07	30
Greenbrier	South of Greenbrier	Gammarus minus	0.33	15
	River ^b	Asellus holsingeri	0.20	15
		Stygonectes spinatus	0.20	15
		Stygonectes emarginatus	0.07	15
		Asellus scrupulosus	0.20	15
		Stygobromus mackini	0.13	15
		Crangonyx sp. n.	0.07	15
		Apocrangonyx sp. n. ^a	0.07	15
Powell ^c		Lirceus sp. n. ^d	0.60	5
		Asellus recurvatus	0.60	11
		Crangonyx antennatus	1.00	11
		Stygobromus sp. n.e	0.09	11
Clinch ^f		Asellus recurvatus	0.44	9
		Asellus richardsonae	0.22	9
		Gammarus minus [®]	0.22	9
		Crangonyx antennatus	0.22	9
		Stygobromus mackini	0.55	9

TABLE 1. Frequencies of occurrence of cave crustaceans in different karst valleys

NOTE: Only nonflooding caves are included because flooding caves tend to have fewer species (Culver 1970a). All macroscopic crustaceans in caves except for crayfish are included. The subdivisions of the Greenbrier Valley correspond to possible dispersal barriers.

Two recently discovered species of Apocrangony x related to A, parvus (Holsinger 1969b).
 Includes only those species found in over 50% of the visits to the cave.
 Only caves in Lee County were investigated.
 An undescribed cave-limited Lirccus is known only from one small valley near Rose Hill. Only caves in this valley are used to calculate the frequency.

 An undescribed cave-imitted Literars is known only from one small valey near Rose Fint. Only caves in this valey are used to carculate the frequency.
 This species is closely related to *Strgobromus mackini* (Holsingre 1969a).
 All caves are in Virginia. The valley should probably be subdivided like the Greenbrier Valley, but there are insufficient data.
 Cammarus minus is known only from caves at the headwaters of the Clinch River. It occurs in springs throughout the valley (Holsinger and Culver) 1970).

changes occur (Simberloff and Wilson 1969). 1 previously presented data for faunal changes in Upper Martha's Cave in the Greenbrier Valley (Culver 1970a). Since then I have gathered similar data for two caves in the southern part of the Greenbrier Valley (Table 2). In Crossroad Cave, each species was present, on the average, 47% of the time; in Hunt Cave each species was present, on the average, 58% of the time. The corresponding figure for Upper Martha's Cave is 44%. Of course, no faunal changes were observed in many of the caves that were visited several times.

When we consider patches of habitat, the same pattern of uncertainty occurs. Since most cave species are rare in most caves where they occur, many patches of habitat will be empty simply because there are not enough animals to go around. But even if we limit our attention to cases where the mean abundance of animals is more than 4 per patch, there are still empty patches (Table 3). Furthermore, the number of empty patches is much greater than expected from a Poisson distribution. For a Poisson distribu-

tion with a mean of 4, the frequency of empty patches should be 0.018, much lower than any of the results given in Table 3. Only Lirceus from Gollahan Cave no. 1 and Crangonyx antennatus from Lucy Beatty Cave come close to occurring in all optimal habitat patches. It is difficult to get data concerning temporal changes in habitat patches occupied by a species because the habitat usually must be disrupted in order to count the animals. However, three incidental observations made in the course of field work indicate that temporal changes are quite common. On my return to Martha's Cave in the Greenbrier Valley in April 1971, after an 18-month absence, the Asellus holsingeri population had shifted downstream about 10 m, and was completely absent in the area where it previously occurred. This shift was undoubtedly caused by a sudden rise in current sometime during the 18 months, but this is the kind of event that regularly occurs in all caves in the study area. Similar changes in the distribution of Stygonectes spinatus in Greenbrier Caverns were observed in a 4month period. Finally, many of the Lirceus and

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TABLE 2. Fauna changes in Crossroad Cave and Hunt (Connel) Cave. Both caves are in Monroe County, West Virginia, in the southern part of the Greenbrier Valley. An x indicates that the species was present

		Crossroad	i Cave		
Date	A. scru- pulosus	G. minus	Crangonyx sp. n.	S. mackini	S. spinatus
Sept. 1, 1967		x	x	x	
April 5, 1971	x				x
Aug. 31, 1971	x	x			
	and the set of the set of the set of the	Hunt C	lave		
	A. scri	upulosus	S. spinatus	Crang	onyx sp. n
Dec. 11, 1965					x
Oct. 14, 1970		x	x		x
April 5, 1971			x		
Sept. 3, 1971		x			T

TABLE 3. Percentage of patches of optimal habitat that do not contain the species listed

Species	Cave	Valley	Percent- age of empty samples	No. of samples
Gammarus minusª	Benedict's	Greenbrier	12	73
Stygonectes spinatus ^a	Court Street	••	23	38
Stygonectes emarginatus*	Court Street		45	38
Asellus holsingerib	Blue Spring	••	41	56
Crangonyx antennatus®	Gollahan #1	Powell	50	20
Crangonyx antennatus ^e	Lucy Beattie	••	8	12
Asellus recurvatus ^b	Gollahan #1		35	20
Lirceusb	Gollahan #1	••	10	20
Asellus recurvatus ^e	Cope	**	25	12

NOTE: One square foot of rocky pools and riffes were sampled. Each mud pool was examined in its entirety. Areas without competing species were used.

b Riffles and rocky pools.
 c Mud pools.

• wide pe

Asellus recurvatus in Gollahan Cave no. 1 are on the tops of rocks and are visible without disturbing the habitat. Between August and October 1971 about half the rocks either had a different species, or the previous species was absent and the habitat was empty. Thus, patches of habitat within a cave are islands of suitable habitat just as caves themselves are islands of suitable habitat.

A riffle in a stream is also not a continuous habitat. Is consists of a series of rocks separated by moving water. Field observations indicate that none of the amphipod and isopod species being considered can maintain position when exposed to the main force of the current. Therefore, moving from rock to rock is a risky operation, and the habitat should not be viewed as a homogeneous environment. Furthermore, in a series of experiments measuring the washout rates of *Gammarus minus* in an artificial stream (Culver 1971b), I found that considerable mortality accompanied washout (dislodgment). Thus, it appears that the microhabitat is also islandlike, i.e., habitable patches (rocks) separated by inhospitable areas (moving water), and the environment can be described as islands within islands within islands.

The second major generalization about the distribution of aquatic cave animals in the central Appalachians is that species do not coexist in the same habitat patch in the same cave at the same time. The scale of exclusion can either be such that coexistence in the same cave is possible or that coexistence in the same cave is impossible. Coexistence in the same cave has two distinct patterns, at least in extreme cases: the species can occur in different patches of the same habitat, or the species can occur in different habitats. In Table 4, I have classified all possible species pairs as to their patterns of codistribution. The only species pairs not listed are those that are rare and have not been found either alone or together enough times to get any field information or enough individuals for laboratory studies.

Species that occur in different patches of the same habitat usually both occur in a variety of habitats. For example, *Crangonyx antennatus* and *Asellus recurvatus* both occur in mud pools, bedrock pools, and small gravels in riffles in Cope Cave in the Powell Val-

TABLE 4. Summary of distribution patterns of macroscopic crustaceans in Clinch, Powell, and Greenbrier Valley caves. All pairs except those for which no information is available are listed

Species	Valley	Cave
A. Coexistence in different patches of th	e same habita	t
Crangonyx antennatus—Asellus recurvatus	Powell	Cope
Asellus recurvatus—Lirceus n. sp.	Powell	Gollahan #1
Asellus scrupulosus—Grammarus minus	Greenbrier	Crossroad
Asellus scrupulosus—Crangonyx n. sp.	Greenbrier	Hunt
Asellus richardsonae—Gammarus		
minus	Clinch	Hugh Young
B. Coexistence in the same cave, in diffe	erent habitats	
Stygonectes emarginatus—Asellus		
holsingeri	Greenbrier	McClung-Zenith
Stygonectes spinatus—Asellus	Greenbrier	Indian Draft
holsingeri		Court Street
Asellus scrupulosus—Gammarus minus	Greenbrier	Jarret's Water
Gammarus minus—Stygonectes emarginatus	Greenbrier	The Hole Greenbrier
Gammarus minus—Stygonectes	Greenbrier	The Hole
spinatus		Benedict's
-		Indian Draft
Gammarus minus—Asellus holsingeri	Greenbrier	Marth a's
		Greenbrier
		Benedict's
Stygonectes emarginatus—Stygonectes	Greenbrier	Court Street
spinatus		The Hole
Crangony'x antennatus—Asellus	Powell	Gollahan #1
recurvatus		Gollahan #2
Crangonyx antennatus—Lirceus n. sp.	Powell	Surgener's
		Thompson-Cedar
Stygobromus mackini—Asellus	Clinch	Mun se y
recurvatus		Jessie
C. Complete exclusion from caves		
Asellus scrupulosus—Asellus holsingeri		Greenbrier
Crangonyx antennatus—Stygobromus m	ackin i	Clinch
Asellus richardsonae—Asellus recurvatus		Clinch
Asellus recurvatus—Gammarus minus		Clinch

^{*} Riffles.



FIG. 1. Schematized map of distribution of *Asellus recurvatus* (solid oblong symbols), *Lirceus* (open oblong), and *Crangonyx antennatus* (solid crescent) in three caves in Lee County, Virginia. The large irregular shapes represent large rocks (> 10 cm), and the small irregular shapes represent small rocks in riffles. The dotted areas are mud pools.

ley (Fig. 1). The most striking example of this pattern is A. recurvatus and Lirceus sp. n. in Gollahan Cave no. 1 in the Powell Valley (Fig. 2). In a 3-ft section of stream in this cave, there were 27 rocks, all between 2 and 4 inches in diameter. Fourteen had only Lirceus, ten had only A. recurvatus, one had neither species, and only two had both species. The expected number of co-occurrences is 7.11, which is significantly different from the observed ($\chi_1^2 = 3.53$, P > 0.95). In most of the remaining stream in the cave, the two species tended to be more separated. In one 6-ft section of cave, the first foot had only A. recurvatus, the next 3 ft had only Lirceus, and the next 2 ft had only A. recurvatus. In this 6-ft section there were 25 rocks; nine had A. recurvatus, nine had Lirceus, and seven had neither species. I will discuss this cave in more detail below.

The most common pattern is coexistence in the same cave but in different habitats. In previous work on the fauna of the central part of the Greenbrier Valley (Culver 1970b), I found that G. minus, Stygonectes spinatus, Stygonectes emarginatus, and A. holsingeri did not coexist in the same habitat even though all but Stygonectes spinatus occupied the same habitat when alone, i.e., rocks over 1 inch in diameter in riffles. Lirceus nearly excludes C. antennatus in

caves where they co-occur in the Powell Valley—C. antennatus is limited to partially isolated stream pools (Fig. 1). In some caves (Fig. 1), there is a similar pattern with C. antennatus and A. recurvatus, although in this case C. antennatus also occurs in very small gravels where its size at maturity is much smaller than in caves where it predominates. Other examples of habitat separation are given in Table 4.

Other species are common in the same karst valley, but never in the same cave (Table 4). The most striking case of this is A. holsingeri and A. scrupulosus in the lower part of the Greenbrier Valley. Asellus scrupulosus is found in caves primarily in Monroe County and in Greenbrier County west of Muddy Creek Mountain, while A. holsingeri has a much broader range (Steeves 1969). Asellus scrupulosus occurs in five of 20 caves in this area, and A. holsingeri occurs in six of 20 caves, and never in the same cave. However, in Benedict's Cave east of Muddy Creek Mountain in Greenbrier County, A. scrupulosus occurs in the entrance stream, and A. holsingeri occurs deeper in the cave. The A. scrupulosus population in Benedict's Cave is anomalous because animals 200 m into the cave have lost all pigments and the eyes are very small (Steeves 1969). Furthermore, A. scrupulosus is not always present



FIG. 2. Schematized map of distribution of *Asellus* recurvatus and *Lirceus* in Gollahan Cave no. 1. The small stream entering on the left is a stream coming directly from the surface, and thus is an important food source for the isopods.

in the entrance stream. The distribution of *G. minus* with *A. recurvatus* and *A. richardsonae* in the Clinch Valley probably fits into this pattern also. *Gammarus minus* is known from caves in the Clinch Valley only in the Maiden Springs karst near the headwaters of the Clinch River, and from springs throughout the valley (Holsinger and Culver 1970). It is probable that *G. minus* is completely excluded from caves by *A. recurvatus*, and in turn *G. minus* almost completely excludes *A. richardsonae* from the Maiden Springs Karst. They only co-occur in Hugh Young Cave, and then in different parts of the cave.

The only exceptions among the cave crustaceans to the patterns discussed above are all cases of coexistence for relatively short periods of time (less than several months) in rimstone pools that collect water from subsurface seeps. Since these pools are usually isolated from the surface stream, there is no possibility of spatial separation, and so we would expect the two species to persist until one of the populations (usually less than 10 individuals) dies off. With this description of the macroscopic crustacean interactions, we have covered the entire macroscopic community except for the predaceous salamander *Gyrinophilus porphyriticus*, the uncommon crayfish *Cambarus*, the occasionally abundant flatworm *Sphal*-

loplana virginiana, and occasionally abundant snails of the genus *Fontigens*.

The Model

From the previous discussion of the distribution patterns of the species, any model must account for both the exclusion of species within a patch of habitat and the uncertain distribution of species among the patches. The most convenient starting place is a model that allows the proportion of patches occupied by a species to be determined by a balance between extinction and migration rate (Levins and Culver 1971). The first problem is to decide what size scale to use. Since the actual interactions between individuals occur within a patch of habitat, an islandlike system of a series of rocks in a riffle will be analyzed.

The basic equation for the rate of change of the number of rocks occupied by a species (N) in the absence of competitors is a function of migration rate (m) and extinction rate (x_0) .

$$\mathrm{d}N/\mathrm{d}t = f(m, x_0, N) \ .$$

For a rock about 1 cm in diameter, it is almost always true that there is only place around it for one animal to avoid the current (Culver 1970b). Larger rocks basically consist of a series of hiding places separated by spaces where the animals are exposed to the current. Thus each patch has either none or one individual, and one extinction occurs every time one individual washes out of the riffle. On the other hand, successful movement from one rock to another rock within the riffle is one migration and one extinction. Therefore, there must be other sources of both migration and extinction. There are two sources of migration: birth and emigrations. Both of these will take the form

m'N(T-N)

in the growth equation where T is the number of rocks. For births, m' would be equal to r/T, but the situation is less clear for emigrations. At first glance it would appear that the migration rate into a riffle would be m'(T-N), which is a constant times the number of empty spaces. However, riffles differ in the current speed and this profoundly affects the emigration rate. The best way to measure this is to know \hat{N} , the number of spaces occupied at equilibrium. Except for a 50-day recovery period after the high washout accompanying spring thaw runoff, N will be close to \hat{N} (Culver 1971b). Therefore our best estimate of the form of the differential equation is

$$dp/dt = mp(1-p) - g(x,p)$$

where p is N/T, m = m'T, and g is a monotonic decreasing function of p.

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The form of the second term, which reflects the loss of animals from the riffle, will not be linear. In previous experiments with the washout rate in an artificial stream, *Gammarus minus* had a washout rate proportional to the square of the density (Culver 1971*b*). The biological meaning of this is that washout usually occurs when two individuals meet. Therefore the simplest form of the equation that is realistic is

$$dp/dt = mp(1-p) - x_0 p^2$$
. (1)

At equilibrium

$$\hat{p} = m/(x_0 + m)$$
. (2)

When the proportion of occupied rocks is small, as it is for most cave populations, m will be small compared to x_0 .

The most reasonable interpretation of competition is that it increases washout rate. When two individuals are put in a finger bowl with one rock, one individual will drive the other off. If this occurs in running water, it increases the washout rate. Let $q = N_2/T$, and x_1 the washout rate when the second species is present:

$$dp/dt = mp(1-p) - p(qx_1 + px_0) .$$
 (3)

At equilibrium

$$\hat{p} = (m - x_1 q) / (x_0 + m)$$
. (4)

If we define the competition coefficient α_{pq} as $\frac{-\delta \hat{p}}{2q}$

(Levins and Culver 1971)

$$\frac{-\delta\hat{p}}{\delta q} = \frac{x_1}{x_0 + m} \ . \tag{5}$$

Equation (4) can be written in the form of Lotka-Volterra equations:

$$\frac{dp}{dt} = mp \left[\frac{\frac{m}{m+x_0} - p - \frac{x_1}{x_0 + m} q}{\frac{m}{m+x_0}} \right].$$
 (6)

Note that $K(=m/(m+x_0))$ is not independent of r(=m), and α is not independent of either K or r. The interconnection of these three variables seems intuitively more realistic than independence of the three variables.

Let us reconsider the nature of x_0 and x_1 . Washout is caused by failures of an individual to get under a rock, which is largely a matter of the physical presence of another individual taking up the hiding place. So it is unlikely that x_1 will be much less than x_0 , and will be greater whenever there is interspecific avoidance. So, coexistence in the same patch is unlikely except when the migration rate is high. We can make this more precise. If current is reduced, both x_1 and x_0 will be reduced by some quantity a. Then

$$\alpha'_{pq} = \frac{x_1 - a}{x_0 - a + m} .$$
 (7)

If resource levels are increased by the same amount, m will be increased because birth rate will increase. Then

$$\alpha''_{pq} = \frac{x_1}{x_0 + m + a} .$$
 (8)

Dividing and rearranging terms,

$$\frac{\alpha'_{pq}}{\alpha''_{pq}} = 1 + \frac{-2ax - a(x_0 + m + a)}{x_1(x_0 + m - a)} < 1.$$
(9)

So, increasing migration rate decreases α_{pq} more than decreasing extinction rate by the same amount. Therefore, the scale of separation should be less in areas of high food input than in areas of low current. In Gollahan Cave no. 1 we find the predicted pattern (Fig. 3). Asellus recurvatus and Lirceus sp. n. show more spatial separation in the area of low current than in the area of high food input.

Some separation within the riffle is possible if the rocks in the riffle are of different sizes and one species goes to large ones while the other goes to small ones. Let θ be the rate of avoidance of one size class of rocks. Then

$$\frac{dp}{dt} = mp(1-p) - p[x_1q(1-\theta) + px_0] \quad (10)$$

$$\alpha_{pq} = \frac{x_1}{x_0 + m} (1 - \theta) .$$
 (11)

This strategy usually involves size differences. The most striking case of this strategy is the larger *Stygonectes emarginatus* preferring larger gravels and the smaller *Stygonectes spinatus* preferring smaller gravels in Greenbrier Valley caves (Culver 1970b).

Thus, the model predicts that the microdistribution of each species will be uncertain, and that coexistence in the same riffle will be uncommon. However, we have no predictions concerning why some species pairs can coexist in the same cave and others cannot. To do this we must consider a model where each riffle is considered a patch. Let m^* be the colonization of empty riffles, and x_0^* and x_1^* be the rate of washout of all the individuals from one riffle. For this model, we assume that extinction is a linear function of the proportion of occupied riffles. It makes no sense to talk of the square of the frequency of occupied riffles as this would imply that animals in different riffles interact to cause washout. Thus

$$\frac{\mathrm{d}p}{\mathrm{d}t} = m^* p(1-p) - p[qx_1^* + (1-q)x_0^*]. \quad (12)$$

Remember that p is the frequency of occupied riffles rather than the frequency of occupied rocks. The properties of eq. (11) have already been worked out (Levins and Culver 1971) so I will only repeat the relevant results. The competition coefficient is

$$\frac{-\delta p}{\delta q} = \frac{x_1^* - x_0^*}{m^*} \,. \tag{13}$$

Note that washing from one riffle to another riffle is not an extinction. The washout rates x_0^* and x_1^* should be proportional to the within-riffle washout rates x_1 and x_0 if either washout results in considerable mortality or if the distance washed is considerable.

If we compare a pair that coexists in the same cave with a pair that cannot coexist, the pair that cannot coexist in the same cave should have one or more of the following characteristics, all of which will increase x_1^* :

- 1) The washout rates will be greater.
- 2) The distance washed out will be greater.
- 3) Mortality will be greater.

TESTING THE MODEL

The extinction rates x_0 of each species are measured by putting 10 animals in a section of gravel 15 cm long and 30 cm wide in an artificial stream (Culver 1971b), and counting the number washed out after 24 hr. This number divided by 10 gives the extinction rate per individual per day. The washout rate in the presence of the competing species was measured by putting five individuals of each species in the artificial stream and counting the number washed out after 24 hr. However, this number, call it z, is a mixture of washouts caused by intra- and interspecific contacts. It is easily seen that $x_1 =$ $(2z/10) - x_0$. The washout rates of Asellus holsingeri and A. scrupulosus from the Greenbrier Valley and Crangonyx antennatus, A. recurvatus, and Lirceus from the Powell Valley will be measured. Asellus holsingeri and A. scrupulosus do not occur in the same cave; Lirceus and A. recurvatus occur in different patches of the same habitat; Lirceus and C. antennatus occur in different habitats; and C. antennatus and A. recurvatus either occur in different habitats or in different patches of the same habitat.

The effect of distance on washout rate will be tested by doubling the length of the gravel in the artificial stream. Mortality in washout will be estimated by examining differences in appendage length compared to body length, which should reflect susceptibility to injury. Only the four isopod species will be used for these two tests in order to minimize differences cause by large differences in taxonomic position.

Table 5 gives the results of the washout experi-

 TABLE 5. Washout frequency of various species combinations from the Powell Valley after 24 hr in a 15-cm section of gravel in an artificial stream

Species	Other species present	Mean fraction washed ou	t Range	<i>x</i> ₁
C. antennatus	— A. recurvatus Lirceus	0.80ª 0.80 0.93	0.70-0.88 0.80-0.80 0.80-1.00	0.80 1.07
A. recurvatus	— C. antennatus Lirceus	0.77ª 0.53 0.93	0.70-0.80 0.40-0.60 0.80-1.00	0.30 1.01
Lirceus	— C. antennatus A. recurvatus	0.45ª 0.40 0.33	0.40-0.50 0.20-0.80 0.20-0.40	0.52 0.22

NOTE: Each combination was run three times. See text for details on how x_1 (washout rate when a second species is present) was calculated. • Equals x_0 .

ments with *C. antennatus*, *A. recurvatus*, and *Lirceus* from the Powell Valley. It should be recalled that we have no way of measuring *m*, although it should usually be small compared to x_0 because *p* is small (see eq. (2)). There appear to be no gross differences in *r*, which determines *m* at least in part. The percentage of ovigerous females at any one time is low for all three species, and the average clutch size is about the same (12–30). If we assume that *m* is equal to 0.01 for all three species, the following matrix of competition coefficients is obtained:

C. antennatus	L 1.00	0.99	1.327
A. recurvatus	0.32	1.00	1.29
Lirceus	1.16	0.49	1.00

These should be viewed as maximum values of α because α will be reduced whenever *m* and therefore \hat{p} become much greater than zero.

There are several points of agreement with field data. First, since Lirceus and C. antennatus barely coexist in the same cave (Fig. 1), we would expect the product of their competition coefficients $(\alpha_{13}\alpha_{31})$ = 1.53) to be higher than the other two symmetric pairs, which it is. We would also expect it to be greater than one because C. antennatus is nearly excluded from caves where Lirceus is present. Since Lirceus and A. recurvatus only coexist in areas where m is high (Fig. 2), we would expect that the product $\alpha_{23}\alpha_{32}$ be intermediate between the value of the product of the other two symmetric pairs of alphas, and greater than one when m is small. It is intermediate but less than one (0.64) when m is small. The product of α_{12} and α_{21} (A. recurvatus and C. antennatus) should be less than one since the species often coexist in the same cave. This is also the case $(\alpha_{12}\alpha_{21} = 0.38)$.

Second, values of α less than one involve species with different sizes so that $x_1/(x_0 + m)$ is probably close to one for all species, but θ is greater than zero

TABLE 6. Relationship between number of individuals (N), washout rates of the species when alone (x_0) , and the "community effect" $(C_i = \sum_{j \neq i} \alpha_{ij})$

Species	Ν	<i>x</i> ₀	C_i
C. antennatus	13	0.80	2.33
A. recurvatus	110	0.77	1.67
Lirceus	400	0.45	1.65

TABLE 7. Washout frequencies of *Asellus holsingeri* and *A. scrupulosus* alone and together after 24 hr in a 15-cm section of gravel in an artificial stream

Species	Other species present	Mean fraction washed out	Range	<i>x</i> ₁
A. holsingeri		0.23ª	0.20-0.30	
0	A. scrupulosus	0.40	0.40-0.40	0.57
A. scrupulosus	·	0.27	0.20-0.30	
-	A. holsingeri	0.93	0.80-1.00	1.59

NOTE: Each combination was run three times. See text for details on how x_1 (washout rate in the presence of the other species) was calculated. • Equals x_0 .

in some cases where there are size differences. The effect of *C. antennatus* on *A. recurvatus* (α_{21}) and the effect of *A. recurvatus* on *Lirceus* (α_{32}) are the only values much less than one (Table 7). *C. antennatus* and *Lirceus* are about the same size at maturity (6–7.5 mm), while *A. recurvatus* is much larger (10–13 mm), and both alphas less than 1 involve the larger *A. recurvatus*.

Finally, we can say a few things about what controls the population size. Population size is both inversely correlated with washout rates when alone, and inversely correlated with "community effect" (Table 6). Community effect (C_i) (see Vandermeer 1972) is the sum of the effect that other species have on the species under consideration, and is equal to

$$C_i = \sum_{j \neq i} \alpha_{ij} \,. \tag{14}$$

Similar experiments were done with A. holsingeri and A. scrupulosus from the Greenbrier Valley in West Virginia, and the results are given in Table 7. Remember that these two species do not occur in the same cave. If we assume once again that m is small and equal to 0.01 for both species, the following maximum estimates of α are obtained:

Α.	holsingeri	$\Gamma^{1.0}$	2.46-
Α.	scrupulosus	5.68	1.0

The effect of *A. holsingeri* on *A. scrupulosus* is more than twice the effect of *A. scrupulosus* on *A. holsingeri*, and this may explain why *A. scrupulosus* is found in fewer caves than *A. holsingeri* (Table 1). In addition, *A. scrupulosus* is usually found in caves with high levels of organic input (e.g., Buckeye Creek Cave in Greenbrier County) and it is possible that *A. holsingeri* cannot do well in such caves. Therefore, *A. scrupulosus* may be limited to caves that are marginally inhabitable by *A. holsingeri*. *Asellus scrupulosus* does occasionally survive in caves with low amounts of organic input (Table 2), so it is not physiologically limited to caves with high organic input.

Since the alpha values for A. holsingeri and A. scrupulosus are much higher than for the species from the Powell Valley, this is at least a partial explanation of why A. holsingeri and A. scrupulosus do not occur in the same cave. Asellus holsingeri and A. scrupulosus do not have proportionally longer appendages than *Lirceus* and *A. recurvatus* and so do not appear to be more susceptible to injury and mortality. Asellus recurvatus (Steeves 1963b) and A. holsingeri (Steeves 1963a) have longer appendages than A. scrupulosus (Williams 1970) and Lirceus (personal observation). When the length of the gravels in the artificial stream increased from 15 cm to 30 cm, all of the isopods except A. scrupulosus showed a reduction in washout rate (Table 8). Thus, A. scrupulosus, when it is dislodged in the current, goes farther than the other three species. Since both A. holsingeri and A. scrupulosus do not drift farther when dislodged, differences in distance moved between the Greenbrier Valley and Powell Valley isopods are not sufficient to account for distributional differences. Differences in α itself seem sufficient to account for distributional differences, although the longer distance moved by A. scrupulosus when dislodged would enhance the separation of A. scrupulosus and A. holsingeri.

DISCUSSION AND SUMMARY

The model presented above almost completely describes and predicts the distribution and codistribution of the aquatic cave species studied. Thus the model predicts that species distribution will be uncertain and that two species will not coexist in the same habitat patch unless there are large size differences between the two species. The model allows us to order the amount of overlap from the value of the product of the competition coefficients determined by independent laboratory experiments. It also appears that exclusion on the scale of entire caves is primarily due to larger values of α for withinriffle competition rather than increased mortality or greater distances moved when dislodged. Finally, details of microdistribution can be predicted by the model. For example, overlap is greater in areas of high food than in areas of low current (Fig. 2).

One important item that the model gives no direct prediction for is the number of species in a community. If some way could be devised for directly measuring the parameters in eq. (13), a prediction could

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 TABLE 8. Washout rates of Asellus holsingeri, A. scrupulosus,

 A. recurvatus, and Lirceus after 24 hr in a 15-cm and 30-cm

 section of gravel in an artificial stream

			A Second se	
	Stream		x	o for 30 cm
Species	(in cm)	<i>x</i> ₀	Range x	₀ for 15 cm
A. recurvatus	30	0.47	0.40-0.50	0.61
A. recurvatus	15	0.77	0.70-0.80	0.61
Lirceus	30	0.30	0.30-0.30	0.67
Lirceus	15	0.45	0.40-0.45	0.6/
A. holsingeri	30	0.15	0.10-0.20	0.65
A. holsinge r i	15	0.23	0.20-0.30	0.65
A. scrupulosus	30	0.25	0.20-0.30	0.00
A. scrupulosus	15	0.27	0.20-0.30	0.93

NOTE: All species were run three times at each stream length except for A. holsingeri and A. scrupulosus in the 30-cm stream, which were run twice.

be obtained. Using a more naive approach to competition at this level in an earlier paper (Culver 1970b), I was able to predict a maximum of 4-5aquatic species, which agrees well with field data. Until a way is devised for directly measuring washout rates from a series of riffles, my previous work based on traditional Lotka-Volterra equations is the only available theoretical estimate for the maximum number of species in these particular communities.

It could be argued that more data are needed before these results are definitive. However, most of the species studied are uncommon in any particular cave or have a very local distribution. Since amphipods and isopods tend to lose appendages from being washed out of the artificial stream and from repeated manipulations, most individuals cannot be used in more than two artificial stream experiments. Thus, large numbers of organisms must be collected. In my last three trips to the Greenbrier Valley I have collected every A. scrupulosus I was able to find. Repeated collecting does have a deleterious effect on populations. Researchers on cave bats, in a 1971 AAAS symposium, presented grim evidence of the toll bat researchers themselves have taken of bats in North America. I hope we can avoid similar problems with aquatic cave invertebrates. Therefore, I have only done those experiments that I believe to be absolutely necessary to demonstrate my points. Since different experiments almost invariably gave nonoverlapping results, I did few replicates of each experiment.

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