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**POSSIBLE COLONIZATION STRATEGIES OF SOME
CARABID BEETLES INHABITING STREAM SHORES
(COLEOPTERA: CARABIDAE)**

Paul M. Holeski¹

ABSTRACT

Certain species of insects appear to be better adapted by virtue of their particular strategy to survive disruption of the habitat than do others sharing the same area. *Bembidion impotens*, a carabid beetle, was especially successful in rapidly recolonizing a defaunated stream shore and in maintaining a relatively high population when the habitat was subjected to normal but severe disruption.

In order to be successful, organisms that inhabit areas subject to disruption must either have the ability, once favorable conditions are restored, to repopulate the area quickly by invasion from an undisturbed area, or enough members of a population must be able to survive the disturbance to repopulate it when normal conditions return. The first of these strategies could be considered to be r-selected. The r-selected species are those which invade and populate ecological "islands" and they have been variously called "fugitive" (Hutchinson 1951), "opportunistic" (MacArthur 1960), "colonizing" (Lewontin 1965), and "tramps" (Diamond 1975). Species using this strategy are considered by various authors to possess, among other characteristics, high reproductive capacity (Force 1974) and poor competitive ability, and to live in areas with unstable climate (Pianka 1970). Barbosa (1977) provides a good review of the characteristics of this strategy as well as those of the contrasting K-strategy, exemplified by species living in habitats of stable, benign conditions.

Greenslade (1972) introduced the concept of a "beyond K" strategy existing in environments which, like the "r" environments, had rather severe limiting factors, but, unlike the "r" environments, were highly stable and somewhat predictable. The stability permits species to become closely adapted to the habitat like those of a "K" environment, while the severity of the limiting factors prevents other species from becoming established. In addition, the specialized adaptations evolved by the beyond K-strategists, required to overcome the severity of the environment, also enable them to successfully outcompete most potential invaders (Matthews 1976). The beyond K-strategy is reported to be evident in species inhabiting caves, mountain streams, intertidal zones, and others (Matthews 1976).

In reality there are probably no absolute criteria by which an organism can be designated as a particular strategist. Pianka (1970) emphasized the relative nature of the selection strategies and stated that, rather than absolutes, there is an r to K continuum with particular organisms occupying positions along it. He did, however, list some general characteristics of organisms possessing the strategies and characterized some groups as being primarily one or the other. For example, terrestrial vertebrates were described as K-selected, while insects were described as being r-selected. Theoretical discussions of colonization models and species-equilibrium models may be found in MacArthur and Wilson (1967), Pianka (1976), and Stubbs (1977), among many others.

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Organisms that occupy the narrow zone of stream shore between permanent vegetation and the water of the stream must contend with periodic disturbances in the form of, among others, flooding and drought. These disturbances may have some pattern of regularity, such as spring floods and late summer drought as would occur in many temperate zone streams, but may also be irregular, such as the results of heavy rainfall or lack of rainfall when seasonal conditions are normally otherwise. The unusual conditions may be widespread, affecting many streams in the area, or may be restricted due to localized storms, or, for example, conditions below dams or other water control facilities.

This paper briefly considers one aspect of the community of beetles that occurs on the stream shore, the colonization by the insects of a defaunated shore. Because the shore is bordered on one side by an aquatic habitat and on the other by a much different terrestrial habitat, it can be considered to be an "island" between the two, albeit an extended one. Community, in this instance, follows the definition of Force (1974) as an aggregate of species living together. On the specific shores discussed in this report, the community consisted of numerous individuals of three families of beetles: Carabidae, Staphylinidae, and Heteroceridae. Other insect groups, principally Diptera and Hemiptera, as well as other invertebrates also inhabited this environment, but made up only a small portion of the immediate invertebrate biomass and are not included in this report.

METHODS

The study area was a stream in northwest Ohio, the Middle Branch of the Little Auglaize River, also called Middle Creek. The actual study site was located approximately 3 km northeast from the confluence of Middle Creek and the main channel of the Little Auglaize River. Two other streams, also tributaries of the Little Auglaize River, were located within 5 km of the site.

During 1972 Middle Creek underwent a major channelization. In this process, the banks were cleared of vegetation, the channel cut deeper and to uniform widths (18 m wide at the study site), and the sharp curves were eliminated by modifying the old channel. In some places such as the study site, a completely new channel was constructed. Because in this modification project, construction was taking place at approximately the same time over several kilometers of the stream, either the entire stream shore essentially was being defaunated or the shore was being newly created.

Samples of the adult fauna were collected by taking all those individuals on the surface or that could be forced to the surface by heavy splashing within two 0.092 m² (1 ft²) areas selected at random along a limited area of shore. An initial sampling was made in late May 1972, immediately before excavation activity began. Due to the construction work in progress no further samples were taken at the site until September, two weeks after excavation was completed. Cold temperatures curtailed insect activity and no additional samples were taken in 1972. Sampling resumed the next spring and was conducted at approximately two-week intervals throughout the 1973 season of activity and again in 1974. Five additional sites, four on the streams closest to the channelized study site and the other on an unchannelized portion of Middle Creek, approximately 9.5 km upstream from the study site, were also sampled. Samples were taken at these sites on the same day, or within a day or two of the sample taken at the channelized site. Collecting hours were staggered so that each site was sampled at several times during the diurnal period throughout the season.

After sorting and determination, quantitative diversity analyses using the Margalef (1951) and Shannon-Weaver (1963) formulas were performed on the data. In addition, because quantitative analyses can provide information measurements of the numbers of taxa and the relationships of these numbers in a given area, but do not provide any information about the similarities of the taxa themselves, a coefficient of similarity (C.S.) analysis based on Estabrook (1973) was used as a measure of the qualitative relationships among the species and individuals making up the community.

RESULTS AND DISCUSSION

The 30 May 1972, pre-channelization sample at the primary Middle Creek site resulted in the capture of 13 individuals in seven species. The 30 September 1972, post-channelization sample at the same site produced 16 individuals in seven species. Individuals of one species, *Tachys vivax* LeConte (Coleoptera: Carabidae) were present at the site both pre- and post-channelization. The other six species present in the sample before construction were replaced by six different species in the post-channelization sample. In this latter sample, eight of the 16 individuals were *Bembidion impotens* Casey (Coleoptera: Carabidae). All other species were represented by one or two individuals. No species of the family Heteroceridae were represented in the post-channelization collection, although two species were present in the early season collection before channelization.

Eight collections from the channelized site were made at approximately two week intervals throughout 1973, from 13 July on. Attempts to sample earlier were prevented by flood waters which inundated the shore area continuously from April through early July. A total of 169 individuals belonging to 17 species was collected in these samples. Seventy-six individuals (45%) were *B. impotens*. Other species were represented by from 1 to 20 individuals. The greatest number of species taken in any one collection during the season was 11. Although some of the species were present in most of the samples taken throughout the season, there was considerable disappearance and replacement of species.

Eight collections at this site were also made from 27 April through 31 October 1974. During this year 121 individuals of 19 species were collected. Again the most abundant species was *B. impotens*, represented by 37 individuals (31%). One other species, as yet undescribed, was present in large numbers (24), while all other species were represented by from 1 to 15 individuals.

In the MacArthur-Wilson model there is a continuous process of extinction and invasion of species in the ecological islands; species diversity at any point is a balance between these forces of invasion and extinction, and represents a state of flux rather than a continuity. On the stream shores described in this report it was observed that individuals of a particular species could appear, disappear, and sometimes reappear from sample to sample. This phenomenon was produced, in part, it is believed, by an actual colonization and replacement of species at the channelized site. The theoretical values of the particular C.S. index used could range from 0 (no species shared) to 1.0 (all species shared and number of individuals in each species approximately equal). In this study, because of the low number of species and individuals involved, it was necessary to pool the samples. This was accomplished by subdividing each season into three periods: April-June, July-August, and September-October. In addition, all of the individuals collected at a site in one season were pooled and compared with each of the pools of the other two yearly total collections. The results of the quantitative analysis are shown in Table 1, while the results of the qualitative analysis are shown in Tables 2 - 3.

Sample data at the end of the second year showed that the species numbers remained nearly the same, but there had been a high rate of species turnover resulting in a very different species composition from that of the first year. Only 35-52% of the total species were common to the censuses of the first and second year.

It would be difficult to construct a species colonization curve for this present report, at least for the immediate period following stream channelization due to the termination of construction close to the end of the season of activity of the insects. Nonetheless, it can be seen that the turnover of species following channelization of the test site existed to a greater extent than at the other nearby control sites. This is especially evident in the first full season (1973) following channelization. As shown in Table 2, the C.S. index value of species and numbers of individuals for the three base periods throughout the season of activity was only 0.259 at the channelized site, while at all but one of the other sites, values ranged from 0.546 to 0.747. However, by the next season the community at the Middle Creek channelized site appeared to have stabilized and a high C.S. value (0.793) was obtained.

Table 1. Summary of quantitative diversity index values.

Middle Creek ^a	Little Auglaize River	West Branch	Prairie Creek	Middle Creek ^b	Dog Creek
1972					
3.56 ^c	5.96	4.80	4.65	5.58	5.63
2.23 ^d	2.85	2.61	2.49	2.82	2.84
1973					
3.12 ^c	3.80	4.42	5.15	4.20	5.18
1.92 ^d	1.98	2.15	2.34	2.17	2.23
1974					
3.75 ^c	5.37	4.77	4.45	5.22	4.84
2.24 ^d	2.45	2.30	2.10	2.47	2.39

^aChannelized

^bUnchannelized

^cMargalef (1951) index.

^dShannon-Weaver (1963) index.

Table 2. Mean coefficient of similarity (Estabrook 1973) based on seasonal comparisons. Each collecting season was divided into three seasonal periods: April–June, July–August, September–October; and the species composition of each of the periods compared for similarity. The higher the value, the more similar the composition of species.

Sample station	1972	1973	1974
Middle Creek, channelized	0.264	0.259	0.793
Little Auglaize River	0.684	0.747	0.678
West Branch	0.747	0.661	0.713
Prairie Creek	0.236	0.178	0.793
Middle Creek, unchannelized	0.638	0.724	0.603
Dog Creek	0.644	0.546	0.649

Table 3. Coefficient of similarity (Estabrook 1973) for yearly data. Values were determined by comparing the species composition at a sampling station each year with the species composition at the same station each of the other two years.

Sample station	1972, 1973	1972, 1974	1973, 1974	Mean
Middle Creek, channelized	0.724	0.672	0.690	0.695
Little Auglaize River	0.569	0.709	0.552	0.609
West Branch	0.552	0.534	0.534	0.540
Prairie Creek	0.483	0.638	0.672	0.598
Middle Creek, unchannelized	0.603	0.621	0.655	0.626
Dog Creek	0.586	0.517	0.586	0.563

FROM WHERE DO THE COLONISTS COME?

As previously stated, the insect communities that exist on the shores of streams are subject to periodic disruption. Unfortunately very little is known about the life cycles and the reproductive strategies of the riparian species, but it is probable that some aspects of both a beyond K and an r-strategy are involved in maintaining the community.

Most of the carabid beetles are believed to be spring breeders, that is, they overwinter as adults and then reproduce from spring to early summer with a new generation appearing in autumn. Lehmann (1965) found that carabid beetles were unable to survive the winter in shore areas of the Rhine which were affected by winter floods. The adults must fly away before winter and return in the spring. Species which were autumn breeders, overwintering as larvae, could not survive in the shore area. The results of several other studies also supported this observation (Theile 1977). This would seem to indicate an r-strategy by these species, with the new generation bound to colonizing a new area each season. In contrast, studies in northern Norway indicated that up to 25% of the species living on river banks were those which were autumn breeders overwintering as larvae (Anderson 1968). Anderson believed that both adults and larvae were capable of surviving the cold flood waters of the rather short duration spring floods of that area, the remaining 75% + being spring breeders. Unfortunately, the reproductive patterns of the Heteroceridae and the Staphylinidae are even less well documented.

The spring floods characteristic of the streams of the area considered in this report are usually of long duration, often several weeks, and usually inundate the area up to several meters from the stream channel. To survive this long period of inundation, the insects must either hibernate beyond the flooded area, which in most cases would place them in cultivated fields which are plowed after harvest and after the insects would go into hibernation, or they must hibernate on the stream shore and survive the long period of inundation. The latter is probable. Palmén (1949) found that some species of adult carabid beetles could survive submerged for over a month in cold water, and it is likely that both adult and immature stages could survive protected in hibernacula created in the fine particle soil typical of shores in northwest Ohio for the duration of the spring flooding. This would indicate a beyond K-strategy for these insects.

Many insects, including the shore-dwelling species, do have spring dispersal flights after emerging from hibernation. Larochelle (1978) noted that a common riparian species, *Bembidion minus* Hayward, among many others, dispersed in early spring in Quebec. It seems likely that should the inhabitants of a particular shore area be decimated by spring floods, migrants could repopulate the area.

Larochelle stated that the dispersal flights were restricted to the spring and were induced by warming temperatures. This observation does not seem to be the case in the present examination of the repopulation of the defaunated channelized stream shore. Many of the species present in 1973 could have and probably did arrive during the spring of 1973, but others arrived during the late summer of 1972, after channelization, and the turnover of species during the 1973 season of activity indicated that species must have arrived throughout the season. In this instance, as the original population had been destroyed, the presence of additional or different species throughout the season would have to come from new arrivals rather than from periodic emergences of adults all ready in the habitat. The colonizers had to originate several kilometers upstream or from one of the nearby streams, a minimum distance of over 1 km. Whether flights throughout the season were random or directed toward a habitat similar to the origin, and why they were made, is not known.

It does appear that one species in particular of those present was an excellent colonizer. As noted in the results, *Bembidion impotens* was the most abundant species at the channelized site in each of the three seasons of the study, declining in numbers each season post-channelization. This species was also a common inhabitant, but not the most abundant species, at any of the control sites except in 1973, a year when high flood waters persisted at all sites until mid-July. During this season, *B. impotens* was the most abundant species at three of the five control sites, but the number of individuals making up the percentage of the total did not approach the 45% found at the test site (Fig. 1). That this species was most abundant at some of the control sites in a season characterized by

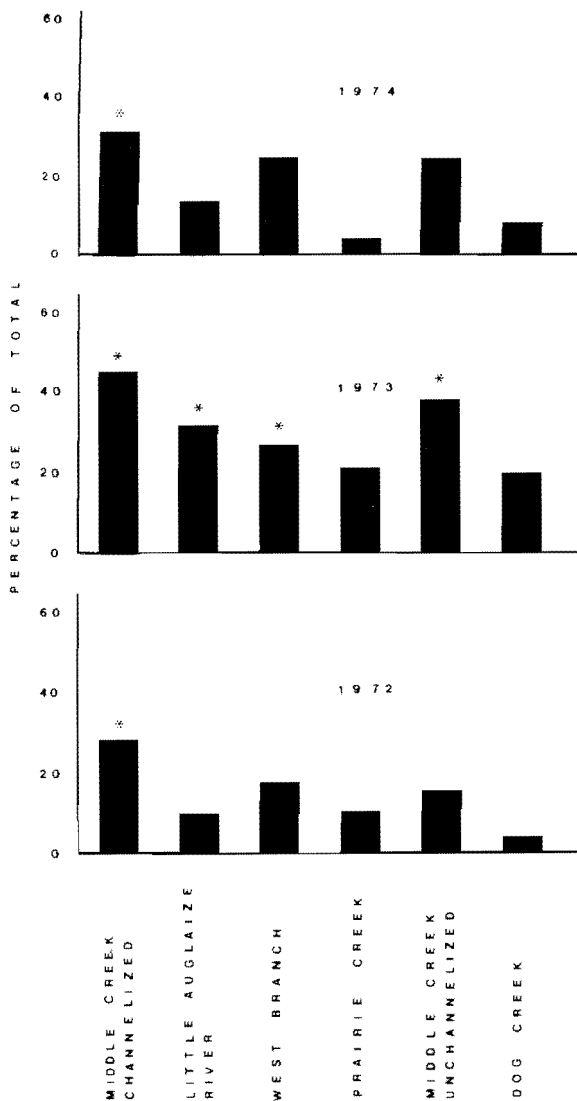


Fig. 1. Percentage of individuals of *Bembidion impotens* in relation to the total number of individuals of all species. * indicates that *B. impotens* was the most abundant species in number of individuals.

adverse conditions would seem to reinforce the opinion that it was an excellent colonizer. As in the MacArthur-Wilson model it seems to follow an r-strategy of being able to invade an area and build up a population, but as conditions stabilize and time progresses, it is replaced in importance by other species.

After sudden disruptions during the season of activity, such as summer floods, it is probably not necessary for colonizers to move into an area from other sources. Immatures

could probably survive in their chambers, although for not as long a period as under colder temperatures, at least the relatively short duration of these disruptions. Adults could survive in the soil or by flying from the area or by climbing exposed vegetation and debris. Many adult riparian species can take flight from water or are good swimmers, as noted by Joy (1910). Thus, some of the original inhabitants could survive and repopulate the disrupted area. In a previous paper, the term "perennial pioneers" was applied to the community of riparian species because they are forced to recolonize their habitat constantly (Holeski & Graves 1978). Although this would appear to involve a beyond K-strategy, the step to r-strategy of migrating to a new area of similar habitat, as in the case of a channelized stream, would not be great.

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