The hellbender (Cryptobranchus alleganiensis) is one of the largest salamanders in North America, growing up to 740 mm in length (Fitch 1947) during its 30 year plus life span (Taber et al. 1975). These purely aquatic salamanders can be found in large swift streams throughout the central Appalachians from southern New York to northern Georgia and in portions of the Ozarks (Fig. 1). A more solidly blotched subspecies, the Ozark hellbender (Cryptobranchus a. bishopi), occupies a smaller range in Missouri and Arkansas where it is apparently confined to the North Fork of the White River and a section of the Black River system. Some hellbender populations, particularly in Missouri and northwestern Pennsylvania, show great abundance (Hillis and Bellis 1971, Nickerson and Mays 1973a). Many investigators, however, have documented declines in populations throughout the range (Nickerson and Mays 1973b, Smith and Minton 1957, Swanson 1948) (Table 1). The status of headwater stream populations in the southeastern Atlantic states remains uncertain due to the lack of concentrated census efforts.

Habitat disruption by man is presumably responsible for the hellbender’s diminishing range. Two major categories of man-related habitat disruption are the submergence of swift water riffles by artificial impoundments and the addition of excess sediment load to moving streams (Nickerson and Mays 1973b). The hellbender is a habitat specialist. Its success is dependent upon the constancy of dissolved oxygen, temperature, and flow

1 Contribution No. 1114—AEL, Center for Environmental and Estuarine Studies, University of Maryland.
found in swift water areas. Such specialists achieve an evolutionary stability within their habitat that magnifies the effects of rapid habitat alteration. The hellbender is confined to a narrow niche by several adaptations of structure, behavior, and physiology brought about by its evolution in a relatively stable environment. It serves as a good example of how a specialist’s adaptive strategies can make it acutely vulnerable to man’s effects.

We would like to thank all the biologists who responded to our letters and telephone inquiries as to the status of the hellbender in their states. We especially thank S. Barkley, F. B. Barick, R. S. Caldwell, B. O. Freeman, T. D. Grelen, T. R. Johnson, J. Laerm, C. T. McAllister, C. J. McCoy, R. H. Mount, R. J. Nemecek, R. A. Pfingsten, M. E. Seehorn, and P. W. Smith. The manuscript was reviewed by R. P. Morgan II and G. A. Feldhamer. F. P. Younger prepared the distribution map. Financial assistance was provided by the Maryland Department of Natural Resources, Wildlife Administration, and the U.S. Fish and Wildlife Service through the Maryland Endangered Species Program.
Table 1. Status of hellbender populations in states throughout its range.

<table>
<thead>
<tr>
<th>State</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alabama</td>
<td>Uncertain: Found in Bankhead National Forest (M. E. Seehorn, U.S. For. Serv., unpubl. data) and Tennessee River drainage; nowhere abundant (Mount 1975).</td>
</tr>
<tr>
<td>Arkansas</td>
<td>Decreasing: Large populations of Ozark hellbender known only in Spring River. Populations in North Fork of White River presumably destroyed by impoundment (Nickerson and Mays 1973b). Recent investigations under guidance of Department of Biological Sciences, Arkansas State University (S. Barkley, Ark. Game and Fish Comm., pers. commun.).</td>
</tr>
<tr>
<td>Georgia</td>
<td>Uncertain: Recorded in upper headwaters of coastal streams (Firschein 1951). Most specimens from Tennessee River drainage. Current surveys by University of Georgia, Museum of Natural History (J. Laerm, pers. commun.).</td>
</tr>
<tr>
<td>Illinois</td>
<td>Endangered or extirpated: Historically known from Mississippi River tributaries. Nickerson and Mays (1973b) knew of no specimens collected since 1956.</td>
</tr>
<tr>
<td>Indiana</td>
<td>Endangered: Only remaining large population is in Blue River (Minton 1972).</td>
</tr>
<tr>
<td>Iowa</td>
<td>Extirpated: May never have been present (Nickerson and Mays 1973b).</td>
</tr>
<tr>
<td>Kansas</td>
<td>Uncertain: Records from Neosho River only (Hall and Smith 1947).</td>
</tr>
<tr>
<td>Kentucky</td>
<td>Decreasing: Known from Cumberland, Kentucky, and Licking rivers and Tripplet Creek (Barbour 1971). Many populations destroyed by impoundments and acid mine drainage. Being considered for population monitoring by Kentucky Nature Preserves Commission.</td>
</tr>
<tr>
<td>Maryland</td>
<td>Endangered: Historically known only from Youghiogheny and Susquehanna river drainages (Hardy 1972). Last verified sighting in Youghiogheny River by Maryland Department of Natural Resources was in 1969. Currently under study by University of Maryland, Appalachian Environmental Laboratory.</td>
</tr>
<tr>
<td>Mississippi</td>
<td>Stable: A population in Bear Creek, Tennessee River drainage, appears to be surviving (Ferguson 1961, C. T. McAllister, Dep. Biol. Sci., Ark. State Univ., pers. commun.). Has also been collected in Lewis Creek (B. O. Freeman, Miss. Game and Fish Comm., pers. commun.).</td>
</tr>
<tr>
<td>Missouri</td>
<td>Stable: Although completely isolated, the 2 subspecies are common in several streams of the Missouri Ozarks. Good populations of Ozark hellbender exist in Black River drainage and North Fork of White River (T. R. Johnson, Mo. Dep. Conserv., pers. commun.).</td>
</tr>
<tr>
<td>Ohio</td>
<td>Uncertain: Historically known throughout Ohio River drainage. Available habitat reduced by industrialization (Nickerson and Mays 1973b).</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>Stable: Historically known throughout Allegheny and Susquehanna river drainages according to Carnegie Museum of Natural History records. Despite pressure from acid mine drainage in western Pennsylvania, large populations occur in a number of localities.</td>
</tr>
</tbody>
</table>
Table 1. Continued.

<table>
<thead>
<tr>
<th>State</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tennessee</td>
<td>Stable: Reported to be common in sections of Cumberland and Tennessee river drainages (Gentry 1955). Some populations destroyed by impoundments, but others exist in Great Smoky Mountains National Park (Nickerson and Mays 1973b) and Cherokee National Forest (M. E. Seehorn, U.S. For. Serv., unpubl. data).</td>
</tr>
<tr>
<td>Virginia</td>
<td>Uncertain: Reported from New River (Hutchison 1956), Jefferson National Forest (M. E. Seehorn, U.S. For. Serv., unpubl. data), and Clinch River.</td>
</tr>
<tr>
<td>West Virginia</td>
<td>Stable: Common in Ohio River drainage, especially Cheat, Monongahela, New, and Little Kanawha rivers (Green 1933).</td>
</tr>
</tbody>
</table>

STRUCTURAL, PHYSIOLOGICAL, AND BEHAVIORAL ADAPTATIONS

A number of structural features illustrate the hellbender’s adaptation to cool swift-water habitats. The adult body form is flattened dorso-ventrally, and it has an oar-like tail. This body shape, which is similar to the larval stage except for the absence of external gills, helps the hellbender remain immobile on the stream bottom despite swift currents. The tail performs a rudder function during swimming that is as effective in swiftly flowing water as in a lacustrian environment. It is, however, the hellbender’s dependence on highly vascularized lateral skin folds for respiration that limits its success in lake habitats. Investigators eliminated gills (Bishop 1941) and lungs (Hughes 1967) from consideration as primary respiratory organs. It became clear from the research of Bernstein (1953), Guimond (1970), and Noble (1925) that the vascularized dermal papillae of the lateral folds are major sites for cutaneous gas exchange. This respiratory strategy has 2 consequences. It limits the hellbender to fairly cool environments with well oxygenated water (Guimond and Hutchison 1973) and requires water flow over the skin. The hellbender exhibits a preferred mean temperature of 11.6 C, 17.7 C, and 21.7 C for acclimation temperatures of 5 C, 15 C, and 25 C, respectively (Hutchison and Hill 1976). The relatively lower dissolved oxygen levels found in warm or standing water do not provide enough countercurrent exchange to meet the hellbender’s respiratory needs. Hellbenders have been observed rocking or swaying in still warm water. This behavior has been linked to cutaneous respiration (Bishop 1941).

Hillis (1969) found that hellbenders prefer den sites under large flat rocks in water that is swifter and cooler than shore areas. Some 92.8% of hellbenders he captured came from water 12–46 cm deep, and 67.1% of these captures were made under rocks 56–109 cm in diameter. Individuals vacated home sites in shallower water in late summer to avoid higher shoreline temperatures. Hillis (1969) calculated a median activity radius of 6.0 m for the hellbender, indicative of a home range of approximately 100 m². This restricted home range demonstrates the hellbender’s behavioral dependence on den sites. These dens are used year-round for concealment during daylight (Nickerson and Mays 1973b) and for egg deposition, fertilization, and brood protection in late autumn (Smith 1907). The burial of these flat rocks by siltation de-
creases the hellbender's survival and reproductive success.

**EVOLUTION AND GEOGRAPHICAL DISTRIBUTION PATTERNS**

The family Cryptobranchidae is at a virtual evolutionary standstill. It has a relict distribution typical of amphibian groups that are not currently undergoing rapid dispersal or evolution. Cryptobranchids were distributed throughout Europe, North America, and Asia during the late Miocene (Meszöly 1966) but are represented today by only 2 isolated species, *Cryptobranchus alleganiensis*, and the giant Japanese salamander, *Andrias japonicus*. Meszöly (1966) presented further evidence of the cryptobranchids' evolutionary impasse by reassigning all North American fossils and the extant Japanese salamander to the European fossil genus *Andrias*.

It has been widely accepted that the hellbender's continent-wide distribution was severely restricted by Pleistocene glaciation. Firschein (1951) suggested that the Ozarkian and Appalachian Highlands served as southern refugia during glaciation. The present arrangement of the Ohio, Monongahela, and Allegheny rivers was formed by the receding glacier (Hocutt et al. 1978), and the hellbender used this newly available habitat as an avenue of northward post-glacial dispersal. It previously has been thought that hellbenders entered the Susquehanna River via stream capture from Allegheny headwaters (Firschein 1951). Recent evidence, however, points to the possibility that allopatric hellbender populations might have survived in the lower Susquehanna River during glaciation. During the Pleistocene, there was repeated formation and destruction of dispersal barriers that could have isolated many aquatic organisms (Briggs 1979). Biochemical analysis of extant hellbender populations has provided some evidence for such an occurrence (Merkle et al. 1977).

**COMPARATIVE BIOCHEMISTRY**

Electrophoretic data have been useful in studying the time of divergence of discrete stocks (Avise 1975). Merkle et al. (1977) found that a Susquehanna population of *Cryptobranchus a. alleganiensis* had a significant electrophoretic difference from Mississippi basin populations of the same subspecies. They considered this variation to be more significant than the differences they found between the 2 subspecies. This conclusion is certainly consistent with our suggestion that the Susquehanna hellbender populations may be of pre-Pleistocene origin.

Although the hellbender's biochemical pattern, as determined by electrophoresis, could be related to factors other than environmental ones, it is consistent with the role of a habitat specialist. There is a large degree of genetic uniformity throughout the hellbender's range that is rare in continent-wide species (Merkle et al. 1977). Analysis of 243 species of plants and animals suggests that the uniformity of their genetic pattern does not vary randomly, but is correlated with habitat types, life zones, and other ecological considerations (Nevo 1978). Nevo (1978) stated that specialization appears to be linked with low genetic variability. The hellbender is a specialist that exhibits extremely low variability. The ecological variability that encourages habitat generalism and high genetic variation (Nevo 1978) in many temperate species is not present in the hellbender’s uniform stream habitat.
CONCLUSIONS AND RECOMMENDATIONS

The hellbender can be characterized as an animal whose adaptation to a constant environment has led to a number of niche-narrowing structural, behavioral, and physiological specializations. Furthermore, it appears that this strategy has removed the hellbender from much of the ecological variation that serves to maintain genetic variability within a species. The effect of man's habitat alterations on the hellbender's range has been swift and, in many cases, irreversible. When assessing our future impact on any ecosystem, care must be taken to identify those animals that are habitat specialists, because the cost of their specialization is an inflexibility towards environmental change.

Management of these specialists is a challenge that can be met with 3 well-known wildlife research procedures. The initial step requires a survey designed to determine the animal's distribution and abundance. Protection of existing habitat takes on increased importance for niche specialists and is the critical second step now needed for hellbender management. Identifying the niche parameters that determine a particular animal's survival and reproductive success is the third step. The biology of the hellbender, like many nongame species, is not as well known as that of commercially important animals. Although information exists on tolerances to certain environmental factors, detailed studies on population dynamics over a wide range of conditions are not yet available. Because the hellbender lives 30 years or more, its mere presence is an incomplete indicator of habitat quality. The monitoring of populations in different stream habitat conditions over a number of years is necessary to completely access the health of this species.

Tributaries and entire watersheds where hellbender populations have been extirpated by man-related pollution may never be repopulated even if habitat quality is improved. This result could be due to the absence of a source of recolonizing individuals. For instance, populations destroyed above stream impoundments may never return, even after water quality has improved, because the dam and lake may function as a barrier to dispersal from below the dam. In this case, relocation could be a viable, cost-effective, management option. In any event, it is a much better management strategy to protect existing populations rather than to correct the situation after the damage has been done.

LITERATURE CITED

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Received 4 August 1980.
Accepted 6 November 1980.