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3-yr drought, but this was due to a reduction in crayfish trapping (J. B., personal observations).

Family Cryptobranchidae

Cryptobranchus alleganiensis (Daudin, 1803)

HELLBENDER

Christopher A. Phillips, W. Jeffrey Humphries

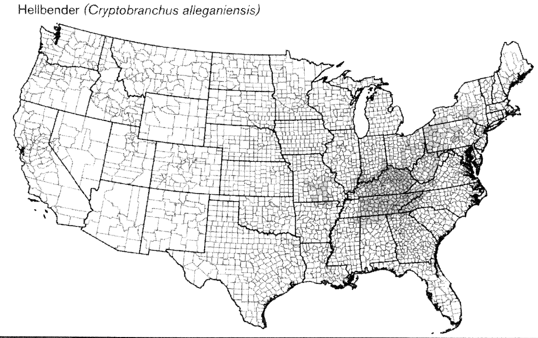
1. Historical versus Current Distribution. Historically, eastern hellbenders *(Cryptobranchus a. alleganiensis)* were found in the Susquehanna system (Atlantic drainage) in New York, Pennsylvania, and Maryland; tributaries of the Savannah River (Atlantic drainage) in South Carolina and Georgia; the Tennessee system in Georgia, Virginia, Alabama, Mississippi, Tennessee, North Carolina, and Kentucky; and the Ohio system in New York, Maryland, Pennsylvania, Virginia, West Virginia, Ohio, Indiana, Kentucky, and Illinois. A second cluster of populations inhabits portions of the Missouri drainage in south-central Missouri and the Meramec (Mississippi drainage) in eastern Missouri. Ozark hellbenders *(C. a. bishopi)* are found in the White River system in southern Missouri and north-central Arkansas. Cope (1889) listed a specimen in the U.S. National Museum from Des Moines, Iowa, and Firschein (1951b) mentioned an unverified record from the Skunk River (Mississippi drainage) in southeastern Iowa. Others have referred to the hellbender's presence in Iowa (e.g., Hay, 1892; McMullen and Roudabush, 1936), suggesting that Iowa might be within the historical range. Firschein (1951b) convincingly discredited a specimen from Vernon County, Missouri (Arkansas drainage). Two specimens from the Neosho River (Arkansas drainage) in southeastern Kansas (Hall and Smith, 1947) have come under scrutiny. Based on the extreme hiatus between the Kansas records and the nearest verified records to the east, several authors have speculated that these specimens were either introduced (Smith and Kohler, 1977) or are otherwise invalid (Dundee, 1971). Records from the Great Lakes, Louisiana, and New Jersey are certainly invalid and represent introductions or confusion with other species (see summary in Nickerson and Mays, 1973a).

Because of the secretive nature of hellbenders and their confusion with mudpuppies *(Necturus maculosus)*, the present range is not known with certainty. They are no longer present in Iowa (if they ever occurred there), and they are almost certainly extirpated from the Ohio drainage in Illinois, although there is a verified 1991 record from the Wabash River in White County. Hellbenders have been eliminated from Indiana except for a small population in the Blue River and the lower portions of the South Fork of the Blue River (Kern, 1986a). In Ohio, Pfingsten (1989a) spent 2,000 person-hours searching for hellbenders from 1985–88 and failed to find any in the Miami River or its tributaries, but did locate them in the other main drainages of the Ohio River. Populations in the remainder of the Ohio drainage are extant, as are most of those in the Tennessee drainage. Green (1934) reported hellbenders to be common in the Ohio River, but not so common in the tributaries near Huntington, West Virginia. Hellbenders were also reported from the Ohio River near Marietta, Ohio (Krecker, 1916). Records for the hellbenders in the Ohio River have not been reported since these early sightings. Humphries (1999) reported hellbenders to still be common in many high elevation streams in West Virginia. Bothner and Gottlieb (1991) studied the distribution and abundance of hellbenders in New York and found the species in both the Allegheny and Susquehanna drainages. The same is true for both systems in Pennsylvania and Maryland (Gates, 1983). No recent data are available for the Savannah drainage populations in Georgia and South Carolina. Populations are also still found throughout the species' historical range in Missouri and Arkansas (Trauth et al., 1992a,b; Trauth et al., 1993b; LaClaire, no date).

2. Historical versus Current Abundance. Historical data on abundance are available for only a few populations and even in those cases, rigorous quantification of effort is lacking. For example, Green (1935) reported catching 34 hellbenders between the hours of 8 (PM) and midnight on 21 June 1934 in the headwaters of the Shavers Fork of the Cheat River (New River drainage of West Virginia). Hellbenders were detected using an acetylene light, but the number of observers or the length of the stream surveyed was not specified. Swanson (1948) reported collecting (and permanently removing) over 650 hellbenders from a 4.8 km (3 mi) stretch of Big Sandy Creek (Allegheny drainage) in Venango County, Pennsylvania, from 1932–48. Other vague accounts are available for Bear Creek in the Tennessee drainage of northeastern Mississippi (Ferguson, 1961b), French Creek in the Allegheny drainage of northwestern Pennsylvania (Hillis and Bellis, 1971), and the streams in the Ohio River drainage of Ohio (Pfingsten, 1989a).

More rigorously documented abundance data are available for the Allegheny River drainage of New York State where Bothner and Goettlieb (1991) performed mark–recapture studies to estimate both abundance and density at eight sites along Ischua Creek, Oswayo Creek, and the Allegheny River. Abundance estimates ranged from 3–58 individuals in study areas that ranged from 424–14,003 m^2 of stream bed. A series of mark–recapture studies has been conducted in Missouri starting with Nickerson and Mays (1973b), who estimated abundance at 1,142 hellbenders in a 2.67-km stretch of the North Fork River (White River drainage) in 1969 and 269 hellbenders in a single riffle (4,600 m^2) in the same river in 1970. Effort, in person-hours, was recorded as 750 in 1969 and 108 in 1970. Peterson et al. (1983) conducted a mark–recapture study in the same riffle during 1977–78, and their estimate of 231 fell within the 95% confidence interval of Nickerson and Mays, indicating no change in abundance in that riffle during a 7-yr period. Mark–recapture estimates of hellbender abundance ranging from 0.9–6.1 hellbenders/100 m^2 were reported for the Spring and Eleven Point rivers (White River drainage of Missouri and Arkansas) and Big Piney and Gasconade rivers (Missouri River drainage of Missouri) during 1980–82 (Peterson et al., 1988). Peterson (1987) captured 110 adults in a 2600-m^2 study site in the Niangua River in Missouri during 1985. Humphries (1999) conducted a mark–recapture study from 1998–99 in the West Fork of the Greenbrier River in West Virginia. An abundance estimate of 31 individuals was found within a 216 m stretch of stream. The density in this section was 0.80 individuals/100 m^2.

Hellbender *(Cryptobranchus alleganiensis)*



Four streams in the White River drainage of Missouri were surveyed in 1992 (Ziehmer, 1992). Numbers encountered and effort were recorded as follows: Jack's Fork, 4 in 66 person-hours; Current, 12 in 60 person-hours; North Fork, 122 in 49 person-hours; Bryant's Creek, 0 in 22 person-hours. Trauth et al. (1992a) surveyed seven sites on the Spring River (White River drainage of Arkansas) in 1991, including two of the same sites that Peterson (1985) had studied between 1980 and 1982. Trauth et al. (1992a) did not encounter any hellbenders at a site where Peterson had marked 60 and encountered only 5 where Peterson had marked 310. This is the only evidence of decline in a hellbender population that has been documented rigorously in the literature.

3. Life History Features.

A. Breeding. Reproduction is aquatic.

i. Breeding migrations. The suggestion by Alexander (1927) that male hellbenders move many km to reach their breeding grounds in the fall has not been supported by recent research. Most authorities agree that no actual breeding migration takes place, although males may move short distances within their home ranges to brooding sites.

ii. Breeding habitat. The breeding season is variable but occurs mainly in September and October, although evidence of breeding activity as late as December and January has been reported for the Spring River in Arkansas (Peterson et al., 1989). Only a few specific breeding dates are given in the literature. Smith (1907) reported egg-laying dates from 28 August–8 September in 6 consecutive years starting in 1906 in northwestern Pennsylvania. Swanson (1948) stated that egg-laying takes place about the 1 September in Venango County, Pennsylvania. The release of milt from captured males and the presence of gravid females was documented between 7 September–11 October during 2 years of study in the Blue River of Indiana (Kern, 1986b). Nests with eggs have been reported in the North Fork River, Missouri, on 13 September (Nickerson and Mays, 1973a), and 2 and 8 October (Nickerson and Tohulka, 1986). Dundee and Dundee (1965) noted a nest containing eggs in the Niangua River, Missouri, on 14 November, and Johnson (1981) noted a clump of eggs in the same river on 19 September. Bothner and Gottlieb (1991) reported nests in the Susquehanna River in New York on 10 and 11 September. Green (1934) reported the spawning season of the hellbender in the vicinity of Elkins, West Virginia, to be from the middle of August to early September. The release of milt from captured males was reported from 20 August–11 September in the West Fork of the Greenbrier River in West Virginia (Humphries, 1999). A nest with eggs has also been reported from the Williams River in Webster County, West Virginia, during September 1997 (S. Blackburn, personal communication).

B. Eggs.

i. Egg deposition sites. The beginning of the breeding season is marked by a change in behavior of hellbenders, especially males. They leave their routine hiding places and move around the stream bottom, even during daylight, exploring cavities under flat rocks and crevices or holes in the bedrock (Smith, 1907). Eventually a male occupies a suitable site and may actively prepare a nest by moving gravel to create a saucer-shaped depression (Bishop, 1941b). Peterson (1988) also reported males using a hole in a mud-gravel bank for nesting. The males lie at the opening of their nests, frequently with their heads exposed, waiting for gravid females. Females may enter nest sites voluntarily or they may be forced into the cavity by the male. As soon as the female starts to deposit eggs, the male moves alongside or slightly above the female and sprays the eggs with snowy-white seminal fluid that may take the form of a cloudy mass or ropy chunks (Smith, 1907).

ii. Clutch size. A single female may deposit from 200 to >400 eggs (Smith, 1907, 1912a; Bishop, 1941b, Nickerson and Mays, 1973a), but this may not represent all the eggs available for oviposition, as >20% of a female's compliment may be resorbed (Topping and Ingersol, 1981; Petranka, 1998). Males may accept several females into their nest cavity, so the total number of eggs in a single nest may be >2,000 (Bishop, 1941b). Deposited eggs are often eaten by both males and females (Smith, 1907; Bishop, 1941b). The eggs are yellow, round, approximately 6 mm in diameter, and surrounded by two transparent envelopes. The inner envelope is attached as a solid rope from egg to egg resulting in long egg strings (Nickerson and Mays, 1973a). The eggs swell with water and eventually increase to 18 mm in diameter (Smith, 1912a). It may take 2 d for a female to expel her eggs, at which time she either leaves the nest or is expelled by the male (Bishop, 1941b). Males usually remain in the nest cavity with the eggs, and both Smith (1907) and Bishop (1941b) witnessed episodes of active nest guarding by males. Bishop (1941b) also observed a brooding male swaying from side to side over the eggs, which may increase the oxygen supply to the eggs. The duration of this brooding period varies, but Smith (1907, 1912a,b) found males attending nests that contained embryos about 3 wk old.

Bishop (1941b) estimated the incubation period at 68–84 d for western New York and Pennsylvania. Peterson (1988) encountered hatchlings in the Niangua River, Missouri, that he believed to be no more than 45 d old. Temperature undoubtedly plays a major role in determining length of embryonic period. Smith (1912) provides the most comprehensive data on embryonic development and should be consulted for details.

C. Larvae/Metamorphosis.

i. Larval stage. Newly hatched larvae are approximately 30 mm TL and are well pigmented dorsally and on the tail. The venter is unpigmented except for the yellow of the yolk sac. The mouth and eyes are conspicuous, the gills are short and flattened, the front limbs terminate in two lobes, and the hindlimbs are paddle-shaped and unlobed (Bishop, 1941b). Development is rapid, and hatchlings double their size during the first year (Bishop, 1941b). Larvae normally lose their external gills in the second summer after hatching, at 100–130 mm TL (Smith, 1907; Bishop, 1941b; Nickerson and Mays, 1973a).

ii. Larval requirements.

a. Food. The diet of larval hellbenders has not been studied but probably includes invertebrates.

b. Cover. Nickerson and Mays (1973a) reported that larval hellbenders utilize small stones and chert for cover. They also reported an anecdotal account of a larval hellbender taken from the interstices of a gravel bed in an area of subsurface percolation. The scarcity of records for larval hellbenders compared to adults supports this suggestion (Kern, 1986c; Petranka, 1998).

iii. Larval polymorphisms. None reported.

iv. Features of metamorphosis. The major morphological features of hellbender metamorphosis are the loss of the external gills and the attainment of adult color pattern.

v. Post-metamorphic migrations. None known.

vi. Neoteny. Not reported.

D. Juvenile Habitat. Same as for adults.

E. Adult Habitat. Adult hellbenders are found in fast-flowing streams containing abundant cover in the form of large flat rocks, bedrock shelves and crevices, and logs (Bishop, 1941b; Nickerson and Mays, 1973a).

F. Home Range Size. Home range has been reported in various forms for several populations of hellbenders. Using minimum area convex polygon in Missouri, average home range size was 28 m^2 for females and 81 m^2 for males (Peterson and Wilkinson, 1996). Coatney (1982) calculated an elliptical home range of 90 m^2 for seven Ozark hellbenders radio-tracked nocturnally for 2 wk. In Pennsylvania, average inter-capture distance was 18.8 m for males and 18.7 m for females (Hillis and Bellis, 1971). The mean activity radius for this population was 10.5 m. Calculated as a circular home range, the average home range was 346.4 m^2. Linear distance between captures in Tennessee ranged from 5–60 m (Casey et al., 1993). Topping and Peterson (1985) provided evidence for size-specific movement in hellbenders in Missouri. They demonstrated a tendency for upstream movements ranging from 2.3–25.7 m/d. In contrast, Peterson (1987) detected no net movement upstream or downstream in the Niangua River, Missouri. Mean linear movement of hellbenders in a West Virginia stream was 20.1 m, ranging from 0.8–70.2 m between captures at least 1 mo apart (Humphries, 1999).

G. Territories. Home ranges of hellbenders overlap (Peterson and Wilkinson, 1996), but they apparently avoid being in the area of overlap at the same time (Coatney, 1982). However, hellbenders have been observed in close proximity to each other at night without conflict between individuals (Humphries, 1999). Rarely is >1 hellbender found beneath the same rock except during the breeding season (Smith, 1907; Hillis and Bellis, 1971; Nickerson and Mays, 1973a; Peterson, 1988), and they are known to defend shelter rocks (Peterson and Wilkinson, 1996; Hillis and Bellis, 1971). Hellbenders will utilize rocks recently vacated by other individuals (Hillis and Bellis, 1971; Peterson and Wilkinson, 1996; Humphries, 1999). Male hellbenders become extremely territorial during the breeding season and will defend nest holes or rocks (Smith, 1907; Bishop, 1941b; Peterson, 1988). Blais (1996) reported that during the breeding season in New York, male hellbender's home ranges tended to overlap more than those of females.

H. Aestivation/Avoiding Desiccation. Not reported; however, Green (1934) stated that hellbenders in West Virginia moved to deeper holes in summer to find colder water.

I. Seasonal Migrations. See "Breeding migrations" above. Seasonal change in nocturnal activity has been reported in high elevation populations in West Virginia (Humphries and Pauley, 2000). Hellbenders were most active during early summer (May–June), with decreased activity in later months. Nocturnal searches with flashlights were most productive in early summer in these populations; however, nocturnal activity shifts have not been reported in other parts of the hellbender's range. Noeske and Nickerson (1979) reported on seasonal changes in activity rhythms in the laboratory.

J. Torpor (Hibernation). In most streams, hellbenders likely become inactive during winter. Overwintering sites in New York included deep pools >2 m deep, fast-flowing riffles that remained free of ice cover, and deep water pockets within riffles 1.5–2 m deep (Blais, 1996). However, hellbenders sometimes breed in Missouri and Arkansas during winter (Dundee and Dundee, 1965; Peterson et al., 1989).

K. Interspecific Associations/Exclusions. None known.

L. Age/Size at Reproductive Maturity. Sexual maturity is reached from 300–400 mm TL, with males normally maturing at a smaller size than females (Taber et al., 1975), although there is much variation reported in the literature (see Petranka, 1998, for a review). Age at sexual maturity has been estimated at 3–4 yr (Smith, 1907) and 5–6 yr (Bishop, 1941b) for eastern populations and 5–6 yr (Dundee and Dundee, 1965; Nickerson and Mays, 1973a) for Ozark populations.

M. Longevity. Hellbenders have survived as long as 29 yr in captivity (Nickerson and Mays, 1973a). Extrapolations from growth rate data suggest that some large individuals may live as long as 30 yr in nature (Taber et al., 1975; Peterson et al., 1983; Petranka, 1998).

N. Feeding Behavior. Crayfish are the most important food item for hellbenders, as indicated by their position at the top of most food lists in the literature (Smith, 1907; Green, 1935; Bishop, 1941b; Swanson, 1948). Other items that have been recorded include fish, insects, earthworms, snails, tadpoles, fish eggs, other hellbenders, and hellbender eggs (Nickerson and Mays, 1973a).

O. Predators. Fishes, turtles, and water snakes are important predators (Nickerson and Mays, 1973a). As noted above, hellbenders and their eggs are eaten by conspecifics (Nickerson and Mays, 1973a). Man is an important predator, as a result of both commercial collecting and scientific research. Swanson (1948) reported taking over 650 individuals from a 4.8-km stretch of Big Sandy River, Pennsylvania. Peterson (1989) killed 108 hellbenders in the Niangua River, Missouri, in 1974 and 62 from the Spring River, Arkansas, in 1985–86 for a study of food habits. Ingersol et al. (1991) killed 127 from the Niangua River in 1979–80 to document their reproductive cycle.

P. Anti-Predator Mechanisms. Hellbenders produce skin secretions that are lethal when injected into white mice and are probably unpalatable to some predators (Brodie, 1971a).

Q. Diseases. Captives are often infected by water mold (*Saprolegnia* sp.).

R. Parasites. Protozoans, nematodes, trematodes, cestodes, acanthocephalans, and leeches have been found associated with hellbenders (see Rankin, 1937 and Nickerson and Mays, 1973a, for a thorough review).

4. Conservation.

Hellbenders are classified as Endangered in Illinois, Indiana, Maryland, and Ohio; Rare in Georgia; Of Special Concern or Species of Concern in New York, North Carolina, and Virginia; Watch List in Missouri; and Deemed in Need of Management in Tennessee. The actual degree of protection each of these designations afford varies by state, but generally, Endangered status requires that a permit be secured before a hellbender can be captured and provides penalties for possessing hellbenders without such a permit. The other categories listed above do not afford this level of protection, but do allow for some acknowledgment that the future of the species within their boundaries is not totally secure. Other states such as Alabama, Arkansas, Kentucky, Mississippi, South Carolina, and West Virginia track hellbender distribution records in a database, but do not generally afford them protection from take. Pennsylvania apparently neither tracks hellbender records nor protects them from take.

The U.S. Fish and Wildlife Service performed a status review of Ozark hellbenders (*C. a. bishopi*) in the early 1990s (LaClaire, no date). This review concluded that "populations of the Ozark hellbender in the majority of its range (in Missouri) are apparently stable and new populations of the species have been found during the recent status surveys." The final recommendation was that the Ozark hellbender did not warrant protection at the time.

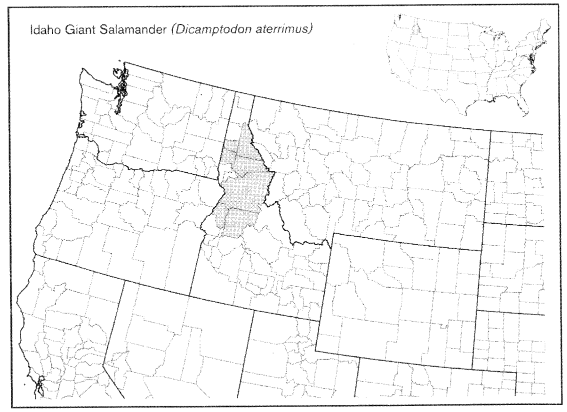
As early as 1957, it was noted that the hellbender's range was rapidly shrinking as a result of human modification of stream habitats (Smith and Minton, 1957). Dundee (1971) listed "siltation, general pollution, and thermal pollution" as being responsible for eliminating the hellbender from "much of the Ohio River drainage, and from other industrialized regions." Bury et al. (1980) mentioned channelization and impoundment of streams and rivers as an agent of decline specifically for Alabama, Maryland, Missouri, Tennessee, and West Virginia. They also cited Nickerson and Mays (1973) when implicating industrialization, agricultural runoff, and mine wastes as contributing factors in Ohio, Pennsylvania, and West Virginia. Other authors have alluded to the range-wide decline in hellbender numbers (Williams et al., 1981; Gates et al., 1985). However, rigorous quantification of effort is lacking in most hellbender surveys, so there are few data to back up these claims. The sole exception of which we are aware, that of Trauth et al. (1992a), documented a drastic decline in hellbenders along the Spring River of Arkansas. They attributed the decline to over-collection of specimens for scientific purposes (see "Predators" above), habitat alteration related to recreational activities, elimination of riparian habitats leading to an increase in the silt burden, and water pollution associated with human occupation and development along the river. Rigorous historical abundance data exist for other streams (see "Historical versus Current Abundance" above) and these areas should be targeted for resurvey.

Family Dicamptodontidae

Dicamptodon aterrimus (Cope, 1867)
IDAHO GIANT SALAMANDER
Kirk Lohman, R. Bruce Bury

1. Historical versus Current Distribution.

Idaho giant salamanders (*Dicamptodon aterrimus*) are found in forested watersheds in north-central Idaho from the Coeur d'Alene River south to the Salmon River (Maughan et al., 1976; Nussbaum et al., 1983) and from two locations in Mineral County in extreme western Montana (Reichel and Flath, 1995). Formerly considered California giant salamanders (*D. ensatus*), Idaho giant salamanders are now regarded as genetically distinct from other species in the genus (Daugherty et al., 1983; Good, 1989). Although the general outline of their range has not changed in recent years, the distribution of Idaho giant salamanders has likely been much reduced within heavily logged watersheds (Fisher, 1989; Hamilton et al., 1998; Hossack, 1998).



2. Historical versus Current Abundance.

Locally abundant in headwater streams in coniferous forest watersheds. Knowledge of historical abundance is scarce, but numbers have likely been reduced in areas of intense timber harvest where larvae may be adversely affected by sedimentation and increases in water temperature (Corn and Bury, 1989a; Bury et al., 1991).

3. Life History Features.

A. Breeding. Reproduction is aquatic.

i. Breeding migrations. The reproductive biology of Idaho giant salamanders is presumed to be similar in most respects to that described for other members of the genus, although breeding behavior of all dicamptodontids is poorly understood. There is circumstantial evidence from population structure that breeding occurs during both spring and fall (Nussbaum, 1969; Nussbaum and Clothier, 1973). Because neoteny is common, asynchronous breeding may also be characteristic of many populations with a high proportion of neotenes (Nussbaum and Clothier, 1973).

ii. Breeding habitat. Courtship likely takes places in hidden nest chambers beneath logs, stones, and crevices in small streams (Nussbaum et al., 1983).

B. Eggs.

i. Egg deposition sites. Nussbaum (1969a) discovered a gravid female buried 60 cm (2 ft) deep in a rock pile at the base of a small waterfall that he believed to be a nest site. Eggs are attached singly on the undersides of rocks within the nest chamber (Nussbaum, 1969a; Nussbaum et al., 1983).

ii. Clutch size. Females lay 135–200 eggs (Nussbaum, 1969a; Nussbaum et al., 1983). Clutch frequency is presumed to be biennial (Nussbaum et al., 1983; Blaustein et al., 1995b). Females remain with the eggs throughout development, apparently guarding them from predators (Nussbaum, 1969a). An incubation period of nearly 9 mo was reported by Henry and Twitty (1940).

C. Larvae/Metamorphosis.

i. Length of larval stage. Metamorphosis occurs during or after the third year (Nussbaum and Clothier, 1973).

ii. Larval requirements.

a. Food. Primarily benthic invertebrates and tailed frog (*Ascaphus* sp.) tadpoles (Metter, 1963). Some predation on juvenile fishes by other *Dicamptodon* sp. has been reported (Antonelli et al., 1972; Parker, 1993a).

b. Cover. Stones and submerged logs (Nussbaum et al., 1983).

iii. Larval polymorphisms. None.

iv. Features of metamorphosis. Transforming individuals are 92–166 mm TL (Nussbaum and Clothier, 1973). Larvae (145–150 mm TL) observed in process of metamorphosis during August in northern Idaho (K. L., personal observations). Complete metamorphosis of Idaho giant salamander larvae required from 11 d to 6 mo in aquaria (Kessel and Kessel, 1944). Mixed populations of neotenic and terrestrial adults are common (Nussbaum, 1976).

v. Post-metamorphic migrations. Move from streams to moist coniferous forest floors (Nussbaum et al., 1983).

vi. Neoteny. Common.

D. Juvenile Habitat. Same as adults.

E. Adult Habitat. Under logs and bark in coniferous forests (Nussbaum et al., 1983). Adults are rarely encountered and knowledge of their habits is scarce.

F. Home Range Size. Unknown.

G. Territories. Large larvae and adults are aggressive toward conspecifics, but whether larvae or adults defend territories is unknown.

H. Aestivation/Avoiding Desiccation. These behaviors have not been reported.

I. Seasonal Migrations. Unknown.

J. Torpor (Hibernation). Unknown.

K. Interspecific Associations/Exclusions. Often occur in the same streams as tailed frogs. Tailed frog tadpoles are an important prey item for larval Idaho giant salamanders.

L. Age/Size at Reproductive Maturity. Sexual maturity in both larval and terrestrial forms usually occurs at sizes greater than 115 mm SVL (Nussbaum et al., 1983).

M. Longevity. Unknown. Based on a 3-yr larval period and a maximum size of 250–300 mm, a lifespan of at least 6–10 yr would not be an unreasonable estimate.

N. Feeding Behavior. Larvae are sit-and-wait predators (Parker, 1994). Adult *Dicamptodon* feed on a wide variety of prey, including terrestrial invertebrates, small snakes, shrews, and mice (Nussbaum et al., 1983).

O. Predators. Predators include fishes, garter snakes, weasels, and water shrews (Sorex palustris) (Nussbaum et al., 1983; Blaustein et al., 1995b).

P. Anti-Predator Mechanisms. Toxic skin secretions, warning postures, and biting (Nussbaum et al., 1983). Adults are also known to growl or squawk (Nussbaum et al., 1983).

Q. Diseases. Unknown.

R. Parasites. Unknown.