United States
Department of
Agriculture

Forest Service

Rocky
Mountain
Region

Black Hills
National Forest

Custer,
South Dakota

May 2003

Conservation Assessment of the Tiger Salamander in the Black Hills National Forest, South Dakota and Wyoming

Brian E. Smith

Conservation Assessment

of the

Tiger Salamander,

in the

Black Hills National Forest,

South Dakota and Wyoming

Brian E. Smith
Department of Biology
Black Hills State University
1200 University Street Unit 9044
Spearfish, South Dakota 57799-9044
BrianSmith@bhsu.edu

Dr. Brian E. Smith is a professor at Black Hills State University, where he teaches a variety of courses in vertebrate biology and ecology. He maintains an active research program on the reptiles and amphibians of the Black Hills and surrounding plains region of South Dakota and Wyoming. He is also active in research on the conservation biology of reptiles and amphibians in the Lesser Antilles island chain in the Caribbean Ocean. He has published several papers on the reptiles and amphibians of the Black Hills and surrounding plains, the Caribbean region, and Central America.

Table of Contents

Tables and Figures

INTRODUCTION

The tiger salamander, *Ambystoma tigrinum*, is the widest ranging amphibian in North America and probably has one of the largest ranges of any amphibian in the world. Despite this, and literally hundreds of studies on the species, many aspects of their natural history remain poorly known. Spring migrations to breeding sites and breeding are fairly well known, but directly following reproduction adult tiger salamanders vanish from breeding ponds at most sites and then are rarely seen for the remainder of the active season. They probably spend most of their adult lives underground. As a result, we are only now beginning to understand the behavior and movements of adults throughout most of the active season, and key aspects of tiger salamander natural history such as survivorship, seasonal movements of adults, reproductive rate, growth rate, size and age at sexual maturity, population density, and maximum life span remain virtually unknown. Because of this it is difficult to manage and even survey the species.

The tiger salamander is considered a sensitive species by the United States Department of Agriculture (USDA) Forest Service in the Black Hills National Forest. With inadequate data on population sizes and survivorship and some evidence that various management actions could adversely affect the species it may be necessary to consider the tiger salamander a sensitive species for some time to come. The following is a technical conservation assessment that addresses the biology of the tiger salamander in light of the management agenda of the USDA Forest Service, as well as suggestions for further research designed to answer questions about the basic biology of the tiger salamander that would help to guide future management actions.

CURRENT MANAGEMENT STATUS

Management Status

Although the tiger salamander is considered endangered in parts of its range (see REVIEW OF TECHNICAL KNOWLEDGE, Distribution And Abundance and Population Trend), its status in South Dakota and Wyoming is generally considered to be secure. According to Natural Heritage Databases maintained in South Dakota and Wyoming it is considered globally secure and secure in both these states. The state governments of Wyoming and South Dakota give the species no special status. It is also not considered threatened, endangered, or a species of concern by the United States Fish and Wildlife Service or by the Convention on International Trade in Endangered Species (CITES). However, *A. tigrinum* is considered a sensitive species by the USDA Forest Service in the Black Hills National Forest.

Existing Management Plans, Assessments, Or Conservation Strategies

Maxell (2000) briefly discusses the conservation and management of the tiger salamander in Montana. Frier and Zappalorti (1983) refer to a management plan for eastern tiger salamanders in New Jersey but this plan was apparently never published. The state of Virginia has drafted an unpublished management plan for the eastern tiger salamander, *Ambystoma tigrinum tigrinum*, which is considered endangered in the state of Virginia (Buhlmann et al., 2000).

REVIEW OF TECHNICAL KNOWLEDGE

Systematics

The systematics of the tiger salamander are controversial (Gehlbach, 1967a; Collins et al., 1980; Shaffer and McKnight, 1996; Irschick and Shaffer, 1997; Petranka, 1998), but most authors recognize a single wide-ranging species with considerable geographic variation (Gehlbach, 1967a; Shaffer and McKnight, 1996; Irschick and Shaffer, 1997; Petranka, 1998). Petranka (1998) provided a good overview of the most common arrangement of the seven subspecies. He also discussed the systematic position of the California tiger salamander, *Ambystoma californiense*, which at one time was considered to be a subspecies of *A. tigrinum*. Black Hills populations are referred to the subspecies *A. t. melanostictum*, the blotched tiger salamander (Petranka, 1998), although a wide range of variation in color exists in Black Hills specimens (Peterson, 1974; B. E. Smith, personal observations).

The tiger salamander is one of the largest terrestrial salamanders in North America and can reach 33-35 cm total length (Petranka, 1998). Branchiate adults[1] are also found in many parts of the range including the Black Hills (Peterson, 1974; B. E. Smith, personal observations). Terrestrial adults in the Black Hills are extensively mottled with black or dark markings on an olive-green background. Petranka (1998) provided photographs of the various subspecies of *Ambystoma tigrinum*; this source should be consulted for definitive identification of the subspecies. However, the tiger salamander is the only salamander in the Black Hills region and cannot be confused with any other naturally occurring amphibian in the area.

Distribution And Abundance

Ambystoma tigrinum is the most widely distributed North American salamander and ranges throughout much of the United States except New England and the west coast. It also ranges south to the southern Sierra Madre Occidentalis in Mexico (Petranka, 1998). The northernmost populations are found in the southern portions of Saskatchewan, Alberta, and Manitoba. The species ranges throughout much of the middle portion of the United States, including most or all of Arizona, Utah, Wyoming, and Montana and all of the plains states east to far eastern Texas, Oklahoma, and Kansas. The range also encompasses much of the Midwest, including northern Arkansas, Missouri, Iowa, Wisconsin, Michigan, Indiana, Illinois, and parts of Kentucky, Ohio, and Tennessee. There are eastern coastal populations from Long Island through Georgia. The species is also found on the Gulf Coast from the panhandle of Florida through southern Mississippi northwards into parts of northern Mississippi, Alabama, and Georgia. There are small disjunct populations in Idaho, Mississippi, and southern Ohio, and a larger disjunct population in the eastern half of Washington. The species is commonly used as bait for sport fishing and introduced populations have been found in Washington, Oregon, California, Nevada, Arizona, Tennessee, Virginia, and Ohio (Petranka, 1998). It ranges from sea level (Petranka,

[1] A word about terminology: The terms “paedomorphic” and “neotenic” are frequently used to refer to salamanders that become reproductively mature but retain larval morphology. Since these terms are used interchangeably but mean different things (see clarification in Pough et al., 2001, pp. 245 – 248), I have elected to use the term “branchiate adults” to refer to salamanders that are sexually mature but retain larval morphology. Another term often used by laypeople (and some scientists) to refer to branchiate adults is the term “axolotl”, which more commonly refers to a species of Mexican salamander, *Ambystoma mexicanum*. This species is a true paedomorph and never transforms to become a terrestrial adult.

1998) to 3660 m in elevation (in the mountains of southwestern Colorado, Hammerson, 1999). Petranka (1998) provided a range map that shows the ranges of all of the described subspecies.

It can be difficult to determine the status and abundance of the tiger salamander since terrestrial adults spend a considerable amount of their time underground in various retreats (Hamilton, 1946; Hamilton, 1949; Bishop, 1941, 1943; Smith, 1961; Nussbaum et al., 1983; Semlitsch, 1983a; Collins, 1993; Oldfield and Moriarty, 1994; Madison and Farrand, 1998). The eastern subspecies, *Ambystoma tigrinum tigrinum*, is considered endangered by state wildlife agencies in a number of eastern states including New Jersey, New York, Delaware, Maryland, and Virginia. It is considered threatened in North Carolina and a species of concern in South Carolina. Web sites for some of the state wildlife agencies in these states usually cite habitat destruction as the cause of endangerment of this amphibian but published studies are rare. Semlitsch (1983b) studied two populations of eastern tiger salamanders during four breeding seasons in South Carolina and found that abiotic factors were very important in controlling annual recruitment. He did not specifically address conservation issues. Frier and Zappalorti (1983) stated that habitat destruction and pollution were the primary causes of population declines in New Jersey. Mount (1975) mentioned that they were scarce in Alabama because suitable breeding sites were few. Travis (1992) described their status in Florida as “unknown”.

The subspecies *Ambystoma tigrinum stebbinsi*, the Huachuca or Sonoran tiger salamander, is considered critically endangered by the state of Arizona. It is thought to be restricted to 16 (Jones et al., 1988) or 17 (Collins et al., 1988) localities in the San Rafael Valley of southeastern Arizona. Jones et al. (1988) clarified its taxonomic and systematic status and collected the species in all known localities in Arizona. Collins et al. (1988) studied some of the factors affecting conservation of this subspecies.

The blotched tiger salamander (*Ambystoma tigrinum melanostictum*) is considered an endangered species in British Columbia (Weller and Green, 1997). Orchard (1992) first noted that tiger salamanders were becoming scarcer in British Columbia. Weller and Green (1997) summarized tiger salamander abundance throughout Canada and stated that they were declining in British Columbia due to a combination of factors including grazing and trampling of pastures by livestock, urbanization, fish stocking, and recreational development of lakes. Cannings et al. (1999) also blamed their decline on the same combination of factors.

Throughout the rest of their range tiger salamanders have been reported to be common to abundant. Nussbaum et al. (1983) found larval tiger salamanders to be quite common in Washington but noted how difficult it was to find terrestrial adults. Koch and Peterson (1995) reported that tiger salamanders were common to abundant throughout Yellowstone and Grand Teton National Parks. Baxter and Stone (1980) said that they were common in Wyoming but were especially abundant in places where game fish were absent. Didiuk (1997) noted that populations were stable throughout the range in Saskatchewan. Weller and Green (1997) mentioned declines in British Columbia but otherwise stated that there were no known declines anywhere else in the range in Canada other than some local declines in Alberta that they attributed to development and cultivation. Oldfield and Moriarty (1994) stated that they were common and distributed statewide in Minnesota, and Moriarty (1998) noted that they were probably the most common salamander species in Minnesota. However, Moriarty (1998) also observed that there had probably been some decline in their abundance over time. Both Casper (1998) and Kline (1998) stated that they remained common in southern Wisconsin, but neither author mentioned their status in northern Wisconsin. Hammerson (1999) found them to be common or locally abundant in suitable habitat in Colorado. He also noted that the creation of small fishless ponds (i.e., "dugouts") throughout the state may have created habitat for salamanders. However, Hammerson (1999) also called attention to the fact that many mountain lakes lacked tiger salamanders due to the introduction of trout. Hovingh (1986) reported that they were common in the Uinta Mountains of Utah. Degenhardt el al. (1996) reported that tiger salamanders were common throughout New Mexico, even in urbanized areas. Collins (1993) reported that they were found statewide in Kansas but did not discuss their status. Phillips et al. (1999) reported that tiger salamanders were locally common in Illinois but that they were adversely affected by agriculture and urbanization. Smith (1961), also reporting on Illinois tiger salamanders, noted that they were abundant only in areas with many ponds but that they could persist even in disturbed habitats. In northeastern Illinois Mierzwa (1998) reported that they were common and widespread, although his data indicated a long-term decline that he attributed to ongoing drought. Brodman and Kilmurry (1998) reported that the species was common in Indiana.

In the Black Hills, tiger salamander status and abundance is unknown. Peterson (1974) found tiger salamanders to be moderately common in surveys conducted in the Black Hills in 1972 and 1973. He noted that larvae were more easily found and could be very abundant. He found tiger salamanders at elevations to 1940 m in the Black Hills. Smith et al. (1996a) found larvae to be extremely abundant in a few ponds on the plains surrounding the Black Hills, but they were found in only 3 of 46 ponds that were searched. I have found branchiate adults to be abundant in some springs and sewage ponds in the Black Hills from 1200-2000 m elevation (personal observations). Larvae and adults have been found in bodies of water of all kinds throughout the region (Jason Kolbe, Washington University, personal communication 1996, and B. E. Smith, personal observations), however no formal surveys other than Peterson (1974) and Smith et al. (1996a, 1996b) have been undertaken in the area.

The status of terrestrial adults is much more difficult to determine than that of larval forms or branchiate adults since the terrestrial adults are frequently found under cover or in burrows in the Black Hills (Kolbe et al., 2002). Terrestrial populations of tiger salamanders may live much of their adult life under ground and this may make it difficult if not impossible to survey adults (Madison and Farrand, 1998). A population found at Wind Cave National Park in the Black Hills may be one of the few populations where a survey of terrestrial adults could be undertaken (Kolbe et al., 2002). Salamanders in this population appear to live as commensals (or possibly predators, see REVIEW OF TECHNICAL KNOWLEDGE, Demography And Community Ecology) of black-tailed prairie dogs (*Cynomys ludovicianus*) in a prairie dog town and the salamanders can be easily surveyed and captured at night at the mouths of prairie dog burrows.

Population Trend

Because the states of New York, New Jersey, Delaware, Maryland, and Virginia have all placed the eastern tiger salamander on their endangered species lists, and because the subspecies is considered threatened in North Carolina and of concern in South Carolina, it can be inferred that this subspecies is in decline in these states. However, there is surprisingly little published information on the conservation status of the eastern tiger salamander. Bishop (1941) indicated that it formerly occurred as far north as Albany in New York but was restricted to Long Island and Rockland County at the time of publication of his monograph. Frier and Zappalorti (1983) studied the eastern tiger salamander in New Jersey. They indicated that the range of the subspecies had declined from eight to three counties in New Jersey. Eastern tiger salamanders were known to breed in only 12 locations in New Jersey at that time. A reintroduction project was started in 1982 and an artificial breeding pond was constructed. Translocation of 1000 eggs to this pond resulted in subsequent recruitment of 400 subadult salamanders in 1982 but there is no other published information on this project or on the status of the eastern tiger salamander in New Jersey. Travis (1992) stated that the eastern tiger salamander's status in Florida was unknown but the subspecies was probably at risk due to destruction or modification of breeding ponds and fish stocking. Buhlmann et al. (2000) reported that population sizes of the eastern tiger salamander were very small in Virginia and breeding ponds were few. They reported wetlands loss as the primary factor leading to declines but also mentioned fish stocking, deforestation, and acid precipitation. Petranka (1998) blamed the decline of the eastern tiger salamander in the southeastern United States on deforestation and the loss of wetlands.

Declines of other subspecies have also occurred. The blotched tiger salamander has declined in British Columbia (Orchard, 1992; Weller and Green, 1997). The decline has been blamed on overgrazing, trampling of pastures by livestock, urbanization, fish stocking, and recreational development of lakes (MacIntyre and Palermo, 1980; Orchard, 1992; Cannings et al., 1999). Moriarty (1998) reported that, while tiger salamanders were still the most common salamander in Minnesota, he felt that they had probably undergone population declines. This conclusion was based on qualitative estimates gathered over a number of years' experience collecting amphibians in Minnesota.

In Colorado and other parts of the intermountain west some evidence exists showing that population declines have occurred while other data suggest the opposite. Population declines have occurred over a number of years in mountain lakes due to trout stocking (Burger, 1950; Blair, 1951; Corn et al., 1997). However, Hammerson (1999) pointed out that the creation of numerous small ponds had probably increased habitat for tiger salamanders in some parts of Colorado. My experience in the Black Hills area, Wyoming, and in Colorado indicates that these small ponds are mostly dug at lower elevations to provide water for cattle so they probably do not affect tiger salamander populations at higher elevations. Also in Colorado, Harte and Hoffman (1989) reported tiger salamander declines that were associated with pulses of acidified snowmelt during spring runoff. The sources of the acidified precipitation have been eliminated since this study but no follow-up studies have been conducted. Levels of acid precipitation are thought to have declined, however (Stebbins and Cohen, 1995). Because of these conflicting reports it is difficult to determine whether there has been any change in the abundance of Colorado tiger salamanders, although Hammerson (1999) believed that they were secure.

Population status and trends in the Black Hills are unknown. A population of terrestrial blotched tiger salamanders was monitored for a few years (from 1995-1997) on Wind Cave National Park (Kolbe et al., 2002). Population trends were not evident in such a short time but we did not observe successful recruitment from the breeding pond at this site during these three years. Populations of branchiate adults have been found throughout the Black Hills but it is not known how many ponds are inhabited by this morph in the area (personal observations). Some of these populations appeared to be very large (personal observations). In a survey of 46 suitable breeding ponds, Smith et al. (1996a) found dense populations of larval (but probably not branchiate adults) populations of tiger salamanders at only three ponds. Rumble et al. (in press) have discussed the abundance of created wetlands (i.e., "dugouts") in the Black Hills region. As noted by Hammerson (1999), tiger salamanders can colonize and use these ponds in Colorado and I am certain that some dugouts are also colonized by tiger salamanders in the Black Hills area (personal observations). However, many of these ponds also have introduced fish such as largemouth bass (*Micropterus salmoides*) that eat tiger salamanders (Jodi Massie, personal communication, 2001).

Except in the rather unusual case at Wind Cave National Park (Kolbe et al., 2002), terrestrial tiger salamanders are seldom encountered in the Black Hills region (personal observations). The size of the Wind Cave National Park population was not estimated, but this population is ideal for a mark-recapture study of an adult tiger salamander population.

Life History

To understand most aspects of the biology of the tiger salamander it is necessary to understand their complex life history and variations on the "typical" life history pattern, if they can be considered to have any one typical pattern. Of course, all amphibians have a complex life history. They hatch from anamniotic eggs laid in an aquatic environment to become an aquatic larval form that metamorphoses into an aquatic or terrestrial adult. Such is also the case for *Ambystoma tigrinum*, but the tiger salamander has the most distinctively complicated life history of all salamanders (Collins et al., 1993). The eggs are laid in ponds of various types and hatch into aquatic larvae, but then the life history of tiger salamanders may diverge from the typical amphibian pattern. As described by Collins et al. (1993), tiger salamanders can be found as two different larval forms (normal morph and cannibal morph) that may become adults of three different types (metamorphic adult, branchiate adult, and cannibalistic branchiate adult). Cannibal morph larvae are distinguished by their diet, which consists largely of other tiger salamander larvae (Collins and Holomuzki, 1984; Holomuzki and Collins, 1987). They can also be distinguished by their morphology, with broader heads and enlarged vomerine teeth (Powers, 1907). They are usually rare in any given pond (Rose and Armentrout, 1976; Collins, 1981). Both forms of larvae can mature in the ponds to become aquatic branchiate adults of either type, cannibalistic or normal morph. They can also metamorphose and leave the ponds to be terrestrial metamorphic adults (i.e., metamorphs), before or after sexual maturity as larval forms. Metamorphic adults that were cannibal morphs can be distinguished from metamorphic adults that were normal morphs by their morphology (Rose and Armentrout, 1976). Rose and Armentrout (1976) have also reported two size classes of metamorphic adults in the Llano Estacado of west Texas and eastern New Mexico, suggesting they metamorphose at different ages.

Sexton and Bizer (1978) described four life history patterns for normal morph tiger salamanders living at their high elevation (ca. 2800-3475 m) study sites in Colorado based on size classes of the animals exhibiting larval morphology in the ponds. The first life history pattern they uncovered consisted of ponds with larvae of a single size class. Sexton and Bizer (1978) believed these were larvae that transformed within a single summer season to leave the pond and overwinter in burrows on land. These types of larvae were found in semipermanent ponds (see REVIEW OF TECHNICAL KNOWLEDGE, Habitat Use or DEFINITIONS for a description of pond types). They referred to this life history pattern as type 1. This seems to be a typical pattern amongst low elevation tiger salamanders in most areas of the country, although branchiate adults (type 4 of Sexton and Bizer, 1978, see below) are also found at low elevations in permanent waters in some parts of the range (Rose and Armentrout, 1976). A second life history pattern was described from some ponds that contained larvae of two size classes, in which Sexton and Bizer (1978) surmised that larvae took two years to reach sexual maturity and then left the pond as terrestrial adults. Presumably the larvae overwintered for one winter in the ponds. They referred to this life history pattern as type 2. Ponds with three size classes were similar to those with two size classes, but in these ponds larvae overwintered for two winters in the natal ponds and metamorphosed in the third warm season. They referred to this life history pattern as type 3. The fourth life history pattern was one that resulted in branchiate adults and consisted of ponds with four size classes, all with a larval morphology. They referred to this life history pattern as type 4. Apparently, these animals became sexually mature and bred as branchiate adults in the fourth warm season following birth. Types 2, 3, and 4 were only found in permanent ponds.

Sexton and Bizer (1978) named the different types solely for illustrative purposes and to categorize the populations; in fact, any of the types may metamorphose at any time or extend development for several seasons to become branchiate adults. The primary distinction that Sexton and Bizer (1978) made was between colonizing morphs (types 1, 2, and 3), which moved between ponds, and the consolidating morph (type 4), which was capable of exploiting permanent ponds indefinitely. However, even type 4 individuals can metamorphose and leave a pond if conditions warrant (Sexton and Bizer, 1978). The advantage to individuals of the colonizing morph is that they can move overland to colonize new aquatic habitats. Meanwhile, individuals of the consolidating morph can take advantage of the fact that permanent fish-free ponds offer protection from terrestrial predators. The selective advantage of phenotypic plasticity in the tiger salamander is that they are capable of switching amongst these morphs depending on the conditions, exploiting favorable situations as they arise (Sexton and Bizer, 1978). Also, the later a salamander metamorphoses, the larger its size, presumably giving it an adaptive advantage (Sexton and Bizer, 1978).

In the Black Hills and associated plains, I have found terrestrial adults at all elevations. At higher elevations (ca. 1200 m and higher), I have found extremely large aquatic tiger salamanders that appeared to be branchiate adults. I have not done detailed studies of these individuals. The only way to be certain that they are branchiate adults is to capture and dissect them to determine if they are reproductively mature. Also, I have usually observed what appear to be branchiate adults in permanent ponds, such as sewage ponds (at Wind Cave National Park and Jewel Cave National Monument), and high elevation springs in the southwestern part of the Black Hills, in South Dakota near Elk Mountain. With the cool continental climate of the Black Hills, especially at higher elevations, it would not be surprising to find that larvae take more than one season to develop, so some metamorphs may spend more than one year in a pond before metamorphosis.

Finally, cannibal branchiate adults or cannibal morph larvae could occur in the vicinity of the Black Hills. Cannibal branchiate adults are known from near Chadron, Nebraska, ca. 80 km south of Hot Springs, South Dakota, which is at the southern edge of the Black Hills (Reilly et al., 1992). I have not carefully examined any specimens from the Black Hills for the cannibal morphology. Cannibal morph larvae and adults are discussed more extensively in "Habitat Use".

Movement Patterns

The movement patterns of metamorphic tiger salamanders throughout the active season are complex. They consist of migrations from terrestrial overwintering sites to aquatic breeding sites in late winter or early spring with subsequent emigration to upland foraging sites after a short breeding season (Hamilton, 1949; Reese, 1969; Botts and Folkerts, 1977; Sever and Dineen, 1978; Whiteman et al., 1994; Hill, 1995; Howard et al., 1997; Hammerson, 1999; Phillips et al., 1999; Russell and Bauer, 2000), terrestrial movements of occasionally large numbers of individuals following spring and summer rains (Carpenter, 1953; Reese, 1969; Whiteman et al., 1994; Koch and Peterson, 1995; Hammerson, 1999), and some fall movements of metamorphs over land, possibly directed towards hibernation sites (Duellman, 1954; Smith, 1961; Reese, 1969; Koch and Peterson, 1995). Smith (1956) believed that there were no mating migrations in Kansas but he did not indicate why. It seems unlikely that migrations to breeding ponds would not exist in one part of the range.

Petranka (1998) gave perhaps the best general discussion of mating migrations in the tiger salamander. The timing of late winter to early spring mating migrations varies according to weather, with mating migrations occurring earlier at lower elevations and latitudes and later at higher elevations and latitudes. Coastal populations tend to breed earlier than inland populations. In southern Macon Co., Alabama, eastern tiger salamanders studied by Botts and Folkerts (1977) were breeding at their study pond on 7 December 1975 and 1 January 1976. Eggs were found as early as November in Tennessee (Gentry, 1955). Breeding salamanders have been found in February in Missouri (Seale, 1980) and Arkansas (Trauth et al., 1990). Breeding occurred in February to March in South Carolina, depending on the weather (Semlitsch, 1983b). Near South Bend, Indiana, breeding salamanders were found from late February to mid-April (Sever and Dineen, 1978). At a study site 5 km west of West Lafayette, Indiana, Howard et al. (1997) collected tiger salamanders during migrations that occurred from mid-February through mid-March in 1991 – 1993. Coastal populations tend to migrate even earlier, even at northern latitudes. They have been found breeding in January and February in New Jersey (Hassinger et al., 1970; Anderson et al., 1971), and eggs were first deposited in mid-January in Kent Co., a maritime county in Maryland between the Chesapeake and Delaware Bays (Stine et al., 1954). However, eggs were first found in Syosset (on Long Island), New York, in the last week of March (Bishop, 1941). Buhlmann et al. (2000) stated that eastern tiger salamanders enter breeding ponds in Virginia in January to mid-March.

Western and northern populations move toward breeding ponds at various times depending on local weather conditions, which vary by elevation and latitude. Nussbaum et al. (1983) recorded courting terrestrial adults on 22 April 1967 near Moscow, Idaho. Reese (1969) observed movements (but not in large numbers) to breeding ponds in the mountains of Colorado in late May or early June. The timing of these movements depended on snowmelt. On the plains around Denver, salamanders migrated as early as mid-April, with the timing dependent primarily on rainfall and secondarily on temperature (Reese, 1969). At a site at 2525 m elevation just west of Boulder, Colorado, Hamilton (1949) found that breeding migrations occurred during the last week of April and first week of May in 1947 and 1948. At Ice Lake Reservoir, a permanent lake on the northern border of Yellowstone National Park, Hill (1995) noted that migrations occurred from April 9-May 15, 1993. Whiteman et al. (1994) studied tiger salamander movements over three seasons at high elevation (ca. 3400 m) sites in the Elk Mountains of western Colorado. They found that salamanders migrated into permanent and semipermanent ponds for breeding in early June, depending on the timing of snowmelt and the onset of higher temperatures. They primarily studied movements following the breeding season and did not give any further data on movements towards breeding ponds.

The study of Hill (1995), completed at Ice Lake Reservoir 3.2 km west of Gardiner, Montana, is one of the most extensive studies of tiger salamander movements ever completed and is also probably the most relevant to managers of tiger salamanders in the Black Hills region. However, because all data were collected in a single year, the data might not be representative. The first male immigrated into the pond on April 9, with the first female captured on April 15. The breeding immigration lasted until June 11. Males entered before females but both sexes stayed in the pond until approximately July 8, when adult metamorphs began to leave the pond. The mean duration of stay for males was 98.0 days and for females was 73.6 days, considerably longer for both sexes than in several other studies (Hassinger et al., 1970; Anderson et al., 1971; Sever and Dineen, 1978; Semlitsch, 1983b; Travis, 1992; Madison and Farrand, 1998). Most movements in and out of the pond were at night (98.8%) and occurred within 12 hours of a precipitation event (82.6%; these data are for all movements during the season). The mean temperature of the evenings on which immigration to the pond occurred was 4.5^{o}C. Immigration rarely occurred at temperatures below freezing, but was observed at temperatures as low as –5.6^{o}C and across fresh snow on four occasions.

Spring breeding migrations probably also occur in the Black Hills area. However, they have not been studied here and my own fieldwork has all been done later in the season. Peterson (1974) has also studied tiger salamanders in the Black Hills but did not do spring fieldwork either. I would suggest that researchers look for salamanders in the ponds of the Black Hills in March and April, or as soon as ice melts off the surface of the ponds (Hamilton, 1949; Hill, 1995). Tiger salamanders seem to be tolerant of cold weather (Hill, 1995; B. E. Smith, personal observations), so searches should be conducted immediately following the springtime melt, even while edges of ponds are still frozen (Hamilton, 1949).

Little is known about the environmental factors that influence tiger salamanders to move towards breeding ponds in the spring, other than obvious conditions such as lack of surface ice on permanent ponds, the filling of temporary ponds, temperatures that are above freezing (but potentially with snow still on the ground), and a predilection to move when humidity is high such as during rains and at night. Carpenter (1953) caught tiger salamanders at night in funnel traps placed in and around ponds in the Grand Teton – Jackson Hole area in Wyoming, but not in the same traps during the day. Hamilton (1949) studied tiger salamanders at 2520 m elevation near Nederland, Colorado (ca. 30 km W of Boulder), and found migrating tiger salamanders around ponds with some ice still in the ponds, snow still on the ground, and air temperatures of 5.5^{o}C. Water temperature in his study pond eight days prior to collection of the first males in the pond was also 5.5^{o}C. Sever and Dineen (1978) noticed that salamanders in northern Indiana tended to migrate during periods of precipitation and that they did not appear until after air temperatures had reached from 8 – 16^{o} C. Reese (1969) also gave quantitative data on temperatures and stated that spring migrations to breeding ponds on the plains in Colorado occurred after ambient air temperatures were at least 10^{o}C. He also noted that movements occurred after two or three days of rainfall (from 1 – 2 cm each day). Springtime movements in the mountains were initiated by snowmelt (Reese, 1969). Where workers have recorded precipitation and temperature and their influence on salamander movements, most movements occurred at night or following precipitation events. Koch and Peterson (1995) reported that, of 400 migration events recorded by Hill (data not reported in Hill, 1995) at Ice Lake Reservoir in Yellowstone National Park, 91% were within 24 hours after a rainfall and 99% occurred at night.

Semlitsch (1983b) and Semlitsch and Pechmann (1985) also found that tiger salamanders moved primarily at night. Semlitsch (1983b) also found that salamanders moved just after or during precipitation events, either rain or snow.

Summer movements seem to be more complex and less well studied. They are most extensively discussed by Reese (1969), Whiteman et al. (1994), Hill (1995), Koch and Peterson (1995), and Madison and Farrand (1998). Koch and Peterson (1995) described movements of hundreds to thousands of salamanders following summer thunderstorms in the Yellowstone and Grand Teton areas. These movements have been known since at least 1863, when Captain DeLacy described movements of thousands of salamanders during one rainy evening (reported by Koch and Peterson, 1995). Two grizzly bear researchers witnessed a migration that consisted of thousands of salamanders moving along a roadway for as far as they could see in either direction following a summer thunderstorm (described in Koch and Peterson, 1995). Summer movements appeared to be from south to north in the Lamar Valley of Yellowstone National Park (Koch and Peterson, 1995), but no reasons were suggested for this pattern. In contrast, Reese (1969) reported that salamanders always moved to the south on the plains of Colorado during the summer. He believed that this had to do with a predilection to hibernate in small mammal burrows on north-facing slopes. Carpenter (1953) also described summer movements in the Yellowstone – Grand Teton area following late summer thunderstorms and noted that most of these movements occurred on sagebrush flats. He did not describe the direction of these movements. Carpenter (1953), Reese (1969), and Koch and Peterson (1995) indicated that movements are more likely to occur in the evening.

In Colorado tiger salamanders may stay in breeding ponds until late summer, depending on the weather, when they may finally leave the breeding ponds to move to upland areas or to semipermanent ponds (Reese, 1969; Heath, 1975; Whiteman et al., 1994). Summertime movements following rains in Colorado were more likely at night but could occur during the day (Reese, 1969; Hammerson, 1999). Whiteman et al. (1994) noted that salamanders moved out of breeding ponds or from pond to pond during rainy periods in late July or August in the mountains in Gunnison County. They stated that summertime movements usually involved movements to and from semipermanent ponds, rather than the permanent ponds used for breeding in the spring.

One of the most extensive studies of summertime (July and August) movements of tiger salamanders was conducted in Colorado by Whiteman et al. (1994). At their high elevation (ca. 3400 m) sites in the Elk Mountains of western Colorado they found that salamanders moved out of permanent ponds towards the terrestrial environment, from permanent ponds to semipermanent ponds, and from semipermanent ponds to other semipermanent ponds. Salamanders breeding in permanent ponds tended to move into the terrestrial environment following reproduction, although a few moved into semipermanent ponds. Salamanders that bred in semipermanent ponds tended to stay in these ponds longer and also tended to move from one such pond to another. Semipermanent ponds tended to have a lower density of salamander larvae and were also slightly cooler (albeit only 1^{o}C cooler) than permanent ponds. Movements were also correlated with the density of fairy shrimp (*Branchinecta coloradensis*). Fairy shrimp constituted 91% of the calories consumed by the adult metamorphic tiger salamanders in this study and salamanders tended to leave semipermanent ponds as the density of fairy shrimp in these ponds dropped. Semipermanent ponds also had more fairy shrimp than permanent ponds. Whiteman et al. (1994) could not explain why tiger salamanders that bred in permanent ponds tended to return to the terrestrial environment following breeding rather than moving to semipermanent ponds.

Again, some of the most extensive data that are relevant to Black Hills populations of tiger salamanders are those of Hill (1995). At Ice Lake Reservoir, the first summertime movements consisted of the emigration of adult metamorphs (i.e., not young of the year), which began on July 8. Emigration events on August 5 and 14 consisted of 45% and 48% immature metamorphs, respectively. Large-scale emigration was largely over in August, but emigrants continued to be observed until October 8. The study concluded October 10, so other individuals may have still been migrating. Prior to July 8, some movement of adult metamorphs out of the pond was recorded, but Hill (1995) considered these to be wanderings in and out of the pond during favorable environmental conditions, since these adults usually returned to the pond almost immediately. As noted previously, most movements of tiger salamanders at this location occurred at night. Because salamanders at Ice Lake Reservoir do not immediately emigrate following the breeding season, Hill (1995) assumed that there is a foraging advantage to remaining in the pond. Emigration may have been stimulated by attainment of a threshold weight gain during aquatic foraging, decreasing day length, and possibly other climatic factors.

Some summertime movements of tiger salamanders are probably associated with a second breeding season that may occur in some southerly parts of the range. Tanner et al. (1971) and Allison et al. (1994) reported summer breeding in Arizona tiger salamanders (*Ambystoma tigrinum nebulosum*) in late July in Utah (Tanner et al., 1971) and sometime prior to late September in Arizona (Allison et al., 1994). Webb (1969) has also reported summer breeding in the barred tiger salamander (*A. t. mavortium*) in southern New Mexico.

No summertime movements of tiger salamanders have been reported in the Black Hills, although at some movements occur given the fact that I and others have found them away from ponds in the summer (Kolbe et al., 2002; Jason Kolbe, Washington University, personal communication, 1996). Given the continental climate in the Black Hills area it seems unlikely that tiger salamanders in the region would be able to breed more than once in an active season. Springtime breeding probably represents their single breeding attempt in a year, and summer movements, if they occur here, are probably for some other reason, such as foraging.

Some of the most detailed information on tiger salamander movements is found in Madison and Farrand (1998) and they are the only authors to study terrestrial movements in any detail. They implanted radiotransmitters in 27 metamorphic adult tiger salamanders and followed their movements throughout the spring breeding season and into the fall, but not over winter. The tiger salamanders spent an average of 11 days in the breeding pond after release and spent most of their time in deeper, more heavily vegetated parts of the pond. Upon emigration from the ponds, they moved in all directions into wooded habitat but avoided grassy fields, paved roads, and developed areas. They made longer movements in the spring or fall, or sometimes in both seasons. Some did not emigrate from the area directly around the pond. Most resident salamanders moved no more than 150 m from the breeding pond and used an area of approximately 300 m around the pond. Salamanders that were displaced from their natal pond stayed in their new ponds to breed but upon emigration traveled farther than residents. More data from Madison and Farrand (1998) is discussed in "Habitat Use".

Fall movements are poorly documented. Duellman (1954) reported large concentrations of tiger salamanders found dead on roadways in Michigan following rainy or foggy weather in October and November. Breckenridge (1944) believed that salamanders found migrating at this time of year were seeking hibernation sites. Smith (1961) observed that fall breeding movements occurred in Illinois but he did not give the precise timing of these events. It is therefore difficult to assess whether these were actually breeding migrations or, more likely, movements toward hibernation sites. Given typical fall weather in much of Illinois, it seems unlikely that tiger salamanders would breed in the state at this time.

Fall movements have been recorded from August through November in Colorado. Reese (1969) noted mass movements as late as November on the plains of Colorado and Hammerson (1999) stated that they moved as late as September in the mountains of Colorado. Reese (1969) believed that many of the late summer (August) and fall movements were toward overwintering sites. He explained the southward movement of salamanders away from ponds at such times as behavior that was designed to seek out mammal burrows on north-facing slopes in which to overwinter. Reese (1969) believed that mammal burrows on north-facing slopes were ideal overwintering sites for tiger salamanders because snow covered such sites and kept them covered until the spring, sheltering the salamanders from cold temperatures that could penetrate exposed burrow entrances.

Tiger salamanders probably move to hibernation sites in the fall. Koch and Peterson (1995) observed that tiger salamanders probably migrated to hibernation sites in the fall in the Yellowstone and Grand Teton area but gave no quantitative data. Hibernation sites are probably spread out across the landscape and fall migrations are probably not as obvious as spring migrations in and out of relatively visible sites such as breeding ponds. However, Reese (1969) reported that fall migrations were more obvious than spring migrations, especially on the plains of Colorado. No fall movements have been observed in the Black Hills.

Habitat Use

Because of their complicated life history amphibians utilize several types of habitat during the course of their lives. However, there are two basic types of habitat of interest to the student of tiger salamander biology: 1) Aquatic habitat, in which eggs and larvae develop and where branchiate adults may live much or all of their lives, and 2) Upland habitat, where metamorphic adults spend the majority of their lives. In addition, aquatic habitat can consist of temporary, semipermanent, or permanent ponds, habitats that can be quite different from each other. Temporary ponds are ponds that dry every year. Semipermanent ponds are ponds that dry periodically or in drought years. Permanent ponds are ponds that generally never dry but may do so during extreme droughts.

Aquatic Habitat

It is well known that metamorphic tiger salamanders use many types of ponds in which to breed and sometimes forage. A variety of papers look at different aspects of these ponds. Reese (1969), Hassinger et al. (1970), Sexton and Bizer (1978), and Hill (1995) probably have the best description of the basic structure of these ponds. Madison and Farrand (1998) used radiotelemetry to determine which parts of ponds are used by metamorphic tiger salamanders. Whiteman et al. (1994) have an especially good discussion of why terrestrial tiger salamanders may choose to remain in ponds of various types to forage. Hassinger et al. (1970), Whitford and Massey (1970), Heath (1975), and Bogart et al. (1987) gave good descriptions of the biotic and abiotic environment of breeding habitat used by terrestrial tiger salamanders. Frier and Zappalorti (1983) designed an artificial pond in which several hundred larval tiger salamanders were successfully reared. Although they did not state how they arrived at the design of this pond, I have assumed that it was based on natural ponds used by tiger salamanders for reproduction in New Jersey. Several authors have discussed the effect introduced predatory fish have on tiger salamanders (Burger, 1950; Blair, 1951; Carpenter, 1953; Reese, 1969; Collins and Wilbur, 1979; Collins, 1981; Olenick and Gee, 1981; Degenhardt et al., 1996; Corn et al., 1997; Hammerson, 1999). Hammerson (1999) offered a general and lengthy discussion of breeding ponds used by terrestrial tiger salamanders in Colorado. His discussion may be especially relevant to managers of the species in western South Dakota and the Black Hills, as many of the habitats he wrote about are similar to those found in western South Dakota.

Reese (1969), working in several different ecoregions in Colorado, did one of the most extensive descriptive studies of ponds used by metamorphic tiger salamanders. He noted that salamanders occurred everywhere in Colorado except in the alpine tundra climax ecoregion (>3500 m elevation). In general, ponds were at least 0.50 m deep if they were muddy and 0.60 m deep if they were clear. In comparison, Koch and Peterson (1995) reported that of 48 ponds examined for tiger salamanders in Yellowstone National Park, 31 were used by tiger salamanders and averaged 1.6 m deep and 17 were not used by tiger salamanders and averaged 0.4 m deep. Reese (1969) reported that breeding ponds characteristically received a lot of sunlight during the day and were seldom shaded with woods, especially in the subalpine forest climax ecoregion (ca. 2860 – 3400 m elevation). At these elevations a large portion of the pond needed to be exposed to the sun at least nine hours of the day, presumably because of the colder daytime temperatures. He noted that salamanders found in ponds in narrow canyons at these elevations took longer to develop. He also noted that salamanders never used ponds for breeding that were stocked with fish. The clear ponds Reese (1969) visited tended to be at high elevations, they had more vegetation in general, and they tended to have populations of branchiate adults rather than metamorphic forms. Reese (1969) believed that tiger salamanders preferred turbid water for concealment from predation and that this could be a reason why they used deeper ponds if the water was clear. Turbid ponds also contained more organic matter that generated food for the salamanders. In general, ponds had a deep water portion as well as a shallow beach-like area. Heath (1975) reported that larvae tended to spend the daytime in warm shallows, moving into deeper water at night, which was warmer than the shallows at night. Ponds with the structure described by Reese (1969) probably have the kinds of temperature gradients described by Heath (1975) as being conducive to larval development. All the ponds Reese (1969) visited that had salamanders had mud bottoms except for one pond. The pH of the ponds varied from 6.8 – 9.6, with half the ponds of pH 8.4. Data are not given, but I assume that this was the mode of his measurements. Several ponds in which salamanders occurred on the plains had pH >9.0. Reese (1969) thought that beaver (*Castor canadensis*) were probably important to tiger salamanders because they provided breeding habitat for them, especially at higher elevations.

Another study that offered good descriptions of the structural and physical environment of ponds used by metamorphic tiger salamanders was that of Hassinger et al. (1970), at ponds in New Jersey near sea level approximately 6.5 km from Delaware Bay. The soil in the area was gravelly and the terrestrial vegetation was described as xerophytic (Hassinger et al. 1970). The ponds were abandoned gravel quarries from 1 – 50 years old and were situated near salt and freshwater marshes, indicating that at least eastern tiger salamanders (*Ambystoma tigrinum*

tigrinum) may have some tolerance to high salinity. Bishop (1943) also stated that adult and larval tiger salamanders occurred in highly saline water, particularly at Devil's Lake, North Dakota. Hassinger et al. (1970) found that recently created ponds lacked aquatic vegetation but the older ponds were more mesophytic, with shrubs surrounding the ponds and reeds in the margin of the ponds (Hassinger et al., 1970). The ponds were from 0.15 – 0.60 m deep and averaged 450 m^2 in area. The three most intensively studied ponds were 0.25 m deep and 900 m^2 in area, 0.60 m deep and 335 m^2 in area, and 0.45 m deep and 295 m^2 in area, respectively. These ponds filled by May and were dry by June. The pH of the water in the ponds was 5.6 – 7.8 and salinity was 38 – 71 ppm. At least seven species of anurans also used the ponds as breeding habitat. Aquatic invertebrates became abundant in these ponds later in the season, but densities and types were not reported.

Frier and Zappalorti (1983) designed and built a pond in New Jersey that was presumably derived from a general study of breeding ponds. They placed 1000 eggs in the pond, successfully rearing to metamorphosis approximately 400 eastern tiger salamanders. Unfortunately, no reason was given behind the design of the pond, however a detailed map was provided. The pond was about 60 X 10 m (ca. 600 m^2) in surface area with gently sloping sides. It was 2 m deep at the center. From their diagram it appears that it was surrounded on all sides by brush that was about 5 m from the edge of the pond. They planned to expand this reintroduction program by digging at least one more pond but no further details were given and I have not turned up any other references to this program.

Again, the study of Hill (1995) is particularly relevant to managers of tiger salamanders in the Black Hills region. Ice Lake Reservoir was at 1670 m elevation and was 0.8 ha in area, 3.7 m deep at its deepest part, and averaged 1.5 m deep. The pond was bordered by a steep rocky hillside, an extensive marshy area, a sagebrush-grassland meadow, and an earthen dam. An extensive diagram of the pond is provided including depth contours. Hill (1995) also discussed the geology of the area. He also included a list of vegetation both surrounding and within the pond. Ice Lake Reservoir contained both type 1 and type 2 larvae of Sexton and Bizer (1978) and would probably be considered a permanent pond, although its permanency is not discussed by Hill (1995).

Sexton and Bizer (1978) studied the effects of temperature on tiger salamanders in the Gunnison River Basin, Gunnison Co., Colorado and discovered that tiger salamanders had two basic life history strategies (colonizing and consolidating morphs) and four types of normal morph growth. They surveyed 60 ponds between the months of June and October in 1973 – 1975. These are generally the only months during which these high elevation ponds remain completely ice-free. They picked ten of these ponds to study in detail plus six ponds that lacked salamanders. They measured water temperature weekly or biweekly at mid-day in 1974 and 1975, both at the surface and at 0.5 m intervals beneath the surface, deriving an index of average water temperature during the warm season (June – September) in each study pond. Ponds with temperatures averaging <10^{o}C never contained larvae, presumably because this temperature is too cold for normal development. Ponds with type 1 larvae averaged 14.5 – 17.0^{o}C during the summer. Ponds with type 2 larvae averaged 13.4 – 16.5^{o}C during the summer. Types 3 and 4 salamanders were usually found together in the same ponds, which averaged 11.2 – 13.9^{o}C during the summer. One pond contained only a type 4 population and averaged 12.1^{o}C during 1974 and 11.7^{o}C during 1975. One pond at 3410 m averaged 11.1^{o}C and larvae did not develop and metamorphose in this pond. The general picture that emerges from this study is that type 1 populations live in the warmest ponds and type 4 populations live in the coldest ponds, with a range of conditions in ponds between these extremes that support types 2 and 3 larvae.

Their data also give some clues into the structure of these ponds. Type 1 populations can occupy temporary ponds, but they must be relatively warm, are usually shallow, and are in open areas. These types of habitat are often fed by runoff water. These populations run a constant risk of failing to metamorphose if ponds are not warm enough or dry too quickly. In contrast, types 2, 3, and 4 larvae require permanent ponds and must metamorphose rapidly if their habitat begins to dry. If these ponds are filled by runoff water, they are usually quite large. If they are small ponds, they are often stream-fed. Types 2, 3, and 4 populations can tolerate shadier conditions at pond margins than type 1 populations. A variety of ponds are simply unsuitable; they may be too shady and cold, or may dry too rapidly for metamorphosis, or can have a variety of other characteristics. Ponds could also be too far away from a source of colonization for salamanders to reach during normal emigration but may appear otherwise suitable (Semlitsch and Bodie, 1998; Semlitsch, 2000a, 2000b).

Heath (1975) was primarily interested in the structure of ponds, the temperature preferences of tiger salamanders, and the behavior of tiger salamanders in the field. He worked at a number of the same ponds studied by Sexton and Bizer (1978). The study sites were primarily glacier-fed ponds <1.5 ha in size, except Rainbow Lake, a reservoir of about 6.7 ha. Depths in these ponds ranged from 1 – 6 m and elevations were from 2865 – 3475 m. In the ponds, larvae and branchiate adults selected the warmest water available. Metamorphic adults did not show any such preferences. In the lab, larvae and branchiate adults preferred temperatures of 23.0 – 25.5°C while metamorphs preferred cooler water, 18.4 – 23.7°C. The larvae and branchiate adults also had a narrower preferred range than the metamorphs.

Heath (1975) found that the typical pond was surrounded by sedges and grasses that extended 1 – 3 m into the pond margins, and that the ponds had bottoms that sloped up gradually into the shallows. This type of structure tended to set up a mid-day thermal gradient that could be as little as 1°C. Nevertheless, larvae and branchiate adults still congregated in the warmest end of the pond and picked warmer parts of the shallows, even if the gradient in the shallows was as little as 1 – 2°C. They moved into the shallows in the morning as the water warmed and then moved back into deeper water, which stayed warmer than the shallows overnight, as the water cooled again in the late afternoon. They began moving before the shallows had fully cooled, implying that some cue other than temperature (perhaps decreasing daylight) triggered the movement. If the ponds remained isothermal due to winds no movements were observed.

Whitford and Massey (1970) also studied the movement of larval tiger salamanders in response to thermal gradients but at a lower elevation pond in southern New Mexico. They found that tiger salamanders exhibited similar movement patterns to those of salamanders studied by Heath (1975) at water temperatures <15°C but that movements were random and activity increased at temperatures >15°C. They believed that light was the most important factor governing summer activity of larval tiger salamanders whereas temperature was more important during winter and spring.

Whiteman et al. (1994) discovered that metamorphic salamanders used different types of habitat (i.e., permanent and semipermanent ponds or terrestrial habitat) at high elevations (ca. 3400 m) in the Elk Mountains, western Colorado, because of the foraging advantages offered by some of these habitats. Salamanders migrated toward permanent and semipermanent ponds during the

June breeding season. Populations that bred in semipermanent ponds tended to remain in semipermanent ponds following breeding, or to move amongst these types of ponds. Tiger salamanders that bred in permanent ponds moved from these ponds to semipermanent ponds or, more typically, from permanent ponds to land following the breeding season. Lauder and Shaffer (1986) established that metamorphic tiger salamanders feed more efficiently on land, which could explain movement to land from permanent ponds. One reason that metamorphic adults moved to semipermanent ponds may have been to avoid competition with conspecific larvae, which were more common in permanent ponds. Semipermanent ponds were also cooler than permanent ponds, and Heath (1975) established that metamorphic salamanders preferred cooler water than larvae. However, Whiteman et al. (1994) believed the primary reason that metamorphic tiger salamanders moved into semipermanent ponds from permanent ponds or moved between semipermanent ponds, was the higher density of fairy shrimp in semipermanent ponds. Fairy shrimp also have a higher caloric content than many other types of prey items (Whiteman et al., 1994). Ninety-one percent of the calories consumed by metamorphic adults in semipermanent ponds were fairy shrimp (Whiteman et al., 1994). When fairy shrimp density dropped, the metamorphic salamanders tended to move out of ponds regardless of pond type.

Metamorphs virtually never breed in ponds in which fish are also found. In New York, Bishop (1941) noted that tiger salamanders only bred in temporary ponds where fish were absent. Carpenter (1953) never found tiger salamanders in ponds with fish in the Grand Teton area of Wyoming. Various other studies from Arizona (Collins, 1981) to Florida (Travis, 1992) have also noted that tiger salamanders are never syntopic with fish. Baxter and Stone (1980) found that tiger salamanders were most common in Wyoming in localities without game fish. Corn et al. (1997) reported that trout and tiger salamanders seldom co-occurred in Rocky Mountain National Park in Colorado. A population of branchiate adult tiger salamanders disappeared from a lake in Colorado following the introduction of trout (Burger, 1950).

Only one study reported the co-occurrence of salamanders and stocked game fish. Olenick and Gee (1981) found that stocked rainbow trout (*Salmo gairdneri*) and tiger salamanders could coexist in prairie pothole lakes in Manitoba, but they were found in different parts of the ponds, with tiger salamanders mostly found on the bottom of ponds and rainbow trout in mid- and upper levels of the ponds. Rainbow trout were also stocked in the ponds following the breeding season of tiger salamanders and were then removed at the end of the warm season. Therefore, trout were never exposed to tiger salamander eggs or very small larvae. Rainbow trout and tiger salamanders both ate similar types of invertebrates in these ponds and Olenick and Gee (1981) explained their differential habitat utilization as a competition avoidance mechanism. However, it seems equally likely that this could be a predator avoidance mechanism on the part of tiger salamanders, a theory not explored by Olenick and Gee (1981).

Eastern tiger salamanders studied by Madison and Farrand (1998) used various parts of their study ponds on Long Island, depending on the habitat in the pond and in one case on bluegill sunfish, *Lepomis macrochirus*, a known predator of *Ambystoma* eggs and larvae (Arndt, 1989; Figiel and Semlitsch, 1990). Salamanders preferred shallow water (<0.6 m) in the one study pond occupied by bluegills, presumably to avoid these predators, which preferred deeper water (Madison and Farrand, 1998). Eastern tiger salamanders in this study usually preferred deeper water as well (>0.6 m). Overall, Madison and Farrand (1998) showed that tiger salamanders were flexible and sophisticated in their use of aquatic habitat.

Other predators also affect habitat use by larval tiger salamanders. Adult diving beetles, *Dytiscus* species, are voracious predators on a variety of amphibian larvae including tiger salamanders (Holomuzki, 1986a). *Dytiscus* are primarily active at night and search shallow vegetated areas where they forage for animal prey. Salamander larvae in ponds without *Dytiscus* used microhabitats at random but larvae in ponds with *Dytiscus* did not use vegetated shallows at night. Holomuzki (1986a) also showed in field and laboratory experiments that larvae altered their behavior in the presence of *Dytiscus* larvae to minimize encounter rates with the beetles.

Other studies may be of relevance because of a common type of habitat encountered in the Black Hills and surrounding plains: Natural or artificial "dugouts" often used to water cattle (Rumble et al., in press). These are similar to playas, depressions of 6 m to 2.4 km in diameter and from <1m to >30 m depth studied by Rose and Armentrout (1976) that serve as the major source of standing water for amphibians found on the Llano Estacado in western Texas and eastern New Mexico. Although the climate is substantially different, features of the Llano Estacado are reminiscent of western South Dakota and northeastern Wyoming. The plains are relatively flat and featureless. Playas are commonly used to water cattle, may often be used as sewage ponds, and are sites frequently used by amphibians for reproduction. The barred tiger salamander, *Ambystoma tigrinum mavortium*, is the most common amphibian in the playas of the Llano Estacado. In the Black Hills and surrounding plains, it is most likely that chorus frogs (*Pseudacris triseriata*) are the most common amphibians found breeding in dugouts (Smith et al., 1996a, 1996b). Most playas fill and dry each year, as do many of the temporary ponds found in the Black Hills and surrounding plains, like the tiger salamander breeding pond studied by Kolbe et al. (2002). Fish are frequently stocked in these playas but ordinarily do not survive long since the playas dry up each year. This would be typical for many temporary ponds in the Black Hills and surrounding plains.

Various other authors have also observed tiger salamanders in man-made habitats such as "cattle tanks" (presumably dugouts, rather than upright steel tanks, into which metamorphs would have difficulty climbing), dugouts, or stock ponds across the range of the tiger salamander, including Gehlbach (1965) in the Zuni Mountains of northwestern New Mexico, Webb (1969) and Webb and Roueche (1971) in southern New Mexico, Collins (1981) in Arizona (only the introduced subspecies, *Ambystoma tigrinum mavortium*, used artificial habitat, whereas the native *A. t. nebulosum* occurred only in natural habitat), Degenhardt et al. (1996) in New Mexico, and Hammerson (1999) in Colorado, where they may occur in ponds heavily polluted with cattle manure.

Terrestrial Habitat

Like all amphibians that live part of their lives as a terrestrial form metamorphic tiger salamanders have at least two types of habitat that they use extensively; ponds for breeding and terrestrial upland habitat in which they may forage and overwinter (Semlitsch, 1983a; Madison and Farrand, 1998; Semlitsch, 1998). Of the two habitat types, the former is usually intensively studied since amphibians often congregate and are quite visible at breeding ponds and because eggs and larvae develop in these ponds. The latter is typically very poorly studied, even though upland habitat is extremely important to terrestrial amphibians because they forage and sometimes overwinter in such habitat and in fact often spend the majority of their lives in such habitat. For example, Travis (1992) reported that the average pond residency time of male tiger salamanders in Florida was 13 days and that females spent even less time in ponds. In New

York, Madison and Farrand (1998) reported average yearly pond residency times of 21.8 days for males and 12.0 days for females. Whiteman et al. (1994) did not explicitly study pond residency but their data imply that adult metamorphs could spend up to three months in ponds in the high mountains of Colorado. However, there was considerable terrestrial movement amongst ponds. Therefore, adult metamorphic tiger salamanders spend from 9 – 11.5 months on land each year, depending on the locality. In the only study to extensively investigate use of the terrestrial environment by tiger salamanders, they spent up to 378 days away from water (Madison and Farrand, 1998). It can therefore be persuasively argued that consideration of upland habitat is critical to the conservation of ambystomatid salamanders (Semlitsch, 1998) and aquatic-breeding amphibians in general (Semlitsch and Bodie, 1998; Semlitsch, 2000a, 2000b).

The most extensive study of terrestrial habitat use by tiger salamanders is that of Madison and Farrand (1998), who studied the movements of eastern tiger salamanders using radiotelemetry on Long Island in New York. Surface movements occurred at night or after rains. Major movements by individual salamanders could occur in the spring or fall or in both seasons. Movements were confined to habitat within 300 m of a breeding pond, nearly twice the 165 m terrestrial buffer zone recommended by Semlitsch (1998), and almost ten times the 30.8 m buffer zone required by law in states with these types of laws (Massachusetts and Florida, Semlitsch, 1998). Individuals were also highly philopatric; displaced individuals used ponds in which they were placed to breed but then left and seldom returned to these ponds. Instead, these displaced individuals wandered randomly. In contrast, individuals that were not displaced continued to use the same pond for breeding and used upland habitat near this pond in which to forage during the active season. Tiger salamanders frequently sheltered in shallow runways that might have been dug by mammals (average usage time of 31.6 days) or in short blind tunnels that salamanders dug themselves (average usage time of 7.1 days). Less frequently, they used deeper runway systems (average usage time of 83.4 days). They also spent a considerable amount of time foraging underground. This predilection to burrow has also been studied by Semlitsch (1983c), who observed that tiger salamanders were the only ambystomatid salamander he studied that dug their own burrows when exposed to detrimental conditions (dry and hot environments) in the laboratory. Local conditions also affected upland habitat use; salamanders did not move as far from breeding ponds if there were many underground shelters near these ponds (Madison and Farrand, 1998). Salamanders restricted their upland habitat use to wooded areas, avoiding grassy areas, roadways, and developed areas.

Only Reese (1969) has made any observations on upland overwintering habitat used by metamorphic tiger salamanders. Branchiate adults, of course, stay in the water for the winter, as do larvae that may take one or more years to develop. Reese (1969) examined a variety of rodent burrows in winter near a breeding pond and found that 65% of the burrows were occupied by adult metamorphic tiger salamanders. These burrows were up to 3.1 m long, but salamanders tended to overwinter in chambers only 5.0 – 7.5 cm beneath the surface. All of the burrows used for overwintering had openings that faced to the north and were on the south bank of the breeding pond. The south side of the pond retained moisture and snow longer than the north side, remaining under 0.15 – 0.60 m of snow throughout January and February. Several burrows contained more than one animal and up to three, but these animals were not found together. Some salamanders seemed to have constructed small side burrows off of the main burrows in which to hibernate, as if they had used the main burrows to get underground, and then built side chambers in which to overwinter. Given that tiger salamanders can dig their own burrows

(Semlitsch, 1983c), it seems likely that they can dig short side burrows once underground.

There have been no extensive studies of habitat use by metamorphic tiger salamanders in the Black Hills. I have found them in virtually all types of water, from small to large ponds, in springs, clear water, turbid water, and heavily polluted stock ponds. Peterson (1974) found them in ponds and springs and in various terrestrial environments later in the season. When I have found them in upland habitats it has always been under stones or logs. Kolbe et al. (2002) found that they made extensive summertime use of prairie dog burrows surrounding a temporary pond on a mixed-grass prairie portion of Wind Cave National Park. They were often found at the entrance to prairie dog burrows at night. However, Kolbe et al. (2002) did not differentiate amongst burrow types and did not capture and mark salamanders. Although tiger salamanders have been found in several types of habitat in the Black Hills, their abundance in these habitats has never been assessed.

Habitat Use By Cannibal Morph Larvae

Larval development of tiger salamanders in at least some populations can lead to four different outcomes, depending on environmental conditions: Typical branchiate adults, typical metamorphic adults, cannibal metamorphic adults, and cannibal branchiate adults (Collins et al., 1993). All four of these types are recognizable by their morphology (Rose and Armentrout, 1976; Collins et al., 1993). When reared under conditions of high conspecific density some tiger salamander larvae become cannibal morphs (Collins and Cheek, 1983; Lannoo and Bachmann, 1984), which usually metamorphose into normal metamorphic adults (but with a distinctive morphology, Rose and Armentrout, 1976) but can become cannibal branchiate adults (Collins et al., 1993). In the wild, conditions of high conspecific density tend to occur in ephemeral wetlands that can undergo rapid drying during the dry season (Rose and Armentrout, 1976; Lannoo and Bachmann, 1984; Pfennig et al., 1991). Because they grow rapidly (due to the large food items they are capable of consuming), metamorphose, and leave such ponds early, cannibal morphs should be at a selective advantage under these conditions (Hoffman and Pfennig, 1999). Ephemeral ponds that dry each year are common in the Black Hills area, particularly at lower elevations.

Cannibal morphs have been reported in four subspecies of *Ambystoma tigrinum*, including *A. t. mavortium*, *A. t. nebulosum*, *A. t. tigrinum*, and *A. t. melanostictum* (Collins et al., 1993). Cannibalistic morphs have been reported from Nebraska (Powers, 1903, 1907; Reilly et al., 1992), Oklahoma (Glass, 1951), Arizona (Gehlbach, 1967a, 1967b; Collins, 1981), Colorado (Reese, 1969), Texas (Rose and Armentrout, 1976), Iowa (Lannoo and Bachmann, 1984), New Mexico (Pedersen, 1993), and Illinois (Hoffman and Pfennig, 1999). However, the exact extent of this phenomenon is probably incompletely known. Cannibal branchiate adults have been found in eastern South Dakota (Larson et al., 1999) and cannibal branchiate adults of the subspecies *A. t. melanostictum* have been collected near Chadron, Nebraska (Reilly et al., 1992). Chadron is about 80 km southeast of Hot Springs, South Dakota, which is at the southeastern corner of the Black Hills.

Research has been conducted on a variety of factors that influence the development of cannibal morph larvae. Of greatest importance is simple crowding with conspecifics (Collins and Cheek, 1983; Pfennig and Collins, 1993; Loeb et al., 1994; Maret and Collins, 1994; Hoffman and Pfennig, 1999). However, crowding with congeners can also induce the development of cannibal larvae (Hoffman and Pfennig, 1999), whereas phylogenetically distant organisms, such as chorus frogs (*Pseudacris triseriata*) do not induce the development of cannibal morphs (Loeb et al., 1994). By virtue of their large size and mouth gape, cannibal larvae will not hesitate to eat various animals, including other developing amphibians such as chorus frog tadpoles, which make up a good portion of the diet of cannibal larvae in some areas (Loeb et al., 1994). Other factors affecting the development and behavior of cannibal larvae are kinship relations (Pfennig and Collins, 1993; Pfennig et al., 1994; Pfennig et al., 1999), size class structure (Maret and Collins, 1994), and pathogen densities (Pfennig et al., 1991).

Regardless of the extensive research on cannibal larvae and their development, the main point of interest to managers of tiger salamander populations is that cannibal morph larvae are likely to be found in the Black Hills area and tend to develop under certain behavioral conditions rather than physical parameters. Cannibal larvae may be most common in ephemeral ponds because the larval densities can be very high in these ponds and behavioral interactions favoring development of cannibal morphology (chemical, visual, and tactile cues; see Hoffman and Pfennig, 1999) are most likely in these sorts of ponds. There is also a selective advantage to becoming a cannibal under this situation since cannibal larvae can mature rapidly, metamorphose, and leave ponds that are rapidly drying faster than non-cannibal conspecifics (Hoffman and Pfennig, 1999). Ponds with a high pathogen density may not be conducive to the development of cannibal larvae because cannibal larvae become sick and die from eating diseased conspecifics (Pfennig et al., 1991). Chorus frog density will probably be correlated with the presence of cannibal larvae since chorus frogs and cannibal morphs tend to occur in similar types of ponds and chorus frogs are extremely common in the Black Hills and other areas (Loeb et al., 1994; Smith et al., 1996a, 1996b). Cannibal branchiate adults could also be found in the Black Hills area but little is known about this morphological type or the conditions under which they develop (but see Powers, 1907; Rose and Armentrout, 1976; Collins, 1981; Larson et al., 1999).

Food Habits

Tiger salamanders are carnivorous throughout their range as both larvae and adults. The dietary preferences of larval tiger salamanders have been extensively studied but the prey consumed by metamorphic adults is virtually unknown. Larval tiger salamanders eat a variety of aquatic invertebrates, and the following authors can be consulted for basic lists of prey items consumed by larval tiger salamanders: Bishop (1941) summarized early studies in New York, Reese (1969) listed food items consumed in Colorado, Webb and Roueche (1971) provided a very short list of some prey consumed in New Mexico, and Rose and Armentrout (1976) gave a similar list for the Llano Estacado of west Texas and eastern New Mexico. More extensive lists with proportions of food items consumed are found in Lannoo and Bachmann (1984; Iowa), Brophy (1980; Illinois), and Miller and Larsen (1986; Washington). Some of the more unusual food items consumed by larvae were *Scaphiopus* and *Spea* (spadefoot toad) tadpoles in New Mexico (Webb and Roueche, 1971), fathead minnows (*Pimephales promelas*) by cannibal morph larvae in eastern South Dakota (Larson et al., 1999), and bullfrog (*Rana catesbeiana*) and green frog (*R. clamitans*) tadpoles in captivity, which are noxious to fish (Werner and McPeek, 1994). Loeb et al. (1994) reported that cannibal morph larvae ate more chorus frogs than conspecifics in some parts of the range.

Few workers have studied the diet of adult metamorphs. Rose and Armentrout (1976) reported that adult salamanders frequently did not have food items in their stomachs. Reese (1969) provided one of the more extensive lists of the prey of adults but did not list proportions consumed. He noted that they ate mollusks, various insects, and annelids. They have also been reported to eat small field mice (species not given; Ditmars, 1905). I have raised adult tiger salamanders on newborn house mice and Lindquist and Bachmann (1982) fed them earthworms in captivity.

Of more relevance to managers of the species in the Black Hills area are more comprehensive lists of food items consumed by tiger salamanders in the Rocky Mountain region. Gehlbach (1965) provided one of the earliest such lists. At his study sites in northeastern New Mexico he found that larval tiger salamanders primarily ate the eggs of the canyon treefrog, *Hyla arenicolor* (27%), and substantial amounts of larval culicids (aquatic dipterans; 24%). Other prey items consumed were gastropods (i.e., snails; 16%) and nymph and adult Corixidae (order Heteroptera or Hemiptera, the "true bugs"; 14%). Collins and Holomuzki (1984) and Holomuzki and Collins (1987) provided what are probably the most extensive lists of prey items consumed by larval tiger salamanders. They worked at various study sites in east-central Arizona. Collins and Holomuzki (1984) summarized data at three ponds sampled in July and at one pond sampled in June, July, August and September. They listed prey items of one vertebrate taxon (*Ambystoma tigrinum*, primarily eaten by cannibal morph larvae) and 34 invertebrate taxa. Holomuzki and Collins (1987) summarized data from two ponds over six years (but not sampled every year) and one pond over two years. They listed prey items of one vertebrate taxon (once again, *A. tigrinum* larvae) and 24 invertebrate taxa. Several things are notable about the lists published by Collins and Holomuzki (1984) and Holomuzki and Collins (1987): 1) Tiger salamanders ate prey of a variety of invertebrate taxa; 2) Cannibal morph larvae primarily ate conspecifics (66% at one pond and 96% at another; Collins and Holomuzki, 1984) but also ate other types of prey (for example, Loeb et al., 1994, found that they primarily ate chorus frogs at some sites); 3) Typical morph larvae did not specialize on eating conspecifics but ate them at times (from 0.2 – 1.7% of the diet at two different ponds during two different months, but usually 0% at most ponds during most months); 4) Tiger salamanders changed their dietary habits as the season progressed; and 5) Dietary habits differed amongst ponds. Because diet varied amongst ponds and months, any general trends in preference are very tentative (Collins and Holomuzki, 1984; Holomuzki and Collins, 1987). However, at a broad taxonomic level, typical morph larvae primarily ate crustaceans (primarily cladocerans) and aquatic insects (primarily chironomids) (Holomuzki and Collins, 1987). However, they are very adaptable and seem to eat whatever is available.

Possibly more relevant to managers in the Black Hills is a study of larval tiger salamander diet over one summer season (June – September) at two high elevation ponds, 2880 m and 3097 m, in the Elk Mountains of western Colorado (Dodson and Dodson, 1971). The larvae ate a variety of crustaceans, mollusks, insects, collembolans, hirudineans, planarians, and rotiferans, but primarily ate crustaceans and various aquatic insects. Crustaceans of the genera *Hyalella* and *Daphnia* were especially common prey items, as were colonies of *Conochilus* (Rotifera). Due to their small size, *Conochilus* may have been ingested incidentally. The proportions of different foods in the diet also changed during the summer. *Hyalella* and *Daphnia*, especially *Daphnia*, were commonly taken from June to August, and *Conochilus* colonies were more commonly found in the diet in September. The results were somewhat confounded by size of the larvae as well, which was different between ponds. Dodson and Dodson (1971) found that differently-sized larvae fed on different food items and behaved differently during food capture. The lower elevation pond contained normal morph type 1 larvae whereas larvae in the higher pond grew more slowly and were normal morph type 2 larvae.

More important than the extensive lists of prey items published by Dodson and Dodson (1971) were generalizations about larval diet they drew from their study. They stated that there were three general classes of diets. The smallest larvae (<2.0 cm long) took small planktonic Cladocera and Copepoda and small chironomid larvae. A mid-sized class (2.0 – 8.0 cm) ate a large number of foods of a variety of size classes, from 0.3 mm diameter rotifer colonies to 20 mm conspecifics. The largest class ate little, as this class underwent metamorphosis to become terrestrial adults. Larvae, regardless of size, tended to eat the largest prey items available to them. Larger larvae were more opportunistic than smaller larvae. Larvae in the two ponds had different diets as well, which reflected food availability in the two ponds. Benthic animals formed a large part of the larval diet. Dodson and Dodson (1971) sampled prey only from the water column so they could not comment on the benthic animals consumed by tiger salamander larvae. They speculated that larvae spent a lot of time disturbing pond bottoms to dig up benthic animals, rather than capturing prey in the water column. Leff and Bachmann (1986) also found that tiger salamanders spent more time foraging on the substrate than in the water column. Dodson and Dodson (1971) did not mention caloric content, which was an important factor in the study of Whiteman et al. (1994).

Zerba and Collins (1992) studied variation of larval tiger salamander diet amongst ponds and also studied variation in diet within ponds (i.e., amongst individuals). Diet varied considerably amongst ponds, showing that larvae are phenotypically plastic in their diet. Diet within a pond varied considerably amongst individuals as well, but virtually all of this variation was size-dependent. Therefore, diet within a pond was largely determined by larval size, and larvae of certain sizes ate similar prey items. However, diet varied considerably amongst ponds depending on the availability of prey items. The most important prey items in the diet of tiger salamander larvae in this study were chironomids (aquatic insects), cladocerans (crustaceans), trichopterans (aquatic insects), pelecypods (mollusks), and odonates (larval dragonflies and damselflies).

Because diet varied according to larval size, it was not surprising that the position of larval tiger salamanders with respect to trophic level changed as they grew. In contrast to Dodson and Dodson (1971), however, Holomuzki and Collins (1987) found that there were only two size classes of larval salamanders at their study sites in Arizona. Larvae that were <30 mm snout-vent length (SVL) ate predominantly daphnids and larval dipterans. When >30 mm SVL, larvae ate a greater variety and size range of aquatic insects and fed on the next highest trophic level, effectively becoming competitors for food with the predaceous diving beetle larvae (genus *Dytiscus*) and with leeches. Tiger salamander cannibal morph larvae, were, of course, on a higher trophic level since they ate larval salamanders and effectively competed for food with adult *Dytiscus*, which are well-known predators of larval salamanders (Holomuzki 1986a).

Because tiger salamanders are phenotypically plastic and have a tremendous range of life history options available to them it should not be surprising to find that they can exploit a wide range of feeding strategies, as studied by Whiteman et al. (1994, 1996) in Colorado. Whiteman et al. (1994) showed that metamorphs moved from pond to pond in search of the high quality aquatic prey, the fairy shrimp, and also to reduce competition with larval forms, especially branchiate adults, which were more abundant in permanent ponds (see REVIEW OF TECHNICAL

KNOWLEDGE, Habitat Use). Whiteman et al. (1996) extended this study to further explore the reasons why some tiger salamanders became metamorphs while others remained branchiate adults. Whiteman et al. (1996) found that only non-permanent ponds contained fairy shrimp. As a consequence, metamorphs had a growth advantage over branchiate adults and were capable of reducing competition with them since metamorphs were able to exploit food resources unavailable to branchiate adults. Whiteman et al. (1996) speculated that there were trade-offs with other life history characteristics that maintained facultative metamorphosis but refused to speculate further. It would seem that branchiate adults might be relatively safe from predation in fish-free ponds, or they might have a less risky overwintering strategy, overwintering in ponds rather than burrows on land. Other hazards could await metamorphic tiger salamanders, such as the risk of dessication or increased likelihood of predation in the terrestrial environment. None of these hypotheses have been investigated, however.

It is also apparent that the density of larval tiger salamanders can have an effect on lower trophic levels in some ponds that in turn affects the life history strategy of tiger salamanders. Sprules (1972) was primarily interested in the structure of zooplankton communities and studied the same ponds visited by Dodson and Dodson (1971) and Whiteman et al. (1994). He considered the study ponds to be "shallow ponds" (i.e., semipermanent or non-permanent) and "deep ponds" (i.e., permanent). Of course, metamorphic tiger salamanders were primary predators on zooplankton in the shallow ponds and branchiate adult tiger salamanders were primary predators in the deep ponds. The zooplankton communities at shallow and deep ponds were stable but different from each other. Some zooplankton appeared to outcompete others, depending on whether the pond was a shallow pond or a deep pond, and some abiotic factors were also important (i.e., some zooplankton couldn't exist in shallow or deep ponds, respectively). However, of most interest to students of salamander biology, the large cladoceran *Daphnia pulex* appeared to be excluded from deep ponds due to heavy predation by branchiate adult tiger salamanders. There was also heavy predation by branchiate adult tiger salamanders on the fairy shrimp, a known high quality food item (Whiteman et al., 1994). These results suggest that predation by branchiate adult tiger salamanders is very important in maintaining facultative metamorphosis in the tiger salamander at these high elevation sites. Metamorphic tiger salamanders are able to gain a fitness advantage by metamorphosing simply because heavy predation by branchiate adult tiger salamanders completely excludes fairy shrimp and other zooplankton from permanent ponds, potentially giving a selective advantage to metamorphs that migrate into shallower ponds to prey upon these favored food items. Also of interest is that the zooplankton community of these ponds appears to be structured by the tiger salamanders, with some zooplankton species excluded from some ponds due to heavy predation by tiger salamanders.

In field experiments, Holomuzki et al. (1994) also showed that heavy predation by tiger salamanders could control lower trophic levels. However, at their sites in central Arizona no effects were seen in the wild at normal densities. Enclosures with larval salamanders maintained at high density contained relatively fewer herbivorous zooplankton, which caused an increase in chlorophyll *a* and a concomitant decrease in orthophosphate levels. There were also changes in relative proportion amongst the zooplankton community, suggesting that larval tiger salamanders could be keystone predators in these ponds. However, in field surveys no such effects were seen, implying that larval tiger salamanders, in normal densities in these ponds, had no effect on lower trophic levels. This study is of interest because it shows that larval tiger salamanders could affect the composition of the herbivorous zooplankton community, the algal community these zooplankton feed upon, and certain abiotic parameters of these ponds as a result.

Although Dodson and Dodson (1971), Brophy (1980), Collins and Holomuzki (1984), and Holomuzki and Collins (1987) have shown that larval tiger salamanders predominately eat various invertebrates in the wild, several authors have shown that they will eat other larval amphibians as well, including chorus frogs (Sredl and Collins, 1991; Loeb et al., 1994; Maret and Collins, 1996), *Hyla eximia* (the mountain treefrog; Sredl and Collins, 1992), and *Rana sylvatica* (the wood frog; Wilbur, 1972). Of these three species, only the chorus frog occurs in the Black Hills and surroundings, and it is probably the most common amphibian in the area (Smith et al., 1996a, 1996b). Although tiger salamanders seldom eat such species in the wild (but see Loeb et al., 1994), there is doubtless a selective advantage associated with the energy reward obtained from eating such a large food item (Maret and Collins, 1996). Reilly et al. (1992) have also shown that cannibal morphs are more efficient predators on large prey items and Lindquist and Bachmann (1982) have shown that tiger salamanders are primarily visually oriented predators that would detect any active prey items, such as tadpoles. Because heterospecific larvae are not common food items for tiger salamanders, one might question how these species avoid predation.

Sredl and Collins (1991) addressed how heterospecific tadpoles avoid predation by larval tiger salamanders in field experiments where the density of tiger salamanders was manipulated in field enclosures in two ponds. Chorus frog tadpoles did not survive as well at high densities of tiger salamander larvae but Sredl and Collins (1991) did not uncover consistent reasons why this occurred. At lower densities tiger salamander larvae had no effect on survival of chorus frog larvae. At higher densities, abiotic effects were important as chorus frog larvae survived better in shallower ponds than did tiger salamander larvae, the chorus frog larvae thereby escaping predation in shallower ponds. Priority effects were important also. Larger chorus frog tadpoles escaped predation simply by being larger and metamorphosing earlier. However, tiger salamanders and chorus frogs breed at about the same time both at the study ponds of Sredl and Collins (1991) in Arizona and in the Black Hills and surrounding plains (Smith et al., 1996a, 1996b). It seems likely that the greatest effect of tiger salamander larvae on chorus frog larvae is on landscape variables; chorus frogs are probably more likely to use smaller ponds, such as ephemeral or semipermanent wetlands, in the Black Hills and surrounding plains if the larval density of tiger salamanders is high enough in larger ponds to affect populations of chorus frog larvae in these ponds. Chorus frogs use ponds of all types in the Black Hills and surrounding plains to breed (B. E. Smith, personal observations) but their reproductive success in these pond types is unknown.

Other studies have investigated the role of habitat structure and the priority effect (i.e., which species hatches first) in survival of tiger salamander prey. Sredl and Collins (1992) added complexity to the environment by adding hay to field enclosures with mountain treefrog (*Hyla eximia*) and tiger salamander larvae. They showed that habitat complexity had no effect on the survival of mountain treefrog tadpoles in these enclosures with larval tiger salamanders. It is surprising that a complex habitat does not increase survival considering that such a habitat should provide microhabitats in which frog tadpoles could escape predation. In other studies, the priority effect has been shown to be very important. The wood frog is another frog similar to chorus frogs in that it is an early breeding frog that breeds in many types of ponds, and may frequently breed in habitat similar to that used by tiger salamanders for breeding. In Michigan it became common prey of tiger salamander larvae if wood frog tadpoles did not hatch early and grow too large for tiger salamander larvae to eat (Wilbur 1972). Interestingly, large wood frog tadpoles became competitors with tiger salamander larvae if the tadpoles were large enough to avoid predation by tiger salamander larvae.

Chorus frog tadpole densities have also been shown to be important in the development of cannibal morph larvae, although they do not directly cause the development of cannibals (Loeb et al., 1994). Instead, the high food reward received from eating extremely large food items like chorus frog tadpoles (relative to the smaller invertebrates typically eaten by tiger salamander larvae) tends to cause differential growth of tiger salamander larvae (Maret and Collins, 1996). Since relative intraspecific size differences are known to cause development of cannibal morph larvae (Maret and Collins, 1994; Ziemba and Collins, 1999; Ziemba et al., 2000), the presence of chorus frog tadpoles in relatively high density may lead to the development of cannibal morph tiger salamander larvae by increasing size differences amongst the tiger salamander larvae. Since chorus frogs often occur in high density in the Black Hills region (B. E. Smith, personal observations), it becomes even more likely that cannibal morph larvae may eventually be found in the Black Hills area.

To summarize the food habits of tiger salamanders, larvae are opportunistic predators that take the largest prey items available to them (Dodson and Dodson, 1971; Brophy, 1980; Leff and Bachmann, 1988). Nevertheless, they can be selective for prey items (Leff and Bachmann, 1988). Larvae are primarily visually oriented predators that use chemical orientation for the final attack (Lindquist and Bachmann, 1982). They also do not show classical satiation; they continue to look for more prey items after a feeding bout (Lindquist and Bachmann, 1982). They also use a wide variety of foraging strategies throughout their ontogenetic development (Leff and Bachmann, 1986). They eat a wide variety of invertebrate prey and can be important in structuring the biotic and abiotic environment of breeding ponds, whether as typical larvae, branchiate adults, or metamorphs (Sprules, 1972; Holomuzki et al., 1994). They are also likely to have effects on other amphibians, especially chorus frogs in the Black Hills, which are natural prey of tiger salamanders (Loeb et al., 1994; Kiesecker, 1996) and whose breeding period and period of larval growth substantially overlap the breeding period and period of larval growth of tiger salamanders (Smith et al., 1996a, 1996b). The diet of metamorphs is nearly unknown except for in high elevation ponds in Colorado extensively studied by Dodson and Dodson (1971), Sprules (1972), and Whiteman et al. (1994, 1996). Some studies have shown that their stomachs may frequently be empty in the wild (Rose and Armentrout, 1976).

Breeding Biology

A variety of studies have addressed breeding in tiger salamanders. Some basic information is available from various parts of the range, including Alabama (Botts and Folkerts, 1977), Alberta (Russell and Bauer, 2000), Arizona (Allison et al., 1994), British Columbia (Green and Campbell, 1984), Colorado (Hamilton, 1949), Maryland (Stine et al., 1954), Montana (Hill, 1995), New Jersey (Frier and Zappalorti, 1983), New Mexico (Gehlbach, 1965; Webb, 1969), the Pacific Northwest (Nussbaum et al., 1983), Tennessee (Gentry, 1955), Utah (Tanner et al., 1971), and Wyoming (Carpenter, 1953; Koch and Peterson, 1995). More extensive studies have been conducted in Colorado (Reese, 1969), Indiana (Sever and Dineen, 1978), the Llano Estacado of eastern New Mexico and west Texas (Rose and Armentrout, 1976), New Jersey (Hassinger et al., 1970; Anderson et al., 1971), southern New Mexico (Webb and Roueche, 1971), and New York (Bishop, 1941). Petranka (1998) wrote a general discussion of tiger salamander reproduction and Hammerson (1999) offered a general description of breeding in Colorado. For metamorphic populations in the Black Hills a typical breeding season is probably similar to breeding seasons of populations studied in Colorado (Hammerson, 1999) or Montana (Hill, 1995).

Breeding starts with spring migration, which has been discussed in "Movement Patterns", and continues with breeding at the ponds. Males arrive at the breeding ponds slightly before females (Hamilton, 1949; Reese, 1969; Semlitsch, 1983b; Hill, 1995). It is not known exactly how long the breeding period lasts at a specific pond because metamorphs sometimes forage for long periods of time in breeding ponds after the breeding period has ended (Whiteman et al.,1994; Hill, 1995). At any rate it would be necessary to follow marked individuals throughout the breeding season, which has seldom been done. In Colorado studies have found that the breeding season can occur any time from mid-March (Reese, 1969) to early August (Sexton and Bizer, 1978), depending on local conditions of elevation and weather. Hill (1995) found that the breeding season in Montana started in early April, which may be a reasonable estimate for the start of the breeding season in the Black Hills region. The start of breeding appears to be tied to periods of precipitation with nighttime temperatures above freezing (Hamilton, 1949; Reese, 1969; Hill, 1995) or should directly follow the thawing of permanent ponds (Whiteman et al., 1994). However, tiger salamanders also move at extremely cold temperatures, even temperatures below freezing (Hill, 1995). Studies at specific ponds have shown median residence times of 11 (Madison and Farrand, 1998) to 13 (Travis, 1992) days for males, with females staying for shorter periods. During the four years of his study Semlitsch (1983b) found that the median time spent in breeding ponds by females was 9 – 13 days, whereas the median residence time for males was 13 – 44 days. Anderson et al. (1971) found that 50% of eggs at their sites were laid in a week. Whiteman et al. (1994) found that breeding at their study sites lasted 10 – 14 days. This implies that the breeding season in any specific pond or at a certain site should be over rather rapidly.

Courtship in metamorphic eastern tiger salamanders was described by Arnold (1976). Fertilization is internal with the males depositing a sperm packet called a spermatophore that the female inserts into her cloaca. Tiger salamanders tend to gather in ponds in widely dispersed groups of two or three individuals and males begin courtship by nudging the cloaca of females. Males then shove against the lateral or ventral surfaces of females and move females up to a meter. Males then lead females in a tail-tapping walk in which the male maintains contact with the female's dorsum by tapping his tail on her dorsum. The female repeatedly touches the male's cloaca, which stimulates the male to move forward and to eventually deposit a spermatophore. He rapidly undulates his tail while depositing the spermatophore. The female moves forward until her cloaca contacts the spermatophore, then she inserts it into her cloaca. Other males may try to shove the courting male away from the female or distract the courting male by mimicking a female. Males may also deposit spermatophores on top of spermatophores left by other males. A single male deposited multiple spermatophores during a single courtship bout (Whiteman et al., 1999). Males deposited an average of 21 spermatophores per night (Arnold, 1976). Females have also been observed picking up spermatophores left by other males in the absence of those males (Whiteman et al., 1999). Whiteman et al. (1999) showed that courtship behavior in Colorado populations of *Ambystoma tigrinum nebulosum* varied slightly from that in the eastern tiger salamander described by Arnold (1976), but most interestingly found that metamorphs and branchiate adults can interbreed with resultant viable young.

A variety of behavioral and morphological traits of males affect their courtship success. Howard et al. (1997) found that larger males generally had an advantage in mating success and males with longer tails were often preferred as mates by females. Larger males tended to interrupt other courting males more frequently than smaller males (Howard et al., 1997). Males that interrupted courting bouts, if larger than the male they had interrupted, began courting the female (Howard et al., 1997). If they were smaller than the courting male then they began a tactic in which they simulated a female to the interrupted male while simultaneously courting the female (Howard et al., 1997). Howard et al. (1997) found that male-male competition should result in selection for larger body size whereas female choice for mates should result in selection for longer tails. Males have also been observed to mimic females in the absence of females, causing the male that courts them to deposit a spermatophore (Whiteman et al., 1999). This was interpreted by Whiteman et al. (1999) as a tactic used by some males to increase their fitness by causing the male courting them to waste reproductive effort.

Some time after courting eggs are laid in ponds, but the gestation period is not known in tiger salamanders. At study sites in New Jersey, Hassinger et al. (1970) found that eggs were laid on underwater objects such as twigs and reeds, from 30 – 45 cm under water and within 15 cm of the bottom, while Petranka (1998) found them from 50 – 100 cm deep at various sites in the Midwest. They are apparently always laid on underwater objects (Bishop, 1941; Stine et al., 1954; Webb, 1969; Hassinger et al., 1970; Tanner et al., 1971; Webb and Roueche, 1971; Rose and Armentrout, 1976; Sever and Dineen, 1978; Petranka, 1998). Eggs are laid in masses of varying sizes reported to average from 10 – 59 eggs per mass (Bishop, 1941; Stine et al., 1954; Hassinger et al., 1970; Rose and Armentrout, 1976; Botts and Folkerts, 1977), with up to 92 eggs per mass (Stine et al., 1954). Eggs may also be laid singly or in strings of up to 15 eggs per string in some southerly populations (Webb, 1969; Tanner et al., 1971; Webb and Roueche, 1971). The number per mass may be geographically variable (Petranka, 1998). Some populations in Colorado lay eggs in masses (Hamilton, 1949) while some lay them singly (Reese, 1969). Eggs are laid in masses at high elevation (Hamilton, 1949) and singly at low elevations (Reese, 1969), suggesting a thermoregulatory benefit to laying eggs in masses. Multiple egg masses are laid by each female, with as many as 12 masses laid by a single female (Stine et al., 1954). Females are known to lay eggs for up to two weeks (Rose and Armentrout, 1976). Reese (1969) reported that green algae were found inside of eggs in Colorado. Gilbert (1942, 1944) showed a symbiotic relationship between a green alga and *Ambystoma maculatum* that benefited salamanders by causing the larvae to be larger at hatching. Green alga has not been found within tiger salamander eggs in the Pacific Northwest (Nussbaum et al., 1983). Webb and Roueche (1971) probably have the best diagrams of eggs and Reese (1969) and Tanner et al. (1971) measured egg morphology. Eggs and egg laying have not been described in the Black Hills region. Given the variation of egg laying behavior range-wide, tiger salamander eggs may be laid singly, in masses of varying sizes, or in strings in the Black Hills area. There may be adaptive value in laying eggs in masses in the Black Hills area, depending on elevation.

The incubation period of eggs is highly variable and probably depends on local pond and weather conditions. It is probably shorter in more southerly areas where incubation periods as short as two to three weeks have been reported under field conditions (Reese, 1969; Tanner et al., 1971). Under laboratory conditions incubation temperatures of 15 – 21^{o}C have resulted in incubation periods of 6.5 – 18 days (Bishop, 1941; Tanner et al., 1971; Webb and Roueche, 1971). Under field conditions at more northerly sites eggs have been reported to hatch in about three weeks (Illinois; Smith, 1961), 36 days (Maryland; Stine et al., 1954), 40 – 50 days (New Jersey; Hassinger et al., 1970), and 30 – 40 days (New York; Bishop, 1941). None of these authors reported pond temperatures. It might be expected that tiger salamander eggs could hatch in about four weeks in the field in the Black Hills area but it should be noted that there is relatively little data on incubation, especially in the field.

Anderson et al. (1971) reported on the survival of eggs under natural conditions in New Jersey. Most egg mortality occurred early in the season. About half of the eggs that were laid during the breeding season were laid by January 28, but by that date 45% of the eggs that had been laid had died. By March 9, within a few days of hatching, 62% of the eggs were dead. Anderson et al. (1971) attributed the high mortality early in the incubation period to low temperatures and extremely harsh climatic conditions. Overall, 96% of the eggs laid at their three study ponds died, with 100% dying at one pond. Mortality agents were not identified but Anderson et al. (1971) determined that eggs laid as part of larger egg masses had higher survival. Masses containing 60 – 89 eggs fared best with mortality being higher in smaller egg masses (Anderson et al., 1971). Eggs are about 3.0 mm in diameter and surrounded by a jelly coat (Bishop, 1941). Photographs of egg masses can be found in Bishop (1941).

Clutch sizes in the tiger salamander are not easily measurable in the field since females lay eggs in multiple masses or singly. There are only a few direct observations of females laying eggs. Using dissection, Wilbur (1977) reported an average clutch size of 421 ova for 14 eastern tiger salamanders from Michigan. One female from Maryland observed in the laboratory laid 344 eggs (Stine et al., 1954). A female tiger salamander from Kelleys Island in Lake Erie produced 250 eggs (Bogart et al., 1987). Some authors (Koch and Peterson, 1995; Petranka, 1998) have erroneously cited a clutch size as high as 7631 in tiger salamanders from data reported by Rose and Armentrout (1976). This may also be the source of an unattributed statement of 7700 eggs per clutch made by Nussbaum et al. (1983). This was the highest estimate made by Rose and Armentrout (1976) of reproductive potential measured using indirect methods in several larval salamanders. It is not clear what Rose and Armentrout (1976) meant by reproductive potential and the term can mean various things, including total lifetime egg production per female or even a population growth parameter that represents maximum growth potential of a population. It probably does not mean clutch size per year. The fact that reproductive potential was measured in larvae by Rose and Armentrout (1976) makes the statement even more suspicious. Rose and Armentrout (1976) went on to say that, on the Llano Estacado, small morph larvae had an average reproductive potential per female of 625; the large morph females had an average reproductive potential of 805. This seems more similar to an estimate of yearly clutch size. At any rate it is unlikely that tiger salamanders are capable of laying thousands of eggs each year and clutch sizes on the order of 200 – 400 yearly are more likely. Tiger salamanders laid over twice as many eggs as any of the three other *Ambystoma* species studied by Wilbur (1977).

Larvae are 11 – 14 mm total length at hatching (Bishop, 1941; Reese, 1969; Hassinger et al., 1970; Tanner et al., 1971), although they may be somewhat smaller (as small as 9 – 10 mm total length) in more southerly populations (Tanner et al., 1971; Webb and Roueche, 1971). Larvae look like small tadpoles with three pairs of external gills at birth (Bishop, 1941; Webb and Roueche, 1971). Bishop (1941) and Webb and Roueche (1971) provided drawings and photographs of newborn larvae.

The larval period of type 1 regular morph larvae (i.e., those that transform in a single season) is highly variable and depends to a certain extent on the drying regime of the specific pond. A variety of authors have recorded time to metamorphosis of 110 – 140 days (Bishop, 1941; Stine et al., 1954; Sever and Dineen, 1978). Other authors have recorded shorter times to metamorphosis, probably because their study sites dried relatively quickly or were fairly warm. For example, Hassinger et al. (1970) found that the larval period was ca. 75 days, only slightly longer than the incubation time, because eggs incubated during the cold early season while larvae developed during a warmer late season. Larvae forced to gulp air in jars in the laboratory metamorphosed in four weeks regardless of their size (Gehlbach, 1965) and one cohort studied by Rose and Armentrout (1976) went from eggs to metamorphs in 39 days. Tanner et al. (1971) recorded two breeding bouts at their study site. Eggs from the earlier breeding bout hatched ca. late June and eggs from the second bout hatched ca. late July. Because of the warmer weather later in the season, both cohorts reached ca. 90 mm SVL in mid- to late August and metamorphosed at about the same time.

Size at metamorphosis of type 1 regular morph larvae is also highly variable, again depending on weather and drying regime of the pond. Most authors report a size at metamorphosis ca. 90 – 110 mm SVL (Bishop, 1941; Tanner et al., 1971; Webb and Roueche, 1971; Rose and Armentrout, 1976). However, various authors have reported size at metamorphosis for type 1 regular morph larvae at ca. 75 mm (Reese, 1969; Hassinger et al., 1970; Rose and Armentrout, 1976) and Sever and Dineen (1978) reported size at metamorphosis of 53 – 60 mm SVL. Rose and Armentrout (1976) stated that the large morph larvae found at their study sites metamorphosed at 140 – 150 mm SVL.

Size at metamorphosis (types 2 and 3 life histories) or size at sexual maturity (type 4 life history or branchiate adults and branchiate adult cannibal morphs) for other larval types have been less well studied. Where Sexton and Bizer (1978) identified several metamorphic larval forms, the various forms metamorphosed at different sizes. Type 1 larvae metamorphosed at 53 – 55 mm SVL, considerably smaller than type 1 larvae in most parts of the range. They bred in the next warm season but their size at that time was not recorded. Type 2 larvae metamorphosed at a considerably larger size, usually 70 – 80 mm SVL. It appeared that type 2 larvae gained some advantage from delaying metamorphosis since they metamorphosed at a larger size (Sexton and Bizer, 1978). There are no data for type 3 larvae. Size at sexual maturity for branchiate adults (i.e., life history type 4) is very poorly known and existing data are contradictory. Gehlbach (1965) found one sexually mature branchiate adult (a dissected specimen containing yolked eggs) of 103 mm SVL. Collins et al. (1988) found that branchiate adults of the Huachuca tiger salamander matured ca. 100 mm SVL and first bred when one year old (method of determination of maturity not given). Most branchiate adults studied by Webb and Roueche (1971) became sexually mature at ca. 235 mm SVL although a few females matured at ca. 170 mm SVL (determined by dissection and examination of reproductive organs). Sexton and Bizer (1978) found "paedogenic larvae" (presumably branchiate adults) that were sexually mature at 75 mm SVL, although the means of determination of sexual maturity was not discussed. Whiteman et al. (1996) found that branchiate adults grew more slowly than metamorphs but it is not known if the larvae grow more slowly as well, maturing later as a result.

The effects of biotic and abiotic factors on size at metamorphosis, time to metamorphosis, and other larval characteristics have seldom been studied. Brunkow and Collins (1996) found that larval density and variation in the size distribution of larvae affected both time to metamorphosis and size at metamorphosis. Larvae reared at high densities in field enclosures metamorphosed later than those reared at low density. Larvae reared in groups with other larvae of various sizes metamorphosed later and had higher survival than those reared in groups with other similarly sized individuals. Fernandez and Collins (1988) found that larvae reared in clear water or on dark substrates were darker, even as metamorphs, than those reared in turbid water or on light substrates.

Larvae are subjected to many mortality factors. Mass mortality of larvae has been observed several times (Sever and Dineen, 1978; Holomuzki, 1986b; Collins et al., 1988; Worthylake and Hovingh, 1989; Pfennig et al., 1991; Jancovich et al., 1997; Petranka, 1998) and has been observed in the Black Hills (personal observations). The main cause of mass mortality is often simply the drying of a pond but other causes have also been postulated (Holomuzki, 1986b; Worthylake and Hovingh, 1989; Pfennig et al., 1991; Jancovich et al., 1997). Only Anderson et al. (1971) have studied survival of larvae at various stages of development. They found 0 – 8.7% survival of larvae to late larval stage in three ponds and estimated that 385 larvae survived from 11,660 eggs laid at their three study ponds, an average of 3.3% survival per pond. Semlitsch (1983b) determined that survival was very low at two study ponds most of the four years of his study. Recruitment exceeded two juveniles only twice at one pond during these four years. However, recruitment was very high during the other two years at this pond, with 410 and 1041 metamorphosing juveniles leaving the pond during these two years. At the other study pond, recruitment did not exceed two salamanders during any of the four years. He attributed the almost complete loss of cohorts during most years at his study sites to abiotic factors such as variation in climate and drying rate of the ponds. Given the general biology of tiger salamanders (i.e., fairly high clutch sizes, large effect of abiotic factors on survival of eggs and larvae, no parental care), the species could be considered to be an r-selected species and is likely to show high variance in population density from year to year (Anderson et al., 1971; Semlitsch, 1983b; Pechmann et al., 1991; Pechmann and Wilbur, 1994).

Cannibal morph larvae are the most poorly known of all the larval morphs of tiger salamanders. Maret and Collins (1994) showed that only larvae in the upper third of a given larval size distribution developed into cannibals, so cannibal morph larvae are larger than other morphs to begin with. Of course, cannibals tend to be much larger than conspecifics in the same pond because they eat those conspecifics (Ziemba and Collins, 1999). Cannibal morph larvae are also considerably larger than similarly-aged typical morph larvae (Maret and Collins, 1997). Cannibal morphs will eat conspecifics that are nearly their own size (Rose and Armentrout, 1976). Lannoo et al. (1989) found that typical morphs that cannibalized grew faster and metamorphosed sooner than typical morphs that did not cannibalize, and it can be assumed that cannibal morphs obtain a considerable selective advantage by rapid growth to either metamorphose sooner or at a larger size. For example, one cannibal morph larvae transformed in the laboratory at a length of 133 mm SVL (Reese, 1969). Cannibal branchiate adults have been discussed by Powers (1907), Rose and Armentrout (1976), Collins (1981), and Larson et al. (1999), but none of these authors determined size at sexual maturity for this morph.

Demography And Community Ecology

The best way to understand the demography of an organism is to build a life table for a representative population of that organism. To build a life table for an organism it is necessary to know how long individuals live, the proportion of individuals that survive from one age interval to the next, and the number of offspring that each female produces during each age interval. This is difficult for tiger salamanders. For branchiate adults, cannibal branchiate adults, or metamorphs that spend more than one year in a larval stage, there are virtually no survival data for any life stage. For the "typical" tiger salamander population (i.e., type 1 life history strategy), only the most meager data are available. Slavens and Slavens (2002) have collected longevity information for tiger salamanders kept in captivity; Anderson et al. (1971) studied survival from egg laying to metamorphosis; Stine et al. (1954), Wilbur (1977), and Bogart et al. (1987) recorded clutch size in a few females; and age at first reproduction was estimated at one year in one study (Pechmann et al., 1991). Incorporating many assumptions a theoretical fecundity schedule could be compiled from these data.

An estimate of longevity can be derived from Slavens and Slavens (2002). Maximum ages recorded in captivity by a variety of institutions reporting to this website are 5 – 20 years. These are all known ages from adults kept in captivity and are not statistical samples. Therefore they should be considered idiosyncratic data. Tiger salamanders in the wild may not live as long, but of course the adults brought into captivity were adults when captured and had already lived in the wild for an unknown length of time. I will estimate maximum age in the wild of seven years.

Survivorship in the first year is known from a single study and adult survivorship is unknown. Anderson et al. (1971) found that 385 larvae metamorphosed from 11,660 eggs laid at three study ponds in New Jersey, an average survival rate of 3.3% in the first year of life. Although other studies have confirmed extremely low survivorship during the first year in eastern tiger salamanders (Semlitsch, 1983b), no others have made direct estimates of survivorship in this species. I will assume that survivorship is steady past the first year until death at seven years.

Three studies have listed clutch sizes in the tiger salamander but in only one study was a statistical sample collected. Wilbur (1977) found that clutch size averaged 421 eggs in 14 female eastern tiger salamanders collected in Michigan. Other workers have reported clutch sizes of 344 and 250 eggs from single females (Stine et al., 1954; Bogart et al., 1987). I will also assume an annual reproductive cycle, which Duellman and Trueb (1986) stated is the norm in most non-plethodontid salamanders.

Age at sexual maturity has largely gone unreported. However, Pechmann et al. (1991) stated that most eastern tiger salamanders breed at one year of age. Sexton and Bizer (1978) reported that tiger salamanders in some high elevation ponds in Colorado do not metamorphose until the second or third active season. However, I will estimate age at first reproduction at one year.

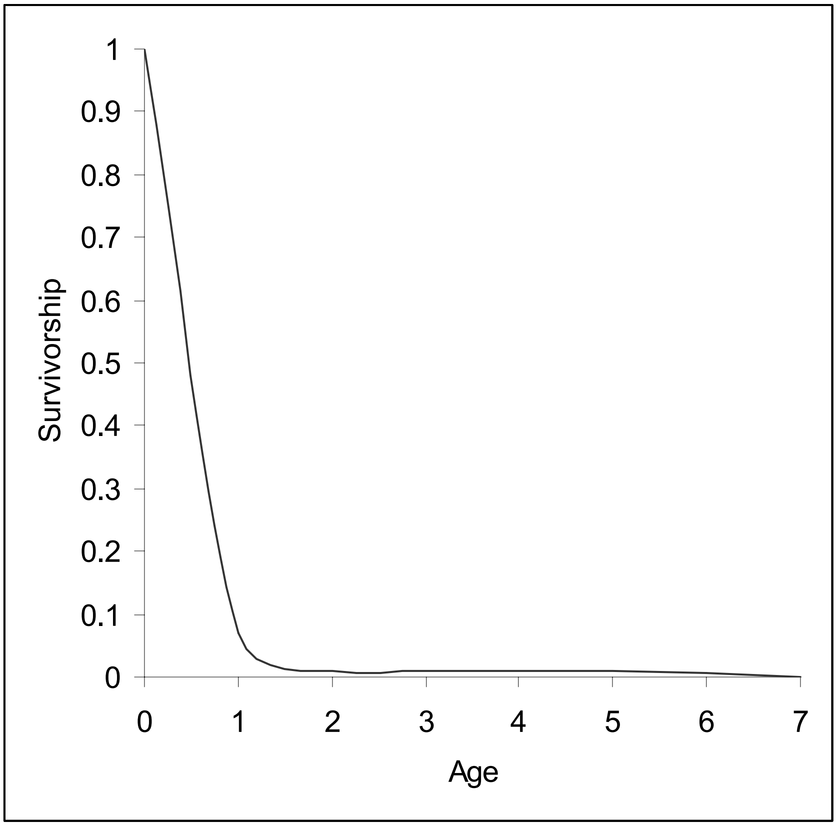
These demographic data are assembled in table 1. There are two things that are notable about this hypothetical fecundity schedule. First, the species clearly has a type 3 survivorship curve (figure 1). Virtually everything about this fecundity schedule is very hypothetical, but data from two different sources (Anderson et al., 1971; Semlitsch, 1983b) and anecdotal evidence on mass mortality of larvae (Sever and Dineen, 1978; Holomuzki, 1986b; Collins et al., 1988; Worthylake and Hovingh, 1989; Pfennig et al., 1991; Jancovich et al., 1997; Petranka, 1998) indicates a type 3 survivorship curve in this species as well. This much seems relatively certain. The second point of interest is that the net reproductive rate, R_0, still exceeds one in this hypothetical population despite enormous mortality in the first year. In fact, R_0 is large enough to indicate that this would probably be a very rapidly growing population. If the maximum age of a female tiger salamander is lowered to six years then $R_0 = 1.29$, still a rapidly growing population. If tiger salamanders lived to five years, then $R_0 = 0.92$, which would indicate a declining population. The net reproductive rate remains high in this species despite heavy mortality in the larval stage because of the high reported clutch sizes.

Table 1. Fecundity schedule for a hypothetical population of type 1 tiger salamanders (*Ambystoma tigrinum*) with life history parameters derived as described in the text.

"Proportion alive" is the proportion of the original cohort alive at the beginning of each time interval. Fecundity per salamander is derived by multiplying hypothesized clutch size per salamander per year (421) by estimated survival of this clutch (3.3%), as explained further in the text. The term "$l_x m_x$" represents the multiplication of the "proportion alive" and "fecundity" columns. $R_0 = \Sigma\, l_x m_x$ and represents net reproductive rate, which is a population parameter but can be thought of as the lifetime reproductive output of an average single female in the population. For these data $R_0 = 1.60545$. $R_0 > 1.0$ is a growing population, $R_0 = 1.0$ is an equilibrial population, and $R_0 < 1.0$ is a shrinking population. For a further explanation of the construction of fecundity schedules see Krebs (2001).

Age interval (years)	**Proportion alive**	**Fecundity**	**$l_x m_x$**
0 – 1	1.000	0.0	0.0
1 – 2	0.033	13.9	0.4587
2 – 3	0.028	13.9	0.3822
3 – 4	0.022	13.9	0.3058
4 – 5	0.016	13.9	0.2294
5 – 6	0.011	13.9	0.1529
6 – 7	0.006	13.9	0.0764

Figure 1. Survivorship curve for hypothetical tiger salamander population plotted using assumptions as outlined in the text.



Of course, there are serious shortcomings in these data. Clutch size has been determined in a total of 16 salamanders in three studies and ranged from 250 – 421 eggs (Stine et al., 1954; Bogart et al., 1987; Wilbur, 1977). The best study used a sample of 14 females and coincidentally is the highest estimate of clutch size in tiger salamanders (Wilbur, 1977). Clutch size could be substantially lower than that used in table 1. I have also assumed constant clutch sizes throughout life in tiger salamanders whereas reproductive output probably declines with age in most organisms. Age at death is estimated from data on a few captive specimens. Survivorship is only known for larval salamanders from a single study (Anderson et al., 1971) and adult survivorship in the wild is unknown. Finally, these data come from just a few studies that have been conducted on the eastern tiger salamander. Demographic data could be substantially different in western populations.

However, the data are at least useful in pointing out that tiger salamanders are almost certainly an r-selected species with characteristics common to such species, including fairly rapid development, potentially high reproductive rate, early age at first reproduction, probably a relatively short life with few episodes of reproduction, high mortality of young, and highly variable population size. Pechmann et al. (1991) and Pechmann and Wilbur (1994) have verified the variable population size of the species. The data of Semlitsch (1983b) also show this inherent variation in population size, with annual recruitment of 0 – 2 juveniles per year at one study pond during the four years of his study. At the other study pond, recruitment was 0 and 1 during two years but 1041 and 410 juvenile salamanders during the other two years. The conservation importance of these data is to recall that species with high growth rates and high variation in population densities can recover rapidly from low population size, although they can also become locally extinct during periods of low density.

Standard ecology textbooks suggest that the mortality of populations of r-selected species is typically controlled by various abiotic factors (Stiling, 2002). Semlitsch (1983b) also suggested that abiotic factors were very important mortality agents in his study ponds and he especially noted climatic variation, the drying rates in ponds, and the structure of ponds as the largest influences on success or failure of a reproductive season in tiger salamanders. However, Anderson et al. (1971) stated that there were two major classes of control exerted on salamanders in their first year of life, one abiotic and one biotic. These factors affected different larval stages. They blamed low early-season temperatures for most embryonic mortality, although they also noted that freezing, predation, and low pH caused the death of many embryos. On the other hand, they noted that hatchlings faced heavy mortality from predation with abiotic sources of mortality being negligible at this stage. After these early stages the larvae were free-swimming and Anderson et al. (1971) felt that they faced little mortality.

Few papers give quantitative data on tiger salamander abundance at any sites and all the published abundance estimates are confounded by the fact that the studies were conducted during the breeding season. At this time, males are typically migrating into ponds, where they are known to stay longer than females (Semlitsch, 1983b; Travis, 1992; Hill, 1995; Madison and Farrand, 1998). Migration will therefore cause abundance in ponds to fluctuate probably on a daily basis. At one 0.25 ha pond near South Bend, Indiana, Sever and Dineen (1978) estimated a population of 360 – 787 individuals in 1976 and 245 – 1132 individuals in 1977. Botts and Folkerts (1977) estimated that 151 salamanders were using a pond of unreported size in southern Macon Co., Alabama. Over four years, Semlitsch (1983b) found an average of 57 male and 30 female metamorphs at one 1 ha study pond (range = 21 – 81 for males; range = 8 – 44 for females) and 13 male and 11 female metamorphs at another 1 ha study pond (range = 3 – >20 for males; range = 0 – >25 for females) in South Carolina. Juvenile recruitment showed tremendous variability during the four years as well, ranging from 1 – 1041 per year at the first pond and from 0 – 2 (0 in three years) per year at the second pond. Deutschman and Peterka (1988) found high variance in salamander population size, even within a single year. At one of their study lakes in North Dakota they found that salamander density varied from ca. 800 – 1000 per ha in May 1981 (overwintering larvae from the 1980 cohort) to ca. 5000 per ha in July 1981 (1980 cohort plus spring 1981 cohort). Wiedenheft (1983) found high variance in salamander densities amongst three closely-spaced and similar prairie pothole lakes in south-central North Dakota. He found 678 salamanders/ha at one 24 ha lake, 4995 salamanders/ha at one 10 ha lake, and 5276 salamanders/ha at one 10.5 ha lake. Salamander biomass ranged from 78 – 182 kg/ha and peaked in late July to mid-September, depending on the lake. In general, tiger salamander densities appear highly variable from year to year and from pond to pond.

For any organism, populations can be limited by the effects of the environment, competition with other organisms, predation by other organisms, the availability of food, the effect of parasitism and diseases, and mutualistic interactions with other species. Despite the large volume of literature on the tiger salamander the influence of most of these factors on populations of tiger salamanders is very poorly known. Analyses of the relative importance of various sources of mortality, such as key factor analysis (Varley and Gradwell, 1960), have not been done on tiger salamanders.

The abiotic environment has obvious effects on populations of tiger salamanders. Anderson et al. (1971) and Semlitsch (1983b) noted that abiotic factors were often important in controlling the population size of larval tiger salamanders at their study sites. Sever and Dineen (1978), Bradford (1993), Vertucci and Corn (1994), Petranka (1998), and Hammerson (1999) have noted periods of mass mortality that seem to be associated with abiotic factors, including deaths while overwintering in ponds (Bradford, 1993; Vertucci and Corn, 1994) and deaths associated with pond drying (Sever and Dineen, 1978; Petranka, 1998; Hammerson, 1999; personal observations). The relative importance of abiotic factors seems potentially large given that tiger salamanders are ectotherms that breed in extremely cold waters early in the season. They are also exposed to pond freezing if overwintering as larvae or branchiate adults.

Competitors have not been examined, although intraspecific competition is probably important where salamander densities are high. Tiger salamanders are usually at the top of the food chain in most ponds, at least as large larvae and as metamorphs (Holomuzki and Collins, 1987; Holomuzki et al., 1994), so they may have few competitors. It is not known what sorts of animals could compete with tiger salamanders on land, but animals that are carnivores that eat smaller prey items and forage in burrows probably potentially compete with tiger salamanders.

Predation clearly has potential to be a major source of mortality affecting tiger salamanders at various stages of their life. Predation caused most mortality of hatchling tiger salamanders at two study ponds in New Jersey (Anderson et al., 1971). Madison and Farrand (1998) found that tiger salamanders frequently succumbed to predation in small mammal runways, apparently by shorttail shrews (Blarina *brevicauda*). They also found that metamorphs avoided bluegills in breeding ponds, suggesting that they were a potential source of mortality or injury. Smith et al. (1996a) found a metamorphic tiger salamander in the stomach of a Plains garter snake (*Thamnophis radix*). Other predators have been known to eat tiger salamander eggs, larvae, or adults, including caddisflies and caddisfly larvae, newts, tiger salamander larvae, dragonfly naiads, diving beetles, other salamanders, garter snakes, killdeers, bitterns, grackles, gray jays, bobcats, coyotes, badgers, owls, and other snakes (Carpenter, 1953; Stine et al., 1954; Dalrymple, 1970; Anderson et al., 1971; Webb and Roueche, 1971; Rose and Armentrout, 1976; Sever and Dineen, 1978; Morin, 1983; Holomuzki, 1985a, b; Holomuzki and Collins, 1987; Wissinger and Whiteman, 1992). Tiger salamanders produce tail secretions that may function to repel predators, indicating that predation is a severe enough threat that anti-predator adaptations have evolved in tiger salamanders (Brodie, 1977). Various fish, including stocked predaceous fish, are well known predators of tiger salamander eggs and larvae (Blair, 1951; Carpenter, 1953; Collins and Wilbur, 1979; Collins, 1981; Degenhardt et al., 1996; Corn et al., 1997; Hammerson, 1999). Tiger salamanders therefore depend on fishless ponds for reproduction sites. An unusual form of population regulation through predation could occur in ponds with cannibal morph larvae. A high density of conspecifics causes the formation of cannibal morphs (Collins and Cheek, 1983) and shows obvious potential for regulation of typical morph populations by cannibal morphs. Predation could be an important but mostly unstudied source of mortality for tiger salamanders at all life stages.

It is hard to determine whether food limits populations. At least one study (Sprules, 1972) showed that populations of branchiate adults seem to prevent colonization of high elevation lakes by certain species of cladocerans, probably because of high levels of predation on this cladoceran by branchiate adults. This suggests that food availability could limit the size of tiger salamander populations, at least as larvae or branchiate adults. However, Holomuzki et al. (1994) found no effect of tiger salamander larvae on the zooplankton community, at least at normally densities of tiger salamander larvae.

The frequency of occurrence of diseases and parasitic infestations is unknown but the effects can be devastating to local populations. Larvae can be heavily infested with leeches but it is unknown to what extent these affect the larvae (Carpenter, 1953; Holomuzki, 1986b). Holomuzki (1986b), Worthylake and Hovingh (1989), and Pfennig et al. (1991) have attributed large die-offs in Arizona and Utah to bacterial infections. Two of these incidents were associated with heavy grazing (Worthylake and Hovingh, 1989; Pfennig et al., 1991), which can increase nitrogen levels in the water and may increase the likelihood of infection from opportunistic bacteria (Worthylake and Hovingh, 1989). The iridovirus *Ambystoma tigrinum* Virus (ATV) has been isolated from populations of the Huachuca tiger salamander and periodically causes mass mortality in populations of this subspecies (Jancovich et al., 1997). It is the first lethal virus isolated from salamanders (Jancovich et al., 1997) and is transmissible to other salamanders, including various ambystomatids (Jancovich et al., 2001). Although poorly studied, diseases could be important episodic mortality agents for tiger salamanders and could periodically wipe out large populations, including entire populations of salamanders inhabiting a single pond. Iridoviruses have also been implicated in mass mortalities of tiger salamanders in Utah, Maine, and North Dakota (United States Geological Survey, 1998).

Mutualistic interactions of tiger salamanders and other species are very poorly known. However, various authors have reported that tiger salamanders are often found in rodent burrows (Vaughan, 1961; Costello, 1969; Reese, 1969; Hoogland, 1995; Hammerson, 1999; Kolbe et al., 2002). Kolbe et al. (2002) recently reported on a population of tiger salamanders living in black-tailed prairie dog burrows (*Cynomys ludovicianus*). In this paper we speculated that tiger salamanders gained a number of advantages from living in prairie dog burrows, including constant high humidity during the relatively dry and hot prairie summer, possibly a ready source of food from insects attracted to the droppings of the prairie dogs (and perhaps even newborn prairie dogs), and a hibernation site. This study system is ideal for a natural history study of metamorphic tiger salamanders similar to the study of Madison and Farrand (1998), since the tiger salamanders are easily observed at the entrances of prairie dog burrows at night and are close by a breeding pond.

From this analysis and published work, it seems that the most important factors controlling tiger salamander populations are abiotic factors including the weather, hydrologic period, and structure of ponds; and biotic factors such as diseases and, at certain points in the life cycle, predation.

Risk Factors

In the previous pages I have outlined a variety of natural factors that could control populations of tiger salamanders. A variety of anthropogenic risks also confront tiger salamanders.

The elimination of wetlands suitable for breeding is the best-known risk factor affecting many pond-breeding amphibians (Semlitsch and Bodie, 1998; Semlitsch, 2000b). Smaller wetlands (<4.0 ha) tend to have the largest and most diverse populations of breeding amphibians (Semlitsch and Bodie, 1998; Semlitsch, 2000b). Semlitsch (2000b) has shown that elimination of wetlands smaller than 4.0 ha (the current U. S. Army Corps of Engineers protection threshold) would not only cause destruction of the amphibian populations at these sites but would also lead to reduced colonization of remaining wetlands. Tiger salamanders can also be highly philopatric (Madison and Farrand, 1998) and it is likely that a metamorphic population using a specific pond, although potentially not directly affected when the pond is eliminated, eventually goes locally extinct because they keep returning year after year to the same site, which of course is no longer available for reproduction.

It should be kept in mind as well that metamorphic tiger salamanders are terrestrial for most of their adult life. They use aquatic habitat in which to breed but then migrate into surrounding uplands to forage for the active season (Madison and Farrand, 1998; Semlitsch, 1998). Semlitsch (1998) determined that a buffer zone of 164.3 m is needed around each wetland to protect at least 95% of the breeding population of a pond, based on movement data collected on six species of ambystomatid salamanders, including tiger salamanders. Current terrestrial buffer zones mandated by law are inadequate to protect salamanders based on these data. For example, both Florida and Massachusetts require protective terrestrial buffer zones of 100 ft (30.8 m) around each wetland (Semlitsch, 1998).

Fortunately for tiger salamanders, they may hibernate close to breeding ponds (Reese, 1969; Kolbe et al., 2002). If this is the case, then protection of the breeding pond and a 150 – 200 m buffer zone surrounding the pond is probably sufficient to protect the population. However, it is important to maintain immigration/emigration routes amongst breeding ponds if they exist. Although longer distance migration has not been studied in tiger salamanders they are frequently discovered in areas far from breeding sources (personal observations; Jason Kolbe, personal communication, 1996; George Rinker, personal communication, 2001). Gene flow from one breeding population to another can be an important pathway to increase genetic variability both within and among populations and it is likely that migratory pathways, if any can be discovered, are important to maintenance of the genetic integrity of metapopulations. Unfortunately, nothing is known about where or how tiger salamanders migrate amongst populations. Developments placed along these pathways will, of course, disrupt normal movement. Migration is an important aspect of the natural history of tiger salamanders that remains poorly studied. Studies of migration would help develop management plans for the species.

Also unknown is the effect of soil manipulation on tiger salamander metamorphs, such as soil compaction or removal by various types of machinery or vehicles. Since tiger salamander metamorphs spend a considerable amount of time underground (Madison and Farrand, 1998), they are susceptible to anything that affects the subterranean habitat, including soil compaction, earth removal, skidding of logs, or excavation. It is possible that any of these manipulations will affect populations of metamorphs. However, if metamorphs stay near water sources to forage during most of the active season, then elimination of developments from water sources and surrounding buffer zones may reduce or eliminate the effects of soil manipulations on tiger salamander populations by machinery. Of course, it is not known where or how salamanders immigrate or emigrate from breeding ponds, nor how often. Therefore, the effect of moving soil in any management area cannot be known with certainty. For example, digging a ditch between two breeding ponds several kilometers apart could cut off a migratory pathway used by metamorphs moving amongst these sites.

Diseases have been discussed (see REVIEW OF TECHNICAL KNOWLEDGE, Demography And Community Ecology"), but they are deserving of mention as a risk factor that can be exacerbated by human intervention. Diseases have been blamed for mass mortalities in tiger salamanders (Holomuzki, 1986b; Worthylake and Hovingh, 1989; Pfennig et al., 1991; Jancovich et al., 1997; United States Geological Survey, 1998). Carey et al. (1999) and Daszak et al. (1999) have recently reviewed diseases in amphibians. Viruses such as iridoviruses have been blamed for population declines or extinctions in ranid frogs (Cunningham et al., 1996, Jancovich et al., 1997, Daszak et al., 1999). There has been recent concern about the fungal disease chytridiomycosis in various species of frogs (Berger et al., 1998; Carey et al., 1999; Daszak et al., 1999, 2000; Morell, 1999; Milius, 2000). However, diseases in salamanders are poorly known.

The first study to report on epizootic diseases of salamanders is that of Jancovich et al. (1997), who found an iridovirus in the endangered Huachuca tiger salamander. This virus was 100% lethal in these populations. The virus is transmissible to other salamander hosts as well (Jancovich et al., 2001). Without safeguards, diseases can be transmitted by humans from one breeding pond to another causing population declines across larger regions, as has apparently occurred in ranid frogs (Daszak et al., 1999). Carey et al. (1999) have suggested a number of ways that diseases can be introduced into natural populations of amphibians, including fish stocking, introduction of non-native amphibians such as bullfrogs or extralimital populations of tiger salamanders, wind-blown insects, the activity of birds or other animals, workers monitoring amphibian breeding sites, anglers, or other tourists.

The acidification of breeding ponds could also have negative effects on tiger salamanders. Corn et al. (1989) studied acidification in Colorado and Wyoming and did not find tiger salamander declines that were associated with acidification. Harte and Hoffman (1989) found significant declines of tiger salamanders in the Mexican Cut Nature Conservancy Preserve in the mountains of Colorado from 1982 – 1988 and attributed them to pond acidification that adversely affected tiger salamander eggs and larvae. However, they were not able to definitively establish that acidification caused the population declines in this area. In an extensive study of the effects of acidification on tiger salamanders, Kiesecker (1991) found that tiger salamanders reared in the laboratory had significantly reduced egg viability and significantly increased time to hatching and time to metamorphosis at $pH < 6.0$. The effects were stronger as pH decreased to 4.5, the lowest pH tested by Kiesecker (1991). Tiger salamanders were also less efficient predators on chorus frogs if raised at $pH < 6.0$ (Kiesecker 1991). This effect was also more pronounced as pH was reduced to 4.5.

Normal pH of snowmelt is ca. 5.6 (Likens et al., 1976; Johnson and Gordon, 1987). Several ponds in Colorado have been found to have $pH < 5.0$, with the lowest of pH 4.82 (National Atmospheric Deposition Program, 1989). Since pH is a multiplicative rather than additive function, a pH of 4.82 is eight times more acidic than normal precipitation of 5.6. Kiesecker (1991) has provided good evidence that tiger salamanders not only contend with adverse effects of low pH under normal situations, but they are also severely affected by pH that is much less than normal. Acidification would present a grave concern for the health of tiger salamander populations living in acidified ponds. It may also explain why tiger salamanders are frequently found in ponds of high pH, up to $pH = 9.0$ (Reese, 1969).

The effects of pollutants have not been well studied in tiger salamanders. Johnson and colleagues (Johnson et al., 1999, 2000a, 2000b) have studied the effects of trinitrotoluene (TNT), a defense-related compound, on tiger salamanders. These researchers were mainly concerned with the metabolic pathways whereby tiger salamanders metabolized TNT, but it did not seem that TNT had major negative effects on salamanders. However, of more relevance to Black Hills populations of tiger salamanders are studies on various environmental pollutants that are probably present in the Black Hills ecosystem. Lefcort et al. (1997) studied the effects of motor oil, silt, and the water mold *Saprolegnia parasitica* on larval ambystomatids, including the tiger salamander. Motor oil and silt reduced the growth of larval tiger salamanders, and ponds with high concentrations of these pollutants produced small salamanders that weighed less than those produced from unpolluted ponds. Presence of these pollutants also increased the susceptibility of tiger salamanders to the parasitic water mold *S. parasitica*. Small size and weight at metamorphosis presumably produce poorly-adapted tiger salamanders, and *S. parasitica* has been linked with amphibian declines in the Pacific Northwest (Blaustein et al., 1994).

The effects of the herbicide atrazine on tiger salamanders were studied by Larson et al. (1998). Amphibians have been shown to be more susceptible to pesticides than many other vertebrates (Boyer and Grue, 1995; Howe et al., 1998). Levels of atrazine in post-planting samples in corn and soybean growing regions in the United States commonly exceed maximum levels allowed by the United States Environmental Protection Agency (Thurman et al., 1992). Larson et al. (1998) found in laboratory experiments that atrazine elevated plasma thyroxine levels and depressed plasma corticosterone levels. Tiger salamanders in their experiments took longer to metamorphose and were smaller and weighed less when they metamorphosed. This study demonstrated that tiger salamander life history traits could be affected by atrazine, but it is not clear whether levels of atrazine commonly encountered in the environment were used in the experiments. Since atrazine is commonly applied in the northern Great Plains (Larson et al., 1998), atrazine should be considered an anthropogenic risk factor that tiger salamanders stand a high chance of encountering and which modifies some of their life history characteristics, probably to deleterious effects. However, studies that address environmentally relevant levels of atrazine are needed.

The stocking of predaceous fish has clear implications for populations of tiger salamanders. Introduction of predaceous fish such as trout is well-known to cause population declines in tiger salamanders (Corn et al., 1997), and tiger salamanders do not breed in ponds with fish (Bishop, 1941; Carpenter, 1953; Travis, 1992). To conserve tiger salamanders, stocking of fish must be eliminated in breeding ponds.

Finally, overcollection of tiger salamanders as fish bait or for biological supply houses can be significant. Tiger salamanders are commonly used as fish bait. They are not commonly used for dissection in high school and university classrooms but are used for some courses. No statistics are kept, but it is known that 174,772 northern leopard frogs were collected from 1994 – 2000 in Nebraska, ca. 120,000 in 1996 alone, mostly by biological supply houses for dissection, so overcollection can clearly be a problem for some species in some cases (Dan Fogell, personal communication, 2002).

Response To Habitat Changes

The response of tiger salamanders to various management activities and natural disturbances is speculative as research into the effects of these activities and disturbances on tiger salamanders has largely not been done. In addition, the natural history of metamorphs is poorly known so the reaction of metamorphs to various management practices and natural disturbances is generally unknown. Various management practices used in the Black Hills National Forest and natural disturbances that occur on the forest are listed below and their possible influences on larval and metamorphic tiger salamanders are discussed.

Timber And Fuelwood Harvest

To maintain 95% of a tiger salamander population at a breeding pond, timber harvest within 200 m of the pond should be discouraged (Semlitsch, 1998). Obviously, large scale habitat alteration directly around a pond is contrary to the objectives of management of tiger salamander populations living in and around the pond. Also, pollution and siltation within a pond is not healthful to tiger salamanders living within that pond and can cause reduced growth in tiger salamanders (Lefcort et al., 1997). Pollution and siltation associated with logging will cause similar problems, making the designation of buffer zones even more important. Semlitsch (1998) emphasized the importance of upland habitat within 150 – 200 m of a breeding pond because he (and Madison and Farrand, 1998) demonstrated that metamorphs use this upland area for foraging during the active season. Disturbance of this area will almost certainly have detrimental effects on populations of metamorphs and larval tiger salamanders living in or around the pond. Pollution and siltation associated with logging could cause problems for breeding ponds even some distance away from the direct effects of logging, so buffer zones may need to be larger depending on local conditions.

In contrast to what is known about the use of upland habitat around breeding ponds, the long distance movements of metamorphic tiger salamanders are almost completely unknown. Timber harvest some distance from ponds could cut off gene flow between two or more breeding ponds, but in the absence of data it is impossible to determine how much this would influence the genetic integrity of the metapopulation of an area. Ponds that are closer together could constitute a metapopulation with some movement amongst these ponds. Potentially, timber harvest should be restricted in the entire area to maintain genetic integrity of the metapopulation. However, in the absence of data a clear determination of management actions is impossible to make.

Fuelwood harvest should probably be under the same restrictions as timber harvest, however fuelwood harvest is probably a less intensive form of habitat modification. Low levels of fuelwood removal are probably not as problematic as large-scale logging operations.

Recreation

Different types of recreation will have different effects on tiger salamanders. Light usage of areas by hikers, cross-country skiers, bird watchers, or other visitors may not damage breeding ponds or terrestrial habitat around the ponds as long as visitors stay out of the ponds themselves to avoid spreading disease from pond to pond. However, other types of recreation could damage tiger salamander populations.

Two of the clearest threats to tiger salamanders are stocking of ponds with predaceous fish (and subsequent use of those breeding ponds by anglers, along with introduction of bait fish), and heavy use of an area by off-road vehicles. The damage caused by predaceous fish has been well-documented (Blair, 1951; Carpenter, 1953; Collins and Wilbur, 1979; Collins, 1981; Corn et al.;

1997) and anglers and stocked fish can introduce diseases to ponds and move diseases from pond to pond (Carey et al., 1999). Off-road vehicles are damaging to ponds, not only because of the physical damage caused to ponds and soil compaction in upland habitat near ponds but also because of pollution caused by any type of motorized vehicle. Although tiger salamanders are surprisingly resistant to pollutants such as silt and motor oil, these pollutants cause reduced growth and affect the prey that tiger salamanders depend on (Lefcort et al., 1997). Off-road vehicles can also cut off migration routes amongst tiger salamander breeding ponds, depending on where the roads are placed. Off-road vehicle use within a buffer zone of 150 – 200 m is undesirable (Semlitsch, 1998), and off-road vehicle use should be restricted in areas where many breeding ponds may be situated close to each other.

Livestock Grazing

Livestock damage ponds by standing in the ponds, eating high quality forage around the ponds that may provide refuges for metamorphic and larval salamanders, and defecating in pond water. Although Hammerson (1999) noted the ability of the tiger salamander to tolerate highly polluted water, others (Worthylake and Hovingh, 1989; Pfennig et al., 1991) have associated some mass mortality events with overgrazing. Livestock can be easily eliminated from breeding ponds and upland habitat around the ponds by simply fencing off the area. Some water can be redirected into stock tanks so that livestock can still obtain water while leaving breeding ponds relatively untouched by livestock. Again, the buffer zone of 150 – 200 m of Semlitsch (1998) is a recommended guide for the management of tiger salamanders.

Mining

Mining produces a variety of heavy metals such as mercury, cadmium, lead, aluminum (often a byproduct of acidification caused by mining), zinc, iron, and copper, and the deleterious effects of mining are well-known for some amphibians (Porter and Hakanson, 1976; Diana and Beasley, 1998). One drainage in Colorado lacked breeding populations of boreal toads due to pollution from one mine that ceased operation ca. 75 years previous (Porter and Hakanson, 1976). Although the effects of heavy metals have not been studied in tiger salamanders it seems reasonable to assume that they would suffer from heavy metal pollution as do other amphibians (Diana and Beasley, 1998). In addition, Kiesecker (1991) has provided conclusive evidence that acidification harms tiger salamanders and has shown that even normal pH levels (i.e., those found in rainwater and snowmelt, pH = 5.6) are not well-tolerated by tiger salamander eggs and hatchlings. It may be important to protect tiger salamanders from sources of acidification, such as mining and abandoned mines. Tiger salamander surveys are needed in areas that were formerly mined in the Black Hills. If no tiger salamanders exist at these localities water quality should be sampled. It is important that new mines not cause acidification of drainages in which tiger salamanders live.

Prescribed Fire And Fire Suppression

The effects of fire on herpetofaunal communities are known from a single study conducted in Florida (Mushinsky, 1985). Contrary to expectations, prescribed fire was found to increase herpetofaunal densities at this study site. The use of fire in national forests has recently been controversial and many differing opinions exist as to how often to burn, whether to burn, and how much effort should be spent suppressing fire. Parrish et al. (1996) have convincingly shown that fire frequency has decreased in the Black Hills from historical levels and that this has caused changes in the Black Hills landscape, including increased windrow pine and fuel buildup, and it has increased the density of ponderosa pine. Compared to pre-European levels, forest fires probably now burn hotter and less frequently (Parrish et al., 1996). Fire has always been part of the ecology of the western United States and the Black Hills and a natural fire regime is probably one of the selective forces alongside which western populations of the tiger salamander evolved. In addition, metamorphic tiger salamanders seem to live a primarily subterranean life. The restoration of a natural fire regime (low intensity fires of ca. 10 – 15 years' frequency, Parrish et al., 1996) would probably not unduly harm tiger salamanders in the Black Hills. However, it would not be advisable to set these fires at times of peak migration or metamorphosis when large numbers of tiger salamanders may be moving across the landscape.

Non-Native Plant Establishment And Control

Non-native plants are an issue of concern in the Black Hills and these plants are controlled through a spraying program. Personnel at the Black Hills National Forest have offered assurances that chemicals are carefully sprayed near water sources and that care is taken in application of sprays. Nonetheless, it is critical that due caution continue to be exercised in this spraying program, especially during the egg laying and larval season, to avoid harming eggs, larvae, and metamorphs of tiger salamanders while they are in breeding ponds. It should also be kept in mind that metamorphs use an area around the pond for foraging after the breeding season and that their skin is highly permeable to any toxin, whether man-made or natural. Care should be used when spraying within the upland buffer zone at any time of year. Atrazine is the only herbicide whose effects on tiger salamanders have been studied (Larson et al., 1998; see REVIEW OF TECHNICAL KNOWLEDGE, Risk Factors).

Natural Disturbances

The effects of various natural disturbances are unknown in many cases except in the case of severe weather, which is uncontrollable and which has been discussed throughout this paper, and disease, which has also been discussed. Unlike weather, the effects of diseases can and should be managed by appropriate management agencies. Fish stocking should be discouraged where possible, especially indiscriminate fish stocking often practiced by the public that is not part of a managed fish stocking program. In my work in the Black Hills I have frequently found various species of fish in a variety of ponds, often not introduced there by any management agency and presumably tossed into ponds as bait fish or for sport by the public. Tiger salamanders are also used as bait and are frequently stocked in ponds and moved around the landscape. Collins (1981) has studied this problem and various individuals are known to raise and stock ponds in the Dakotas (Diane Larson, personal communication, 1996, and personal observations). Fish stocking and stocking of extralimital amphibians have both been described as risk factors for the spread of disease (Carey et al., 1999). Other risk factors are the movement of anglers, tourists, and investigators from one breeding pond to another (Carey et al., 1999). Persons that monitor breeding ponds need to be aware of the risks of moving from pond to pond and take appropriate countermeasures, such as disinfecting clothing, equipment, and machinery used in sampling breeding ponds. Although iridoviruses are natural disturbances, they cause 100% mortality (Jancovich et al. 1997) and can rapidly become a management problem if human agents pass them indiscriminately from pond to pond.

SUMMARY

As suggested in the introduction to this paper the tiger salamander may need to be considered a sensitive species by the USDA Forest Service in the Black Hills National Forest for some time to come. However, the reason I suggest this is because we know so little about critical aspects of tiger salamander biology, such as movement patterns, survivorship of adults and juveniles, population densities, and other critical population parameters. There is no evidence whether tiger salamanders are rare or common in the Black Hills. However, evidence suggests that some management decisions made by the USDA Forest Service on the Black Hills National Forest are potentially not in the best interests of the tiger salamander. Through a sustained survey and inventory program and detailed follow-up studies of specific populations, the biology of Black Hills tiger salamanders could become well known in the area. Many studies in other parts of the range point the way to designing such studies. Through collaboration with professional herpetologists, the USDA Forest Service in the Black Hills National Forest could provide further understanding of a complex and poorly known salamander, in a part of its range where it is little known, in spite of all the studies that have been done on this species.

REVIEW OF CONSERVATION PRACTICES

Management Practices

Although endangered in a number of eastern states, tiger salamanders have not been managed in any state. Therefore, no data exist with which to design management strategies for the species. However, from what we know about tiger salamanders an attempt at a management strategy can be made.

Probably most relevant in this context are the reviews by Semlitsch (1998, 2000a, b) and Semlitsch and Bodie (1998). Although protection of breeding ponds is an obvious first step it is important to realize that upland habitat around the breeding ponds must also be protected (Semlitsch, 1998). To determine the size of a terrestrial buffer zone the extent of use of upland habitat needs to be determined, as Madison and Farrand (1998) have done. As Semlitsch (1998) has shown, the size of a terrestrial buffer zone that would protect 95% of the tiger salamander population around a breeding pond can then be determined. Given data for other ambystomatids and Madison and Farrand (1998), a buffer zone size of 164.3 m may be sufficient. To protect breeding ponds and their metamorphic breeding populations in the Black Hills, it is important to locate breeding ponds and establish buffer zones of 150 – 200 m around them. Only low impact or no impact activities should be allowed within this zone. This would mean the elimination of grazing, timber harvest, off-road vehicle use, and mining within these areas. Low impact recreation, such as hiking or cross-country skiing, would probably not cause population declines as long as these visitors stay out of the breeding ponds.

Clearly inimical to survival of tiger salamander breeding populations are predaceous fish (Blair, 1951; Carpenter, 1953; Collins and Wilbur, 1979; Collins, 1981; Corn et al., 1997). Predaceous fish could completely eliminate tiger salamanders from breeding ponds. To protect breeding populations of tiger salamanders, fish stocking should be eliminated at tiger salamander breeding ponds. Accidental or intentional unmanaged stocking (i.e., introduction of game fish or bait fish by the public) also needs to be discouraged. This can only be done through increased awareness and enforcement of existing law.

Although we do not know the potential for disease to regulate tiger salamanders, it is possible to transfer deadly pathogens through fish stocking, introduction of extralimital amphibians (especially tiger salamanders used as bait by anglers), anglers traveling from pond to pond, tourists or hikers, and biologists (Carey et al. 1999). Elimination of fish stocking and the use of appropriate sterile safeguards by investigators would reduce the potential for transfer of disease through these pathways. Reduction of the potential for transfer of diseases through other agents is much more difficult and can probably only be done through educational programs.

There are many other things we do not know about tiger salamanders and an effective management strategy can only be derived through more research. Migration and movement needs to be more thoroughly researched. Movements made by tiger salamanders amongst breeding ponds are particularly important. Although they are philopatric they are often found far from water. The question of what they are doing and where they are headed when found so far from water remains. Leopard frogs, for example, move along water courses to colonize new breeding habitat or to migrate amongst breeding habitats (Merrell, 1977), and this movement is probably an important part of gene flow amongst leopard frogs in a metapopulation. However, nothing is known of this sort of movement in tiger salamanders. If it were known that tiger salamanders used certain corridors along which to move amongst breeding ponds these movement corridors could be protected to conserve the genetic integrity of metapopulations.

Models

There are no published management models for the tiger salamander. The Black Hills National Forest is in a unique position to provide leadership in this potentially critical area.

Survey And Inventory

There are two basic approaches to survey and inventory studies; basic surveys in which investigators attempt to determine occupation of breeding ponds without estimating the numbers of metamorphs or larvae in these ponds, and intensive surveys in which an attempt is made to estimate the size of the breeding or larval population. Simple surveys can consist of brief visits to breeding ponds to find either breeding metamorphs during the breeding season or to observe larvae (or branchiate adults) later in the active season. Intensive surveys require detailed studies to determine population sizes of metamorphs, larvae, or branchiate adults. There is no “middle ground”; it is probably not possible to derive an index of population size that is easily measured in the field. Obviously, it is more expensive and time intensive to conduct intensive surveys than simple presence/absence surveys. If salamanders are found at breeding ponds during the breeding season, that pond could be considered to have a population of salamanders. However, the size of this population could be small or the salamander could be transient at this locality. If salamanders are not found at specific ponds, these ponds will need to be revisited several times (three surveys would be adequate), to determine with reasonable certainty that salamanders may be absent at these ponds. Even then, the pond should be periodically revisited.

Metamorphs are difficult to survey following the breeding season. Newly metamorphosed tiger salamanders leave the pond following the larval period and are then equally hard to find. Also, salamander eggs can look very similar to the eggs of several other amphibians that are found in the Black Hills, and they would be difficult for the non-specialist to distinguish in the field.

Tiger salamander larvae can be somewhat unique in that they are oblong (rather than round, as are frog tadpoles) and have external gills, and branchiate adults are obvious since they are large, gilled, and look otherwise like the metamorphs. However, other than the metamorphs, branchiate adults, and possibly the larvae, tiger salamanders could be very difficult for a non-specialist to survey at any life stage in the Black Hills. The most successful survey technique should probably concentrate on metamorphs during the breeding season or might concentrate on identifying larvae later in the active season. Larvae may be difficult for most observers to correctly identify.

Most of the extensive studies covered in this conservation assessment have been completed using drift fences that completely encircle a breeding pond (Dodd and Scott, 1994). Drift fences are difficult to build, costly to maintain, and must be checked daily during the study period. The cost will largely depend on the size of the pond and the amount of material necessary to encircle the pond. Cost will also depend on the time spent driving to and checking traps at the pond during the breeding season. Also, the breeding season begins early in the year and access to breeding ponds could be a problem. However, drift fences used during the breeding season would be the most efficient way to survey all breeding metamorphs in a population. This would require that metamorphs in the population be marked and recaptured.

Since tiger salamanders are amongst the largest terrestrial salamanders in North America, they should tolerate invasive marking techniques rather well. Donnelly et al. (1994) reviewed marking techniques, but I would recommend using PIT (passive integrated transponder) tags with tiger salamanders for a simple and easily read marking technique. These tags are inserted into the body cavity and are a unique magnetic tag that readable using a PIT tag reader for a number of years. However, PIT tags have not been used in tiger salamanders and their utility and possible health effects are unknown, but health effects should be slight. Madison and Farrand (1998) used small radiotransmitters, which are larger than PIT tags, to track tiger salamanders with minimal ill effects to their study organisms. Radiotransmitters can also be used if the intent of the study is to track tiger salamanders for some time. Madison and Farrand (1998) can be consulted for methodology. Toe-clipping is commonly used to mark a variety of vertebrates but can be difficult with amphibians, since toes regenerate, limbs may need to be anesthetized, and health problems can result (Donnelly et al., 1994).

Another method of surveying metamorphic tiger salamanders is to set out minnow traps and collect metamorphs in the breeding ponds. Bradley Shaffer (personal communication, 1996) has successfully collected various ambystomatids in the southwestern United States and Mexico using minnow traps. Carpenter (1953) also collected salamanders using funnel traps (similar to commercially available minnow traps) placed in ponds and other aquatic habitats. However, this would not be an efficient method of sampling and would provide only presence/absence information. Minnow traps could be used efficiently as part of a basic presence/absence survey, or to determine study sites to be more extensively studied using drift fences in later field seasons.

Metamorphic tiger salamanders can also be collected by seining or dip-netting in the water at breeding ponds. For instance, metamorphic tiger salamanders court in water (Arnold, 1976; Whiteman et al., 1999) and they would be found most easily in their greatest abundance in breeding ponds at night while courting. However, collecting during the breeding season could disturb breeding metamorphs and eggs laid in the water. Collection of metamorphs at ponds should probably be restricted to limited dip-netting to determine the presence or absence of tiger salamanders at breeding ponds. Once again, this would probably be an effective means to determine breeding sites for presence/absence surveys, or identify sites for later intensive study. The technique would not efficiently capture the large numbers needed for accurate estimation of population densities at breeding ponds.

Larval tiger salamanders can be seined or dip-netted at breeding ponds later in the season after they have hatched and grown to some minimum size at which they are relatively easy to collect and identify. The best timing for such surveys in the Black Hills is not currently known. However, provided suitable marking techniques are available a rather simple Peterson mark-recapture index could be derived of a larval population in a pond (Krebs, 1999). Of course, large numbers of larvae would have to be marked to ensure the accuracy of the mark-recapture survey (Krebs, 1999). Donnelly et al. (1994) reviewed marking techniques useful in amphibian surveys. They noted that larval amphibians are difficult to mark and it might be necessary to develop new marking techniques to survey larval tiger salamanders at ponds.

Metamorphs could be surveyed using the technique of Pechmann (1995). In this study, large square drift fences were constructed in upland habitats near breeding ponds, such that large sections of terrestrial habitat were completely enclosed by a drift fence. Metamorphic populations were then captured when moving overland by traps placed along the drift fence, marked, and placed back inside the drift fences. Other kinds of traps, such as pitfall traps, were also placed within the fenced-off areas to more accurately determine population density and survivorship. The technique is time-intensive and expensive, but possibly superior to other types of survey techniques. It may be the only technique that could be used to survey tiger salamanders in their terrestrial phase, although Kolbe et al. (2002) were successful in finding salamanders at rodent burrows at night using flashlights. I have successfully used their technique to find tiger salamanders at various sites in Nebraska and South Dakota.

Monitoring

Monitoring techniques would be similar to the survey techniques described above. Tiger salamanders could be intensively monitored at specific ponds or could be simply monitored through presence/absence surveys at many ponds. A reasonable compromise might be to establish a few ponds at which tiger salamanders would be intensively studied. This could determine detailed population trends at specific sites and could be combined with ongoing presence/absence surveys at several sites to establish general trends. Yearly surveys as described in the "Survey and Inventory Techniques" section would be appropriate for monitoring populations of tiger salamanders.

ADDITIONAL INFORMATION NEEDS

Basic Natural History Information For Black Hills Populations

The tiger salamander is a cryptic amphibian that breeds early in the active season and rapidly disappears from breeding ponds. Larvae grow and metamorphose in these ponds and then also leave. Tiger salamanders are best known from several studies in the Rocky Mountains of Colorado (summarized by Hammerson, 1999), various locations in Arizona (Collins and co-workers' numerous studies), and various scattered works completed in the central and eastern

United States (Bishop, 1941; Anderson et al., 1971; Hassinger et al., 1970; Webb and Roueche, 1971; Rose and Armentrout, 1976; Sever and Dineen, 1978; Semlitsch, 1983b; Lannoo and Bachmann, 1984; Larson et al., 1999). Other than some work by Peterson (1974) and our own work (Smith et al., 1996a, 1996b; Kolbe et al., 2002) the natural history of the tiger salamander is not known in the Black Hills. The Black Hills are further north than localities studied in Colorado, but lower in elevation. They are further east than the site in Yellowstone National Park studied by Hill (1995), and they are on the edge of the Great Plains. The Black Hills vary in elevation from 1100 – 2150 m. It is difficult to apply the lessons learned at other study sites to tiger salamander populations in the Black Hills. For example, it is hard to know exactly when and where to look for tiger salamanders in the region.

A preliminary step to study of the tiger salamanders in the Black Hills would be basic surveys and inventories throughout the area. Surveys for branchiate adults could be completed at any time of the active season and should concentrate on permanent ponds and springs. Surveys for metamorphic populations should begin as early as feasible in the active season in an attempt to locate breeding congregations. Surveys should probably begin as soon as ice melts off of temporary and permanent ponds. Surveys for larvae should continue through the larval period, but it is not known exactly what the extent of the larval period may be in the Black Hills, and this period probably varies from year to year. Basic surveys would concentrate on spotting active tiger salamanders, whether they are breeding metamorphs, growing larvae, or branchiate adults. To verify identification, tiger salamanders can be visually observed (if metamorphs or branchiate adults) or dip-netted or seined (if larvae). Metamorphs can also be spotted by shining flashlights into rodent burrows. This may be effective only if there is a substantial concentration of rodent burrows near a breeding pond (Kolbe et al., 2002), although I have used the technique on prairie dog towns in a number of sites in Nebraska, North Dakota, and South Dakota.

For a number of reasons basic surveys and inventory work should probably be performed by professionals trained in herpetology. This work will require intimate knowledge of the basic biology and natural history of salamanders and will also require that workers be well-trained in field identification of tiger salamanders, especially small larvae and potentially salamander eggs.

Basic survey work will only provide the most minimal information about where tiger salamanders live and what kinds of ponds they occupy. It will not supply answers to the major topic of this conservation assessment, namely, how to properly manage tiger salamander populations in the Black Hills. However, basic surveys would be a good start to understanding the natural history of tiger salamanders in the Black Hills.

Detailed Population Surveys

After preliminary surveys have located populations detailed work needs to be performed at specific study sites. Little is known about population sizes and recruitment and the few detailed studies have indicated that tiger salamanders have a life history strategy of "boom and bust", with enormous yearly swings in population sizes (Anderson et al., 1971; Semlitsch, 1983b; Pechmann et al., 1991). Populations like this are susceptible to extinction at low points in the population cycle, whereas they can seem very abundant before and after these points (Pechmann et al., 1991). In such populations, it can also be difficult to ascertain whether animals are being affected by anthropogenic modifications of the environment or whether they are simply exhibiting normal yearly variation in population size (Pechmann et al., 1991; Pechmann and

Wilbur, 1994). It can also be difficult to tell whether management actions are working as intended, since yearly population density is unpredictable. Therefore, knowledge of natural fluctuations in population sizes becomes critical to determining the success of management programs.

The only way to examine yearly variation in population size is to conduct long-term detailed population studies of Black Hills populations. Once preliminary surveys have located populations a determination will need to be made of which populations are most suitable for further study. From three to five ponds should be studied for at least four or five years and potentially for much longer (Semlitsch, 1983b; Pechmann et al., 1991; Pechmann and Wilbur, 1994). These populations should be reasonably accessible yet fairly typical for the area. Detailed studies will involve encircling breeding ponds with a drift fence (Dodd and Scott, 1994) and marking all metamorphs moving in and out of the breeding pond. These studies will also involve detailed surveys of the eggs and larvae in the pond and an attempt to determine mortality of eggs and larvae at various stages, similar to work completed by Anderson et al. (1971). A herpetologist will have to perform such a study and the cost could be considerable depending on the data to be gathered. However, to effectively manage Black Hills tiger salamander populations it will be necessary to learn much more about their population sizes, population variability, and population mortality agents in the area.

Detailed Studies Of Tiger Salamander Movements

Of all the aspects of tiger salamander biology, yearly movements are the most poorly known. Spring migrations and the factors triggering them seem to be well understood (Reese, 1969; Semlitsch and Pechmann, 1985; Whiteman et al., 1994; Hill, 1995), but after leaving the breeding pond the activities of metamorphic tiger salamanders are nearly unknown (but see Madison and Farrand, 1998). Recent advances in technology have made it possible to track animals as small as adult tiger salamanders using radiotransmitters, and Madison and Farrand (1998) have pioneered these techniques in tiger salamanders. In their study, they showed that they could establish the size of buffer zones for management of tiger salamanders, they could understand some anti-predator behaviors of metamorphs, and could identify sources of predation on tiger salamanders. Although their study did not extend through the hibernation season, radiotracking of metamorphic tiger salamanders throughout the year would allow determination of typical hibernation habitat and possibly discover any long-distance movements that tiger salamanders might make. Identification of migration pathways could help to determine whether salamanders frequently move from pond to pond and would help to conserve the genetic integrity of metapopulations. These kinds of data are obviously invaluable to designing a management strategy for the tiger salamander at any location. In particular, long-distance movements are completely unknown in tiger salamanders.

Prioritization Of Costs

Clearly, presence/absence surveys are the least expensive of these endeavors but, aside from providing some very basic data about where tiger salamander breeding ponds and branchiate adult populations are located, they provide fairly little information. However, they are a start to management of tiger salamanders in the Black Hills. If all breeding ponds are protected from disturbance, with a 150 – 200 m terrestrial buffer zone surrounding each (Semlitsch 1998), this would go some way towards establishing minimal protection for the tiger salamander in the

Black Hills. To obtain a good idea of tiger salamander population sizes and yearly variation in population sizes intensive study of three to five breeding ponds over several years would be necessary. Semlitsch (1983b) worked at two study sites for four years to obtain the most minimal estimates of variability, and Pechmann et al. (1991) analyzed 12 years of data in their groundbreaking work on variability in amphibian population sizes. Such studies are expensive and time intensive. Studies of movement similar to that conducted by Madison and Farrand (1998) are also time intensive since tiger salamanders with implanted radiotransmitters must be frequently located in the field.

To summarize, simple presence/absence surveys can help design a minimal management strategy if all ponds with salamanders are protected with a terrestrial buffer zone. Detailed population studies would be costly but would provide considerable feedback on population sizes and their variability. Intensive radiotelemetry studies would also be costly but would help to determine the size of terrestrial buffer zones and any migratory pathways that might exist, thereby conserving the genetic integrity of metapopulations.

LITERATURE CITED

Allison, L. J., P. E. Brunkow, and J. P. Collins. 1994. Opportunistic breeding after summer rains by Arizona tiger salamanders. Great Basin Naturalist 54:376-379.

Anderson, J. D., D. D. Hassinger, and G. H. Dalrymple. 1971. Natural mortality of eggs and larvae of *Ambystoma t. tigrinum*. Ecology 52:1107-1112.

Arndt, R. G. 1989. Notes on the natural history and status of the tiger salamander, *Ambystoma tigrinum*, in Delaware. Bulletin of the Maryland Herpetological Society 25:1-21.

Arnold, S. J. 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. Zeitshrift fur Tierpsychologie 42:247-300.

Baxter, G. T., and M. D. Stone. 1980. Amphibians and Reptiles of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming. 137 pp.

Berger, L., R. Speare, P. Daszak, D. E. Green, A. A. Cunningham, C. L. Gogging, R. Slocombe, M. A. Ragan, A. D. Hyatt, K. R. McDonald, H. B. Hines, K. R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proceedings of the National Academy of Sciences 95:9031-9036.

Bishop, S. C. 1941. The Salamanders of New York. New York State Museum Bulletin 324:1-365.

Bishop, S. C. 1943. Handbook of Salamanders: The Salamanders of the United States, of Canada, and of Lower California. Cornell University Press, Ithaca, New York. 555 pp.

Blair, A. P. 1951. Note on the herpetology of the Elk Mountains, Colorado. Copeia 1951:239-240.

Blaustein, A. R., D. G. Hokit, R. K. O'Hara, and R. A. Holt. 1994. Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. Biological Conservation 67:251-

254.

Bogart, J. P., L. A. Lowcock, C. W. Zeyl, and B. K. Mable. 1987. Genome constitution and reproductive biology of hybrid salamanders, genus *Ambystoma*, on Kelleys Island in Lake Erie. Canadian Journal of Zoology 65:2188-2201

Botts, D. A., and G. W. Folkerts. 1977. Observations on the breeding ecology of the tiger salamander, Ambystoma *tigrinum*. Journal of the Alabama Academy of Science 48:66-67.

Boyer, R., and C. E. Grue. 1995. The need for water quality criteria for frogs. Environmental Health Perspectives 103:352-357.

Bradford, D. F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa.* Ecology 64:1171-1183.

Breckenridge, W. J. 1944. Reptiles and Amphibians of Minnesota. University of Minnesota Press, Minneapolis, Minnesota. 202 pp.

Brodie, E. D., Jr. 1977. Salamander antipredator postures. Copeia 1977:523-535.

Brodman, R., and M. Kilmurry. 1998. Status of amphibians in northwestern Indiana. Pages 125-136 in M. J. Lannoo, ed., *Status and Conservation of Midwestern Amphibians.* University of Iowa Press, Iowa City, Iowa. 507 pp.

Brophy, T. T. 1980. Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. Journal of Herpetology 14:1-6.

Brunkow, P. E., and J. P. Collins. 1996. Effects of individual variation in size on growth and development of larval salamanders. Ecology 77:1483-1492.

Buhlmann, K. A., S. Q. Croy, J. C. Mitchell, R. Reynolds, S. M. Roble, and D. J. Schwab. 2000. *Ambystoma tigrinum* tigrinum, recovery plan. Wildlife Diversity Division. Virginia Department of Game and Inland Fisheries, Richmond, Virginia. 40 pp.

Burger, W. L. 1950. Novel aspects of the life history of two ambystomas. Journal of the Tennessee Academy of Science 75:252-257.

Cannings, S. G., L. R. Ramsay, D. F. Fraser, and M. A. Fraker. 1999. Rare amphibians, reptiles, and mammals of British Columbia. Wildlife Branch and Resources Inventory Branch, B. C. Ministry of Environment, Lands and Parks, Victoria, British Columbia. 198 pp.

Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: An immunological perspective. Developmental and Comparative Immunology 23:459-472.

Carpenter, C. C. 1953. An ecological survey of the herpetofauna of the Grand Teton-Jackson Hole area of Wyoming. Copeia 1953:170-174.

Casper, G. S. 1998. Review of the status of Wisconsin amphibians. Pp. 199-205 in M. J. Lannoo, ed., *Status and Conservation of Midwestern Amphibians.* University of Iowa Press, Iowa City, Iowa. 507 pp.

Collins, J. P. 1981. Distribution, habitats, and life history variation in the tiger salamander, *Ambystoma tigrinum*, in east-central and southeast Arizona. Copeia 1981:666-675.

Collins, J. P., and J. Cheek. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. American Zoologist

23:77-84.

Collins, J. P., and J. R. Holomuzki. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). Canadian Journal of Zoology 62:168-174.

Collins, J. P., and H. M. Wilbur. 1979. Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes. Occasional Papers of the Museum of Zoology, University of Michigan 686:1-34.

Collins, J. P., T. R. Jones, and H. J. Berna. 1988. Conserving genetically distinctive populations: The case of the Huachuca tiger salamander (*Ambystoma tigrinum stebbinsi* Lowe). Pp. 45-53 in *Management of Amphibians, Reptiles, and Small Mammals in North America*, R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, Technical Report RM-166.

Collins, J. P., J. B. Minton, and B. A. Pierce. 1980. *Ambystoma tigrinum:* A multi-species conglomerate? Copeia 1980:938-941.

Collins, J. P., K. E. Zerba, and M. J. Sredl. 1993. Shaping intraspecific variation: Development, ecology and the evolution of morphology and life history variation in tiger salamanders. Genetica 89:167-183.

Collins, J. T. 1993. Amphibians and Reptiles in Kansas. The University of Kansas Natural History Museum, Lawrence, Kansas. 397 pp.

Corn, P. S., M. L. Jennings, and E. Muths. 1997. Survey and assessment of amphibian populations in Rocky Mountain National Park. Northwestern Naturalist 78:34-55.

Corn, P. S., W. Stolzenburg, and R. B. Bury. 1989. Acid precipitation studies in Colorado and Wyoming: Interim report of surveys of montane amphibians and water chemistry. United States Fish and Wildlife Service Biological Report 80(40.26). 56 pp.

Costello, D. F. 1969. The Prairie World. Thomas Y. Crowell, New York.

Cunningham A. A., T. E. S. Langton, P. M. Bennett, J. F. Lewin, S. E. N. Drury, R. E. Gough, and S. K. MacGregor. 1996. Pathological and microbiological findings from incidents of unusual mortality of the common frog (*Rana temporaria*). Philosophical Transactions of the Royal Society of London 351:1539-57.

Dalrymple, G. H. 1970. Caddisfly larvae feeding upon eggs of *Ambystoma t. tigrinum*. Herpetologica 26:128-129.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife: Threats to biodiversity and human health. Science 287:443-449.

Daszak, P., L. Berger, A. A. Cunningham, A. D. Hyatt, D. E. Green, and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. Emerging Infectious Diseases 5:735-748.

Degenhardt, W. G., C. W. Painter, and A. H. Price. 1996. Amphibians and Reptiles of New Mexico. University of New Mexico Press, Albuquerque, New Mexico. 431 pp.

Deutschman, M. R., and J. J. Peterka. 1988. Secondary production of tiger salamanders

(*Ambystoma tigrinum*) in three North Dakota prairie lakes. Canadian Journal of Fisheries and Aquatic Sciences 45:691-697.

Diana, S. G., and V. R. Beasley. 1998. Amphibian toxicology. Pp. 266-277 in Lannoo, M. J., ed., *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, Iowa. 507 pp.

Didiuk, A. 1997. Status of amphibians in Saskatchewan. Pages 110-116 in D. M. Green, ed., *Amphibians in Decline: Canadian Studies of a Global Problem.* Herpetological Conservation, Volume 1. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Ditmars, R. C. 1905. The batrachians of the vicinity of New York City. American Museum Journal 5:161-206.

Dodd, C. K., Jr., and D. E. Scott. 1994. Drift fences encircling breeding sites. Pp. 125-141 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds., *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D. C. 364 pp.

Dodson, S. I., and V. E. Dodson. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. Copeia 1971:614-624.

Donnelly, M. A., C. Guyer, J. E. Juterbock, and R. A. Alford. 1994. Appendix 2: Techniques for marking amphibians. Pages 277-284 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds., *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D. C. 364 pp.

Duellman, W. E. 1954. Observations on autumn movements of the salamander *Ambystoma tigrinum tigrinum* in southeastern Michigan. Copeia 1954:156-157.

Duellman, W. E., and L. Trueb. 1986. Biology of Amphibians. McGraw-Hill Book Company, New York, New York. 670 pp.

Fernandez, P. J., and J. P. Collins. 1988. Effect of environment and ontogeny on color pattern variation in Arizona tiger salamanders (*Ambystoma tigrinum nebulosum* Hallowell). Copeia 1988:928-938.

Figiel, C. R., and R. D. Semlitsch. 1990. Population variation in survival and metamorphosis of larval salamanders (*Ambystoma maculatum*) in the presence and absence of fish. Copeia 1990:818-826.

Frier, J. A., and R. T. Zappalorti. 1983. Reptile and amphibian management techniques. Transactions of the Northeast Section of the Wildlife Society 40:142-148.

Gehlbach, F. R. 1965. Herpetology of the Zuni Mountains region, northwestern New Mexico. Proceedings of the United States National Museum 116:243-332.

Gehlbach, F. R. 1967a. *Ambystoma* tigrinum (Green). Catalogue of American Amphibians and Reptiles, pp. 52.1-52.4.

Gehlbach, F. R. 1967b. Evolution of tiger salamanders (Ambystoma *tigrinum*) on the Grand Canyon rims, Arizona. Yearbook of the American Philosophical Society 1967:266-269.

Gentry, G. 1955. An annotated checklist of the amphibians and reptiles of Tennessee. Journal of the Tennessee Academy of Science 30:168-176.

Gilbert, P. W. 1942. Observations on the eggs of *Ambystoma maculatum* with special reference to the green algae found within the egg envelope. Ecology 23:215-227.

Gilbert, P. W. 1944. The alga-egg relationship in *Ambystoma maculatum*, a case of symbiosis. Ecology 25:366-369.

Glass, B. P. 1951. Age at maturity of neotenic *Ambystoma tigrinum mavortium* Baird. The American Midland Naturalist 46:391-394.

Green, D. M., and R. W. Campbell. 1984. The Amphibians of British Columbia. British Columbia Provincial Museum, Handbook Number 45:1-100.

Hamilton, R. 1949. Natural history of the Rocky Mountain tiger salamander *Ambystoma tigrinum* and the occurrence of polydactylism in a local population. M. A. Thesis, University of Colorado, Boulder.

Hamilton, W. J., Jr. 1946. Summer habitat of the yellow-barred tiger salamander. Copeia 1946:51.

Hammerson, G. A. 1999. Amphibians and Reptiles in Colorado. University Press of Colorado, Niwot, Colorado. 484 pp.

Harte, J., and E. Hoffman. 1989. Possible effects of acidic deposition on a Rocky Mountain population of the tiger salamander *Ambystoma tigrinum*. Conservation Biology 3:149-158.

Hassinger, D. D., J. D. Anderson, and G. H. Dalrymple. 1970. The early life history and ecology of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. American Midland Naturalist 84:474-495.

Heath, A. G. 1975. Behavioral thermoregulation in high altitude tiger salamanders, *Ambystoma tigrinum*. Herpetologica 31:84-93.

Hill, S. R. 1995. Description of migratory chronology of adult tiger salamanders (*Ambystoma tigrinum*) and survey of larvae of the tiger salamander in the Northern Range of Yellowstone National Park. M. S. Thesis, Montana State University, Bozeman, Montana.

Hoffman, E. A., and D. W. Pfennig. 1999. Proximate causes of cannibalistic polyphenism in larval tiger salamanders. Ecology 80:1076-1080.

Holomuzki, J. R. 1985a. Diet of larval *Dytiscus dauricus* (Coleoptera: Dytiscidae) in east-central Arizona. Pan-Pacific Entomology 61:229.

Holomuzki, J. R. 1985b. Life history aspects of the predaceous diving beetle, *Dytiscus dauricus* (Gebler), in Arizona. Southwest Naturalist 30:485-490.

Holomuzki, J. R. 1986a. Predator avoidance and diel patterns of microhabitats used by larval tiger salamanders. Ecology 1986:737-748.

Holomuzki, J. R. 1986b. Effect of microhabitat on fitness components of larval tiger salamanders, *Ambystoma tigrinum nebulosum*. Oecologia 71:142-148.

Holomuzki, J. R., and J. P. Collins. 1987. Trophic dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae), in a lentic community. Copeia 1987:949-957.

Holomuzki, J. R., J.P. Collins, and P.E. Brunkow. 1994. Trophic control of fishless ponds by tiger salamander larvae. Oikos 71:55-64.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal. University of Chicago Press, Chicago, Illinois. 557 pp.

Hovingh, P. 1986. Biogeographic aspects of leeches, mollusks, and amphibians in the intermountain region. Great Basin Naturalist 46:736-744.

Howard, R. D., R. S. Moorman, and H. H. Whiteman. 1997. Differential effects of mate competition and mate choice on eastern tiger salamanders. Animal Behavior 53:1345-1356.

Howe, G. E., R. Gillis, and R. C. Mowbray. 1998. Effect of chemical synergy and larval stage on the toxicity of atrazine and alachlor to amphibian larvae. Environmental Toxicology and Chemistry 17:519-525.

Irschick, D. J., and H. B. Shaffer. 1997. The polytypic species revisited: Morphological differentiation among tiger salamanders (*Ambystoma tigrinum*) (Amphibia: Caudata). Herpetologica 53:30-49.

Jancovich, J. K., E. W. Davidson, J. F. Morado, B. L. Jacobs, and J. P. Collins. 1997. Isolation of a lethal virus from the endangered tiger salamander *Ambystoma tigrinum stebbinsi*. Diseases of Aquatic Organisms 31:161-167.

Jancovich, J. K., E. W. Davidson, A. Seiler, B. L. Jacobs, and J. P. Collins. 2001. Transmission of the *Ambystoma* tigrinum virus to alternative hosts. Diseases of Aquatic Organisms 46:159-163.

Johnson, M. S., L. S. Franke, R. B. Lee, and S. D. Holladay. 1999. Biphenyls through two routes of exposure in a terrestrial amphibian: Is the dermal route significant? Environmental Toxicology and Chemistry 18:873-878.

Johnson, M. S., J. K. Vodela, G. Reddy, and S. D. Holladay. 2000a. Fate and the biochemical effects of 2,4,6-Trinitrotoluene exposure to tiger salamanders (*Ambystoma tigrinum*). Ecotoxicology and Environmental Safety 46:186-191.

Johnson, M. S., S. D. Holladay, K. S. Lippenholz, J. L. Jenkins, and W. C. McCain. 2000b. Effects of 2,4,6-Trinitrotoluene in a holistic environmental exposure regime on a terrestrial salamander, *Ambystoma tigrinum*. Toxicologic Pathology 28:334-341.

Johnson, R. W., and G. E. Gordon. 1987. The Chemistry of Acid Rain. ACS Symposium Series, American Chemical Society, Washington DC. 337 pp.

Jones, T. R., J. P. Collins, T. D. Kocher, and J. B. Mitton. 1988. Systematic status and distribution of *Ambystoma tigrinum stebbinsi* Lowe. Copeia 1988:621-635.

Kiesecker, J. M. 1991. Acidification and its effects on amphibians breeding in temporary ponds in montane Colorado. M. S. Thesis, University of Northern Colorado, Greeley, Colorado. 78 pp.

Kiesecker, J. M. 1996. pH-mediated predator-prey interaction between *Ambystoma tigrinum* and *Pseudacris triseriata*. Ecological Applications 64:1325-1331.

Kline, J. 1998. Monitoring amphibians in created and restored wetlands. Pages 360-368 in M. J. Lannoo, ed., *Status and Conservation of Midwestern Amphibians.* University of Iowa

Press, Iowa City, Iowa. 507 pp.

Koch, E. D., and C. R. Peterson. 1995. Amphibians and Reptiles of Yellowstone and Grand Teton National Parks. University of Utah Press, Salt Lake City, Utah. 188 pp.

Kolbe, J. J., B. E. Smith, and D. M. Browning. 2002. Burrow use by tiger salamanders (*Ambystoma tigrinum*) at a black-tailed prairie dog (*Cynomys ludovicianus*) town in southwestern South Dakota. Herpetological Review 33:95-99.

Krebs, C. J. 1999. Ecological Methodology, 2nd ed. Benjamin Cummings, Menlo Park, California. 620 pp.

Krebs, C. J. 2001. Ecology: The Experimental Analysis of Distribution and Abundance, 5th ed. Benjamin Cummings, Menlo Park, California.

Lannoo, M. J., and M. D. Bachmann. 1984. Aspects of cannibalistic morphs in a population of *Ambystoma t.* tigrinum larvae. American Midland Naturalist 112:103-109.

Lannoo, M. J., L. Lowcock, and J. P. Bogart. 1989. Sibling cannibalism in noncannibal morph *Ambystoma tigrinum* larvae and its correlation with high growth rates and early metamorphosis. Canadian Journal of Zoology 67:1911-1914.

Larson, D. L., S. McDonald, A. J. Fivizzani, W. E. Newton, and S. J. Hamilton. 1998. Effects of the herbicide atrazine on *Ambystoma tigrinum* metamorphosis: Duration, larval growth, and hormonal response. Physiological Zoology 71:671-679.

Larson, K. L., W. Duffy, E. Johnson, M. F. Donovan, and M. J. Lannoo. 1999. "Paedocannibal" morph barred tiger salamanders (*Ambystoma tigrinum mavortium*) from eastern South Dakota. American Midland Naturalist 141:124-139.

Lauder, G. V., and H. B. Shaffer. 1986. Functional design of the feeding mechanism in lower vertebrates: Unidirectional and bidirectional flow systems in the tiger salamander. Zoological Journal of the Linnean Society 88:277-290.

Lefcort, H., K. A. Hancock, K. M. Maur, and D. C. Rostal. 1997. The effects of used motor oil, silt, and the water mold *Saprolegnia parasitica* on the growth and survival of mole salamanders (genus *Ambystoma)*. Archives of Environmental Contamination and Toxicology 32:383-388.

Leff, L. G., and M. D. Bachmann. 1986. Ontogenetic changes in predatory behavior of larval tiger salamanders (Ambystoma *tigrinum*). Canadian Journal of Zoology 64:1337-1344.

Leff, L. G., and M. D. Bachmann. 1988. Basis of selective predation by the aquatic larvae of the salamander, Ambystoma *tigrinum*. Freshwater Biology 19:87-94.

Likens, G. E., N. M. Johnson, J. N. Galloway, and F.H. Bormann. 1976. Acid precipitation: Strong and weak acids. Science 194:643-645.

Lindquist, S. B., and M. D. Bachmann. 1982. The role of visual and olfactory cues in the prey catching behavior of the tiger salamander, *Ambystoma tigrinum*. Copeia 1982:81-90.

Loeb, M. L. G., J. P. Collins, and T. J. Maret. 1994. The role of prey in controlling expression of a trophic polymorphism in *Ambystoma tigrinum nebulosum*. Functional Ecology 8:151-158.

MacIntyre, D. H., and R. V. Palermo. 1980. The current status of the Amphibia in British

Columbia. Pages 146-151 in R. Stace-Smith, L. Johns, and P. Joslin, eds., *Proceedings of the Symposium on Threatened and Endangered Species and Habitats in British Columbia and the Yukon*. Victoria, BC: British Columbia Ministry of Environment, Fish and Wildlife Branch.

Madison, D. M., and L. Farrand, III. 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. Copeia 1998:402-410.

Maret, T. J., and J. P. Collins. 1994. Individual responses to population size structure: the role of size variation in controlling expression of a trophic polyphenism. Oecologia 100:279-285.

Maret, T. J., and J. P. Collins. 1996. Effect of prey vulnerability on population size structure of a gape-limited predator. Ecology 77:320-324.

Maret, T. J., and J. P. Collins. 1997. Ecological origin of morphological diversity: A study of alternative trophic phenotypes in larval salamanders. Evolution 51:898-905.

Maxell, B. A. 2000. Management of Montana's amphibians: A review of factors that may present a risk to population viability and accounts on the identification, distribution, taxonomy, habitat use, natural history, and the status and conservation of individual species. Report to USFS Region 1, Order Number 43-0343-0-0224. University of Montana, Wildlife Biology Program. Missoula, Montana. 161 pp.

Merrell, D. J. 1977. Life history of the leopard frog, *Rana pipiens*, in Minnesota. Bell Museum of Natural History Occasional Papers No. 15:1-23.

Mierzwa, K. S. 1998. Status of northeastern Illinois amphibians. Pages 115-124 in M. J. Lannoo, ed., *Status and Conservation of Midwestern Amphibians.* University of Iowa Press, Iowa City, Iowa. 507 pp.

Milius, S. 2000. New frog-killing disease may not be so new. Science News 157:133.

Miller, B. T., and J. H. Larsen, Jr. 1986. Feeding habits of metamorphosed *Ambystoma tigrinum melanostictum* in ponds of high pH (>9). Great Basin Naturalist 46:299-301.

Morell, V. 1999. Are pathogens felling frogs? Science 284:728-731.

Moriarty, J. J. 1998. Status of amphibians in Minnesota. Pages 166-168 in M. J. Lannoo, ed., *Status and Conservation of Midwestern Amphibians.* University of Iowa Press, Iowa City, Iowa. 507 pp.

Morin, P. J. 1983. Competitive and predatory interactions in natural and experimental populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. Copeia 1983:628-639.

Mount, R. H. 1975. The Reptiles and Amphibians of Alabama. Auburn University Agriculture Experiment Station, Auburn, Alabama. 347 pp.

Mushinsky, H. R. 1985. Fire and the Florida sandhill herpetofaunal community: With special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica 41:333-342.

National Atmospheric Deposition Program. 1989. NADP Data Report – Precipitation Chemistry, Volume 8, Number 3. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado.

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. The University Press of Idaho, Moscow, Idaho. 332 pp.

Oldfield, B., and J. J. Moriarty. 1994. Amphibians and Reptiles Native to Minnesota. University of Minnesota Press, Minneapolis, Minnesota. 237 pp.

Olenick, R. J., and J. H. Gee. 1981. Tiger salamanders (*Ambystoma tigrinum*) and stocked rainbow trout (*Salmo gairdneri*): Potential competitors for food in Manitoba prairie pothole lakes. The Canadian Field-Naturalist 95:129-132.

Orchard, S. A. 1992. Amphibian population declines in British Columbia. Pp. 10-13 in C. A. Bishop, and K. E. Pettit, eds., *Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy*. Ottawa: Canadian Wildlife Service. Occasional Paper 76.

Parrish, J. B., D. J. Herman, and D. J. Reyher. 1996. A Century of Change in Black Hills Forest and Riparian Ecosystems. U.S. Forest Service Agricultural Experiment Station, U.S. Department of Agriculture. South Dakota State University. No. B722. 20 pp.

Pechmann, J. H. K. 1995. Use of large field enclosures to study the terrestrial ecology of pond-breeding amphibians. Herpetologica 51:434-450.

Pechmann, J. H. K., and H. Wilbur. 1994. Putting declining amphibian populations in perspective: Natural fluctuations and human impacts. Herpetologica 50:65-84.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. Science 253:892-895.

Pedersen, S. C. 1993. Skull growth in cannibalistic tiger salamanders, *Ambystoma tigrinum*. Southwest Naturalist 28:316-324.

Peterson, C. R. 1974. A preliminary report on the amphibians and reptiles of the Black Hills of South Dakota and Wyoming. M. S. Thesis, University of Illinois, Urbana-Champaign. 59 pp.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D. C. 587 pp.

Pfennig, D. W., and J. P. Collins. 1993. Kinship affects morphogenesis in cannibalistic salamanders. Nature 362:836-838.

Pfennig, D. W., J. P. Collins, and R. E. Ziemba. 1999. A test of alternative hypotheses for kin recognition in cannibalistic tiger salamanders. Behavioral Ecology 10:436-443.

Pfennig, D. W., M. L. G. Loeb, and J. P. Collins. 1991. Pathogens as a factor limiting the spread of cannibalism in tiger salamanders. Oecologia 88:161-166.

Pfennig, D. W., P. W. Sherman, and J. P. Collins. 1994. Kin recognition and cannibalism in polyphenic salamanders. International Society for Behavioral Ecology 5:225-232.

Phillips, C. A., R. A. Brandon, and E. O. Moll. 1999. Field Guide to Amphibians and Reptiles of Illinois. Illinois Natural History Survey, Champaign, Illinois. 282 pp.

Porter, K. R., and D. E. Hakanson. 1976. Toxicity of mine drainage to embryonic and larval boreal toads (Bufonidae: *Bufo boreas*). Copeia 1976:327-331.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. Herpetology, 2nd ed. Prentis Hall, Upper Saddle River, New Jersey. 612 pp.

Powers, J. H. 1903. The causes of acceleration and retardation in the metamorphosis of

Ambystoma tigrinum: A preliminary report. American Naturalist 37:385-410.

Powers, J. H. 1907. Morphological variation and its causes in *Ambystoma tigrinum.* University of Nebraska Studies 7:197-274.

Reese, R. W. 1969. The taxonomy and ecology of the tiger salamander (*Ambystoma tigrinum*) of Colorado. Ph. D. dissertation, University of Colorado, Boulder.

Reilly, S. M., G. V. Lauder, and J. P. Collins. 1992. Performance consequences of a trophic polymorphism: Feeding behavior in typical and cannibal phenotypes of *Ambystoma tigrinum.* Copeia 1992:672-679.

Rose, F. L., and D. Armentrout. 1976. Adaptive strategies of *Ambystoma tigrinum* (Green) inhabiting the Llano Estacado of west Texas. Journal of Animal Ecology 45:713-729.

Rumble, M. A., D. Willis, and B. E. Smith. In press. Wildlife, fish, and herpetofauna of created impoundments in the intermountain west. In Anderson, S., M. McKinstry, and W. Hubert, eds., *Palustrine Habitats of the Intermountain West*.

Russell, A. P., and A. M. Bauer. 2000. The Amphibians and Reptiles of Alberta: A Field Guide and Primer of Boreal Herpetology. University of Calgary Press, Calgary, Alberta.

Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531-1550.

Semlitsch, R. D. 1983a. Terrestrial movements of an eastern tiger salamander, *Ambystoma tigrinum*. Herpetological Review 14:112-113.

Semlitsch, R. D. 1983b. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia 1983:608-616.

Semlitsch, R. D. 1983c. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Canadian Journal of Zoology 61:616-620.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond breeding salamanders. Conservation Biology 12:1113-1119.

Semlitsch, R. D. 2000a. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631.

Semlitsch, R. D. 2000b. Size does matter: The value of small isolated wetlands. National Wetlands Newsletter, January-February: pp. 5-6, 13.

Semlitsch, R. D, and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 5:1129-1133.

Semlitsch, R. D, and J. H. K. Pechmann. 1985. Diel pattern of migratory activity for several species of pond-breeding salamanders. Copeia 1985:86-91.

Semlitsch, R. D, D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pp. 217-248 in M. L. Cody and J. Smallwood, eds., *Long-Term Studies of Vertebrate Communities*. Academic Press, San Diego, California.

Sever, D. M., and C. F. Dineen. 1978. Reproductive ecology of the tiger salamander, *Ambystoma* tigrinum, in northern Indiana. Proceedings of the Indiana Academy of Science

87:189-203.

Sexton, O. J., and J. Bizer. 1978. Life history patterns of *Ambystoma tigrinum* in montane Colorado. American Midland Naturalist 99:101-118.

Shaffer, H. B., and M. L. McKnight. 1996. The polytypic species revisited: Genetic differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. Evolution 50:417-433.

Slavens, F., and K. Slavens. 2002. Reptiles and amphibians in captivity: Longevity homepage. World Wide Web page at http://www.halcyon.com/slavens/longev.html. Last updated 26 Jan 02.

Smith, B. E., D. M. Browning, E. Taylor, R. S. Ferguson, and K. Yturralde. 1996a. Herpetofaunal surveys of the Fall River Ranger District, U. S. Forest Service, southwestern South Dakota and Badlands National Park. U. S. G. S./Biological Resources Division. Northern Prairie Science Center, Jamestown, North Dakota. 27 pp.

Smith, B. E., J. J. Kolbe, and R. S. Ferguson. 1996b. A herpetological survey of Wind Cave National Park, South Dakota. U. S. G. S./Biological Resources Division. Northern Prairie Science Center, Jamestown, North Dakota. 66 pp.

Smith, H. M. 1956. Handbook of Amphibians and Reptiles in Kansas. University of Kansas, Lawrence, Kansas. 356 pp.

Smith, P. W. 1961. The Amphibians and Reptiles of Illinois. Illinois Natural History Survey Bulletin 28:1-298.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375-386.

Sredl, M. J., and J. P. Collins. 1991. The effect of ontogeny on interspecific interactions in larval amphibians. Ecology 72:2232-2239.

Sredl, M. J., and J. P. Collins. 1992. The interaction of predation, competition, and habitat complexity in structuring an amphibian community. Copeia 1992:607-614.

Stebbins, R. C., and N. W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press, Princeton, New Jersey. 316 pp.

Stiling, P. 2002. Ecology: Theories and Applications. Prentice Hall, Upper Saddle River, New Jersey. 403 pp.

Stine, C. J., Jr., J. A. Fowler, and R. S. Simmons. 1954. Occurrence of the eastern tiger salamander, *Ambystoma tigrinum tigrinum* (Green) in Maryland, with notes on its life history. Annals of the Carnegie Museum 33:145-148.

Tanner, W. W., D. L. Fisher, and T. J. Willis. 1971. Notes on the life history of *Ambystoma tigrinum nebulosum* Hallowell in Utah. Great Basin Naturalist 31:213-222.

Thurman, E. M., D. A. Goolsby, M. T. Meyer, M. S. Mills, M. L. Pomes, and D. W. Kolpin. 1992. A reconnaissance study of herbicides and their metabolites in surface water of the midwestern United States using immunoassay and gas chromatography/mass spectrometry. Environmental Science and Technology 26:2440-2447.

Trauth, S. E., R. L. Cox, B. P. Butterfield, D. A. Saugey, and W. E. Meshaka. 1990.

Reproductive phenophases and clutch characteristics of selected Arkansas amphibians. Proceedings of the Arkansas Academy of Science 44:107-113.

Travis, J. 1992. Eastern tiger salamander. Pp. 70-76 in P. E. Moler, ed., *Rare and Endangered Biota of Florida Volume III: Amphibians and Reptiles*. University Press of Florida, Gainesville, Florida.

United States Geological Survey. 1998. Wildlife Health Alert No. 98-02. Memorandum dated October 21, 1998.

VanBuskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. Ecology 72:1747-1756.

Varley, G. C., and G. R. Gradwell. 1960. Key factors in population studies. Journal of Animal Ecology 29:399-401.

Vaughan, T. A. 1961. Vertebrates inhabiting pocket gopher burrows in Colorado. Journal of Mammalogy 42:171-174.

Vertucci, F. A., and P. S. Corn. 1994. A reply to Harte and Hoffman, acidification and salamander recruitment. BioScience 44:126.

Webb, R. G. 1969. Survival adaptations of tiger salamanders (*Ambystoma tigrinum*) in the Chihuahuan Desert. Pp. 143-147 in C. C. Hoff and M. L. Riedesel, eds., *Physiological Systems in Semiarid Environments*. University of New Mexico Press, Albuquerque, New Mexico.

Webb, R. G., and W. Roueche. 1971. Life history aspects of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan Desert. Great Basin Naturalist 31:193-212.

Weller, W. F., and D. M. Green. 1997. Appendix I: Checklist and current status of Canadian amphibians. Pp. 309-328 in D. M. Green, ed., *Amphibians in Decline: Canadian Studies of a Global Problem.* Society for the Study of Amphibians and Reptiles, St. Louis, Missouri.

Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368-1382.

Whiteman, H. H., S. A. Wissinger, and A. J. Bohonak. 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. Canadian Journal of Zoology 72:1780-1787.

Whiteman, H. H., S. A. Wissinger, and W. S. Brown. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum.* Evolutionary Ecology 10:433-446.

Whiteman, H. H., S. A. Wissinger, and R. S. Moorman. 1999. Courtship behavior in a polymorphic population of the tiger salamander, *Ambystoma tigrinum nebulosum*. Journal of Herpetology 33:348-351.

Whitford, W. G., and M. Massey. 1970. Responses of a population of *Ambystoma tigrinum* to thermal and oxygen gradients. Herpetologica 26:372-376.

Wiedenheft, W. D. 1983. Life history and secondary production of tiger salamanders (*Ambystoma tigrinum*) in prairie pothole lakes. M. S. thesis, North Dakota State University, Fargo, North Dakota. 47 pp.

Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma – Rana sylvatica* community. Ecology 53:3-21.

Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. American Naturalist 111:43-68.

Wissinger, S. A., and H.H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: Anthropogenic acidification or natural variation? Journal of Herpetology 26:377-391.

Worthylake, K. M., and P. Hovingh. 1989. Mass mortality of salamanders (*Ambystoma tigrinum*) by bacteria (*Acinetobacter*) in an oligotrophic seepage mountain lake. Great Basin Naturalist 43:687-692.

Zerba, K. E., and J. P. Collins. 1992. Spatial heterogeneity and individual variation in diet of an aquatic top predator. Ecology 72:268-279.

Ziemba, R. E., and J. P. Collins. 1999. Development of size structure in tiger salamanders: The role of intraspecific interference. Oecologia 120:524-529.

Ziemba, R. E., M. T. Myers, and J. P. Collins. 2000. Foraging under the risk of cannibalism leads to divergence in body size among tiger salamander larvae. Oecologia 124:225-231.

DEFINITIONS

Abiotic: Refers to characteristics of the environment that are not biotic in nature, such as water and soil chemistry and weather.

Adult stage: In an amphibian, the stage of life history during which the amphibian is sexually mature.

Anamniotic egg: The egg of an amphibian, which lacks the amnion, an egg membrane derived in the reptiles and higher vertebrates. Anamniotic eggs lack shells and are usually laid in water. Tiger salamanders and most amphibians must lay their eggs in water.

Biotic: Typically used to refer to biological features of the environment and how they affect organisms. Biotic factors include predators, competitors, diseases, and mutualists of an organism of interest.

Branchiate adult: A sexually mature salamander that retains gills. A branchiate adult will look like a larval salamander but will be much larger.

Cannibal morph: A specialized type of tiger salamander larva or branchiate adult that primarily eats conspecifics. Cannibal morphs have a broad head and enlarged vomerine teeth.

Cannibalistic branchiate adult: A sexually mature cannibal morph that retains gills. It will look like a cannibal morph larva but will be much larger.

Cladoceran: An organism in one of four orders (Anomopoda, Ctenopoda, Onychopoda, and Haplopoda), all of which are freshwater Crustaceans (a subphylum). Cladocerans are common freshwater zooplankton. The most well known cladocerans are in the genus Daphnia, but cladocerans comprise hundreds of species and a diverse array of life histories.

Colonizing morph: Defined by Sexton and Bizer (1978) as a metamorphic adult tiger salamander that colonizes new habitats by moving overland to temporary or semipermanent ponds. Sexton and Bizer (1978) contrast this morph with the consolidating morph, defined below.

Congeners: Species within the same genus.

Consolidating morph: Defined by Sexton and Bizer (1978) as a branchiate adult tiger salamander that resides in permanent ponds. Consolidating morphs can reach high densities in these ponds, "consolidating" the population of tiger salamanders in that pond. Consolidating morphs do not colonize new habitat as do colonizing morphs (see above), although they can metamorphose into terrestrial adults that then act as colonizing morphs. For a further explanation, see "Life History" or Sexton and Bizer (1978).

Conspecifics: Individuals within the same species.

Dugouts: Ponds that are created by scooping out small depressions in small drainages or by blocking natural depressions in such drainages. Sometimes the term is used to refer to natural depressions in such drainages. Dugouts are typically not very large. The term is often used by farmers and ranchers in the intermountain west to refer to small ponds used to water livestock.

Egg stage: The stage of amphibian life history during which the embryo develops inside of an anamniotic egg.

Facultative metamorphosis: Refers to metamorphosis in the tiger salamander, in which the tiger salamander may undergo metamorphosis to become a typical terrestrial adult (or metamorph) or may not undergo metamorphosis and remain a branchiate form, perhaps eventually to become a branchiate adult. This is the opposite of obligate metamorphosis, found in most amphibians. Obligate metamorphs always metamorphose and become an adult.

Heterospecific: Not of the same species.

Isothermal: This refers to any fluid body that retains the same temperature throughout. In this paper, it refers to bodies of water in which the same temperature is measured throughout the pond.

Keystone predators: Predators whose influence in the community appears to be inordinately important. It is suspected that removal of a keystone predator from a biotic community would significantly change the character of the community.

Larval stage: The stage of amphibian life following the egg stage and before the adult stage. The larval stage ends with metamorphosis into the adult stage, although in tiger salamanders larvae can become branchiate adults without transformation into a terrestrial adult.

Mesophytic: Wet areas or vegetation characteristic of wet areas.

Metamorphic adult: A tiger salamander that has metamorphosed into a terrestrial adult rather than a branchiate adult.

Metamorphosis: In the tiger salamander this refers to the period of change from a larval form to a metamorphic adult. Larvae or branchiate adults may metamorphose to become metamorphic adults.

Morph: A particular form of an organism. Organisms of the same species can occur as different forms, such as different colors or morphologies. The difference between the sexes is the most obvious example of two different morphs of a species. In the tiger salamander, larvae can occur as cannibal or typical morph larvae, branchiate adults can occur as cannibal or typical morphs, and adults can also appear different as metamorphic adults (which are themselves a morph apart from the branchiate adults) depending on whether they spent their larval stage as cannibal or typical morph larvae.

Morphology: Refers to the external and internal form (i.e., anatomy) of an organism.

Natal: Referring to birth or early rearing. Typically used here to refer to the pond in which larvae are born and reared to metamorphosis.

Neotenic or neoteny: Used synonymously with paedomorphic or paedomorphosis in the literature but correctly restricted to a delay in development of an organism resulting in sexually mature forms with larval characteristics. Because of the confusion between neoteny and paedomorphosis, I have chosen to use the term branchiate adult to refer to adult tiger salamanders that have retained the larval morphology. See Pough et al. (2001) for a further explanation of neoteny in evolution.

Paedomorphic or paedomorphosis: A change in the development of an organism resulting in sexually mature forms with larval characteristics. Frequently used synonymously with neoteny, I have chosen to use the term branchiate adult to refer to adult tiger salamanders with larval characteristics. See Pough et al. (2001) for a further explanation of paedomorphosis in evolution.

Permanent ponds: Ponds that do not normally dry up except in especially dry years.

Phenotypic: Pertaining to the external appearance of an organism.

Phenotypic plasticity: Refers to situations when morphology may be changeable, depending on the conditions. Tiger salamanders are phenotypically plastic because external conditions (pond drying, for example) can cause branchiate adults to metamorphose and become metamorphic adults. If the ponds do not dry, then tiger salamanders remain as branchiate adults.

Philopatric: Tending to return to the same area. For example, many amphibians typically return to the natal pond repeatedly for reproduction.

Playa: A small depression full of water. Playas are found in the southwestern United States and are often temporary ponds. They are frequently used as breeding sites by southwestern amphibians. Playa is a Spanish word meaning beach or shore.

Recruitment: The addition of new organisms into a population through reproductive events.

Semipermanent ponds: Ponds that hold water in most years but frequently dry during drought years.

Temporary ponds: Ponds that typically hold water for only part of a year. They are usually small or shallow.

Trophic: Pertaining to the food web relationships of an organism. Typically used to refer to trophic level, the level at which an organism produces biomass or feeds in a community. For example, an organism may be a producer (plant), a primary consumer (herbivore), or a secondary consumer (carnivore). Each of these successive trophic levels is higher than the one below.

Upland habitat: Terrestrial habitat, usually surrounding a pond, in which metamorphic tiger salamanders feed following the reproductive season.

Xerophytic: Dry habitat or organisms characteristic of such habitat. Often used to refer to vegetation that is found in arid or semiarid regions.