Migratory chronology of adult tiger salamanders (Ambystoma tigrinum) and survey of larvae of the tiger salamander in the northern range of Yellowstone National Park
by Steven Ralph Hill, Jr

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
The movement chronology and patterns and time required for metamorphosis of the tiger salamander, Ambystoma tigrinum, were studied in a permanent lake in Yellowstone National Park by a drift fence and pitfall traps.

Permanent lakes in Yellowstone National Park were sampled with minnow traps and an aquatic box trap to determine whether reproductively mature (paedomorphic) larvae existed. During the period of 9 April-10 October 1993, 280 metamorphosed individuals were intercepted at the drift fence. The pattern of migratory movement was influenced by a combination of environmental and biological factors. Ninety-six percent of the immigration occurred when the minimum daily air temperature was 0 C or greater, and 83% of the immigration occurred within 24 hours of a precipitation event. All emigration occurred when the minimum daily air temperature was 0 C or greater, arid 95% of the emigration occurred within 24 hours of a precipitation event. Factors that may be involved in the initiation of immigration and emigration are discussed. Males immigrate to the lake earlier than females, and males and females emigrate at approximately the same time. Observed migratory events were nocturnal 99% of the time. Most larvae undergo metamorphosis during their second summer in the lake. Six larvae from one lake were determined to be reproductively mature, demonstrating the presence of paedomorphosis in tiger salamanders in Yellowstone National Park.

MIGRATORY CHRONOLOGY OF ADULT TIGER SALAMANDERS (*Ambystoma tigrinum*) AND SURVEY OF LARVAE OF THE TIGER SALAMANDER IN THE NORTHERN RANGE OF YELLOWSTONE NATIONAL PARK.

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A thesis submitted in partial fulfillment
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APPROVAL

of a thesis submitted by

Steven Ralph Hill, Jr.

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

24 May 1995 — Robert S. Moore
Date — Chairperson, Graduate Committee

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Signature Steven R Hill JR

Date 24 May, 1995

It is to my wife, Sharon, and son, Jacob, that I dedicate this work. Their love and support meant more than they realize. I am also grateful to my parents, Steve and Mary Hill, for the support that they have given me in all my endeavors, and for instilling in me the fortitude to finish what I start regardless of the obstacles.

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ABSTRACT

The movement chronology and patterns and time required for metamorphosis of the tiger salamander, *Ambystoma tigrinum*, were studied in a permanent lake in Yellowstone National Park by a drift fence and pitfall traps. Permanent lakes in Yellowstone National Park were sampled with minnow traps and an aquatic box trap to determine whether reproductively mature (paedomorphic) larvae existed. During the period of 9 April-10 October 1993, 280 metamorphosed individuals were intercepted at the drift fence. The pattern of migratory movement was influenced by a combination of environmental and biological factors. Ninety-six percent of the immigration occurred when the minimum daily air temperature was 0 C or greater, and 83% of the immigration occurred within 24 hours of a precipitation event. All emigration occurred when the minimum daily air temperature was 0 C or greater, and 95% of the emigration occurred within 24 hours of a precipitation event. Factors that may be involved in the initiation of immigration and emigration are discussed. Males immigrate to the lake earlier than females, and males and females emigrate at approximately the same time. Observed migratory events were nocturnal 99% of the time. Most larvae undergo metamorphosis during their second summer in the lake. Six larvae from one lake were determined to be reproductively mature, demonstrating the presence of paedomorphosis in tiger salamanders in Yellowstone National Park.

INTRODUCTION

Ambystoma tigrinum (Caudata, Ambystomidae) is the most widely distributed species of salamander in the world (Sever and Dineen 1977). A New World species, it is widely distributed in North America, including the Atlantic seaboard, Mississippi River Valley, Great Plains, Rocky Mountains, and Mexican Plateau. A disjunct population inhabits the Central Valley of California. It can be found across an elevational gradient ranging from sea level to 3,669 meters in the Rocky Mountains (Stebbins 1985).

Six subspecies of *A. tigrinum* are recognized (Collins 1990). The blotched tiger salamander, *Ambystoma tigrinum melanostictum*, is the subspecies in Yellowstone National Park.

A study of *A. tigrinum* in Yellowstone National Park was initiated for two reasons. First, this study seeks to determine whether reproductively mature *A. tigrinum* larvae exist in Yellowstone National Park. Although anecdotal evidence exists for their presence in the Park (Turner 1955), their presence has never been confirmed.

The second reason is that the study of a breeding population of salamanders would serve as baseline data against which future studies of *A. tigrinum* might be compared. Movement chronology and patterns around a breeding pond, time required for metamorphosis of larvae, and age and sex ratios have been studied in other regions of the United States; however, there is little information available from the region in and around Yellowstone.

In addition, this study would provide baseline data that may be valuable in the search for explanations for the recent worldwide declines in amphibian populations (Milstein 1990, Wake 1991, Blaustein et al. 1994), including a population of *A. tigrinum* in central Colorado (Harte and Hoffman 1989, Wissinger and Whiteman 1992). Amphibians are likely to be very susceptible to human-produced pollutants and to climatic changes because of their thin, specialized skin and variable body temperatures that reflect environmental temperatures. Furthermore, since they inhabit both aquatic and terrestrial ecosystems, they can be indicators of the health of both types of environments.

If amphibian declines lead to local or regional extinctions, a significant loss in biodiversity will result. Amphibians are an important part of aquatic and terrestrial food webs. They are major consumers of invertebrates and in turn provide a significant prey base for birds, mammals, and reptiles (Martin 1990, Ross 1991) because of their high efficiencies of biomass conversion (Pough 1983). *Ambystoma tigrinum* populations appear to be stable in Yellowstone National Park at present, but because the Park is relatively undisturbed and distant from large population centers, studies conducted here may provide insights into testing hypothesized causes of declines elsewhere (Koch and Peterson 1989).

The objectives of this study were to:

1) describe the migratory (immigration and emigration) chronology of a population of *A. tigrinum* in a permanent lake,
2) determine the relationship between migratory events and environmental parameters such as temperature and rainfall,
3) determine the approximate size and sex ratio of a population of *A. tigrinum*, the larval growth rate, and the size of new metamorphs,
4) determine, in a series of permanent lakes along an elevational gradient, the number of years required by *A. tigrinum* to metamorphose and whether or not reproductively mature larvae exist in Yellowstone National Park.

LITERATURE REVIEW

Migration

Ambystoma tigrinum follows the classical annual reproductive pattern of aquatic breeders that begins in the spring with the saturation of the ground by melting snow or spring rains (Duellman and Trueb 1986). The sequence of events during the reproductive season has been characterized by Salthe and Mecham (1974) as being a "cold region pattern" and consists of an "explosive" migration of adults to the breeding pond in early spring followed by courtship, mating, and oviposition. Following oviposition the sequence can be variable, depending on the locale and nature of the breeding pond, but includes the development and hatching of the eggs, growth and transformation of the larvae, and emigration of the adults and juveniles from the pond.

In variable climates, amphibians typically hibernate or estivate to avoid unfavorable weather. Estivation and hibernation take place below ground in ambystomids (Stebbins 1951). They often utilize burrows excavated by ground squirrels, pocket gophers, badgers, and other mammals. Vaughan (1961) found that other than pocket gophers, *A. tigrinum* were the vertebrates most commonly observed in pocket gopher burrows in Colorado. He found that *A. tigrinum* was the only vertebrate to have a mutually tolerant relationship with pocket gophers. However, *A. tigrinum* is also capable of digging its own burrows (Gruberg and Stirling 1972, Semlitsch 1983c).

The breeding migrations of ambystomid salamanders have been of particular interest to many researchers. Hoy (1871) first described the breeding migration of an ambystomid. It has since been suggested that land-directed migration events (emigrations) in ambystomids are stimulated by thyroxine whereas water-directed migration events (immigrations) are stimulated by prolactin (Duvall and Norris 1978, 1980). It was not clear to Packer (1960) whether these hormones were stimulated by favorable environmental conditions, such as moisture or favorable temperature ranges, or whether these environmental conditions merely permit the occurrence of migration after some other stimulus is presented for hormonal release. The existence of favorable environmental conditions during a season other than the normal breeding season failed to produce migrations of *A. tigrinum* (Semlitsch 1983a) or *A. maculatum* (Sexton et al. 1990), suggesting that perhaps the environment does trigger hormonal release but that there may also be genetic (Semlitsch 1983a) or physiological (Sexton et al. 1990) controls to prevent the salamanders from responding until the appropriate season.

The stimulus to release prolactin is considered by some researchers to be changing temperature (Chadwick 1940, Grant and Grant 1958, Semlitsch 1985a). Anderson (1967) found increasing temperature, enough to produce snow melt, was the primary factor that initiated immigration in montane populations of *A. macrodactylum*. Many investigators have found a threshold air temperature (Baldauf 1952, Beneski et al. 1986, Douglas 1979, Sever and Dineen 1977, Gentry 1968) or soil temperature at hibernation depth (Sexton et al. 1990) above which immigration of ambystomids to the breeding pond can occur; Semlitsch (1985a), however, failed to find such a threshold temperature.

Other researchers argue that temperature is of secondary importance to precipitation in triggering immigration. Semlitsch (1983b) and Botts (1978) found that immigration of *A. tigrinum* was limited to periods preceded by or during precipitation. Semlitsch (1981) and Blanchard (1930) found that precipitation was the most important stimulus to immigration behavior of other species of ambystomids.

Despite disagreement on the primary environmental factor that initiates immigration, most researchers agree that a combination of appropriate temperature and precipitation is involved in sustaining the immigration event after it has been initiated (Botts 1978, Williams

1970, Sexton et al. 1990, Douglas 1979, Semlitsch 1981 and 1985a, Gentry 1968, Baldauf 1952, Blanchard 1930, Beneski et al. 1986). There is disagreement on whether precipitation or temperature accounts for the most variation in the intensity of immigration. Beneski et al. (1986) and Sexton et al. (1990) found that air temperature explained most of the variation in the intensity of migration in ambystomids, while Botts (1978) and Semlitsch (1983b) found that the amount of precipitation explained most of the variation in the intensity of migration in *A. tigrinum*. Furthermore, the diel rainfall regime has been found to have an important influence on the intensity of migration. Douglas (1979), Botts (1978), Semlitsch (1983b, 1985a, 1981a), Sexton et al. (1990), and Anderson (1967) found that large migration concentrations often occur during nocturnal precipitation events. Botts (1978) and Douglas (1979) were able to show that rainfall was required during a specific portion of the night in order for migration to occur in two species of ambystomids.

It is likely that the factors that initiate and sustain immigration in ambystomids vary by region and species. Anderson (1967) found that immigration of coastal populations of *A. macrodactylum* were initiated by rainfall, with temperature being of little importance, whereas the immigration of montane populations of the same species were initiated by temperature, with precipitation being of little importance. Semlitsch (1985a) also suggests that immigration is triggered by different conditions in different locales. Beneski et al. (1986) suggest that the findings of some investigators that precipitation is the most important factor in migration may be biased due to the fact that temperature is rarely limiting in those locales. Thus, the broad overlap between the occurrence of favorable temperatures and favorable precipitation during most migration events makes it difficult to discern which is more influential on migratory behavior (Beneski et al. 1986). Large migrations of *A. tigrinum* have been documented in Yellowstone National Park (Turner 1955) but no quantitative information is known regarding environmental conditions during or prior to the observations.

Results from different studies appear more consistent on other aspects of migration and population demographics of ambystomids. Males generally arrive at the breeding sites prior to females (Beneski et al. 1986, Botts 1978, Douglas 1979, McClure 1943, Semlitsch 1983b and 1985a, Sexton et al. 1990, Williams 1970), presumably to gain a breeding advantage. It is not clear whether males are able to arrive earlier than females because they have a lower threshold for cues than females (Douglas 1979, Sexton et al. 1990), hibernate at a shallower depth (Sexton et al. 1990) or closer to the breeding pond, or move faster than the gravid females (Anderson 1967). Movement also tends to be nocturnal, regardless of whether more favorable conditions exist during the day (Blanchard 1930, Botts 1978, McClure 1943, Semlitsch 1981, 1983b, and 1985a, Semlitsch and Pechmann 1985, Sexton et al. 1990, Williams 1970). Also, sex ratios are usually skewed toward males (Beneski et al. 1986, Douglas 1979, Semlitsch 1983b, Sever and Dineen 1977, Sexton et al. 1990).

Paedomorphosis

The ability of certain salamanders to attain sexual maturity while at the same time retaining their larval external morphology has been known since the middle of the last century (Duellman and Trueb 1986). The phenomenon is the result of heterochrony, or a change in the relative timing of developmental events (Harris 1987).

Gould (1977) has defined terms describing the developmental pathways by which heterochrony can come about. Paedomorphosis (literally, "shaped like a child") was coined by Garstang in 1922 and, according to Gould, is the all-encompassing term for describing an animal that attains sexual maturity while retaining its larval external characteristics. Paedomorphosis is the result of either progenesis or neoteny. Progenesis was coined by Giard in 1887 and describes an animal that becomes paedomorphic as a result of accelerated reproductive development relative to somatic development (Gould 1977). The term paedogenesis (as contrasted with paedomorphosis) is synonymous with progenesis. Neoteny (literally, "retention of young features") was coined by Kollman in 1885 and describes an animal that becomes paedomorphic as a result of retarded somatic development relative to reproductive development (Gould 1977).

Some investigators feel that neoteny is the most common cause of paedomorphosis and use the terms interchangably (Duellman and Trueb 1986, Peters 1964). However, most investigators have chosen to use the more inclusive term paedomorphosis rather than neoteny (Shaffer 1984, Semlitsch and Gibbons 1985, Harris et al. 1990, Whiteman and Wissinger 1990, Semlitsch 1985b, 1987a, and 1987b, Semlitsch and Wilbur 1989, Harris 1987 and 1989). I will also use the term paedomorphosis throughout this paper.

Among the ambystomids, five species are known to be obligate paedomorphs, that is, they do not normally metamorphose in nature (Duellman and Trueb 1986). Four species of *Ambystoma* (including *A. tigrinum*) are known to be facultatively paedomorphic (Duellman and Trueb 1986). Paedomorphic and metamorphic life history pathways are thus not necessarily mutually exclusive, as individuals of both morphs often coexist in the same population (Eagleson 1976, Sexton and Bizer 1978, Collins 1981, Semlitsch

1985b, Webb and Roueche 1971, Whiteman and Wissinger 1990). Indeed, a population that maintains a facultative flexibility has an advantage over a population that is locked into either obligate paedomorphosis or obligate metamorphosis (Duellman and Trueb 1986), especially in montane or arid environments that are characterized by harsh terrestrial conditions such as severe temperature fluctuations (Sprules 1974a). Such a population can capitalize on the relatively stable conditions (temperature, food, etc.) of a permanent aquatic site by remaining paedomorphic, yet escape from the site during unfavorable periods (e.g., severe drought) by metamorphosing. In addition, those individuals that can respond to change may leave more offspring (Semlitsch 1987a).

Sexton and Bizer (1978) stated that paedomorphosis is the result of an interruption in an endocrinological pathway. The evidence suggests that the interruption of normal development results from low activity in the hypothalamo-pituitary-thyroid axis (particularly the hypothalamus) of paedomorphs (Duellman and Trueb 1986). Experiments with *A.tigrinum* paedomorphs have shown that injections of thyroxine induce metamorphosis, and also that their thyroids are sensitive to thyroid-stimulating hormone (Duellman and Trueb 1986). Thus there has been a search for ecological correlates that might cause the endocrinological interruption that results in paedomorphosis.

Sexton and Bizer (1978) summarized some of the existing data, citing authors who suggested that paedomorphosis might be associated with pond permanency, high dissolved oxygen concentration, low iodine concentration, or low water temperatures at high elevations. In addition, high salinity, high food concentration, and low population density have been suggested (Sprules 1974b). Stebbins (1951) suggested that an iodine deficiency in breeding ponds could prevent metamorphosis by inhibiting the production of thyroxine, but this theory has little support today (Rose and Armentrout 1976). Bizer (1977, 1978), Sexton and Bizer (1978), Snyder (1956) and Sprules (1974b) found that the life history pattern exhibited by *A. tigrinum* was correlated with the temperature of the ponds. They suggested that the low water temperatures of high elevation sites retard or inhibit metamorphosis by inhibiting thyroxine release or the ability of tissues to respond to its presence. In response, larval growth continues, a larger body size is attained, and paedomorphosis may result. Collins (1981) disagreed with these findings, arguing that the high elevation sites were generally more permanent in nature than the lower elevation sites, where normal metamorphosis occurred.

Sprules (1974a) and Collins (1981) suggested that the permanence of the site was a better correlate to paedomorphosis than temperature. This was confirmed by Semlitsch (1985b, 1987c) for *A. talpoideum* in the southeast U.S. Paedomorphosis does not occur in temporary bodies of water (Semlitsch 1985b), and it usually does not occur in permanent bodies of water inhabited by fish (Sprules 1974a) because the fish prey on or compete with the salamanders. Furthermore, in experimental permanent and temporary ponds, Semlitsch (1987a, 1987b) and Semlitsch et al. (1990) found that larvae raised under constant water level treatments grew faster and became sexually mature more frequently than those that received the drying treatment.

Harris (1987) and Whiteman and Wissinger (1990) suggested that abiotic factors alone are not sufficient to predict the occurrence of paedomorphosis and proposed a density dependent effect. Harris (1987) observed that low larval density was associated with a rapid growth rate, rapid reproductive maturity, and paedomorphosis. Semlitsch (1987a) also found that the frequency of paedomorphosis was inversely related to larval densities. He furthermore suggested that lower larval density favors paedomorphosis by providing a higher per capita resource base and less competition. Such conditions allow for a faster growth rate, attainment of the minimum size necessary for metamorphosis, and thus the ability to "choose" to become paedomorphic if the pond conditions remain constant. It appears, then, that pond permanence, larval density, and food concentration may vary in importance with species and locale. Wissinger et al. (1990) suggested that pond permanence increases the frequency of paedomorphosis directly through increased survival of larvae and indirectly through increased prey abundance.

Sprules (1974a) suggested that both genetically determined physiological differences and environmental factors cause paedomorphosis because both paedomorphs and metamorphs of the same species can occur in the same site. Subsequent experimentation by other researchers has shown that individuals taken from populations at different elevations (Eagleson 1976) or ponds within the same region (Semlitsch and Gibbons 1985) and raised under common conditions varied with respect to frequency of paedomorphosis, suggesting a genetic basis. Harris et al. (1990) tested for such a genetic basis by making crosses within and between three local but isolated populations that exhibited both the metamorphic and paedomorphic patterns, and then raising the offspring under common conditions. Their results confirmed that the variation in life history pathways observed between local but isolated populations is due to a genetic difference between the populations. They suggested that the degree of paedomorphosis exhibited by a population can evolve independently among populations as a result of varying selective pressures. Therefore, it follows that paedomorphosis (both facultative and obligate) in ambystomids may be an adaptive response to unfavorable terrestrial conditions which have resulted from Pleistocene and Recent climatic changes (Duellman and Trueb 1986, Rogers 1985).

STUDY AREA

The primary area utilized for this study was Ice Lake Reservoir, a permanent lake in Yellowstone National Park. It is an impoundment of Landslide Creek, a spring-fed stream that issues forth from Sepulcher Mountain. It was created prior to the 1890's to provide ice for the town of Gardiner, Montana. The lake is located approximately 3.2 kilometers west of Gardiner, Montana, and 1.2 kilometers south of the Gardiner-Cinnabar Road (UTM coordinates: Zone 12; 4986300 mN, 519700 mE) in a region that has been part of the Park since 1932. Ice Lake Reservoir has an elevation of 1,670 meters, making it the lowest elevation lake in Yellowstone National Park. The lake was surveyed on July 25-26, 1974, by the U.S. Fish and Wildlife Service as part of the Fishery and Aquatic Management Program in Yellowstone National Park. They measured its surface area to be approximately 0.8 hectares and its maximum and mean depth to be 3.7 meters and 1.5 meters, respectively. They set one large-mesh and one small-mesh gillnet overnight and captured 165 *A. tigrinum* but no fish (USFWS Technical Reports for Calendar Years 1964-1982).

The geology of the region was described by Pierce (1979), who reported the presence of some andesitic volcaniclastic and intrusive rocks and dikes from the

Tertiary, as well as thin sandstones from the Landslide Creek formation from the upper Cretaceous. Subsequently, during the Quaternary period, sediments from river and glaciers were deposited in the area. Thus the area is dominated by colluvial deposits, products of mass wasting including slides, slumps, flows, and frost rubble.

The lake is bounded by a steep rocky hillside on the northeast shore, a marshy area on the south and southeast shores, a sagebrush-grassland meadow to the southwest, and the earthen dam on the northwest shore. Landslide Creek enters the lake on the south shore, and I have characterized this area as a delta. The stream becomes braided in nature and much sediment is deposited here, creating the marshy area that characterizes the southern shoreline. There are two outlets from the lake. One is a deep water outlet that exits beneath the dam via a rock and wood culvert. The other is a surface water outlet that flows from the north side of the lake through a breech between the dam and the steep slope. The two outlets join a short distance below, and the stream continues toward the Yellowstone River. The lake bottom substrate is composed mainly of organic muck, though the northwest and northeast shores have gravel and rock mixed in with the muck.

The lake and the surrounding area were divided into several vegetational zones. Within the lake itself two main zones exist, an open water aquatic zone and a shoreline aquatic zone. Vegetation in the open water aquatic zone was submerged, whereas vegetation in the shoreline aquatic zone grew in the thin band of saturated soil, either slightly above or below water level, that surrounded the lake. The shoreline terrestrial zone similarly occupied a thin band around the lake just outside of the shoreline aquatic zone, but its soil was rarely if ever saturated by the lake water. The terrestrial zone was essentially a band 10-20 meters in width occupied by dry-land vegetation. The vegetation in each zone varied by position along the shoreline (Table 1).

Amphibians, other than *A. tigrinum*, that were observed using Ice Lake Reservoir include two species of anurans, the striped chorus frog (*Pseudacris triseriata*) and the spotted frog (*Rana pretiosa*). The only reptile species observed at the lake was the wandering garter snake (*Thamnophis elegans*), which is an important predator of *A. tigrinum*.

Table 1. Taxonomic list of plant species and corresponding locations at Ice Lake Reservoir. An "X" indicates presence in that zone. (OWA= Open Water Aquatic; SLA= Shoreline Aquatic; SLT= Shoreline Terrestrial; TRL= Terrestrial).

Family *Species*	Zones OWA	 SLA	 SLT	 TRL
Asteraceae				
Artemesia tridentata Nutt.			X	X
Aster adscendens Lindl.				X
Chrysothamnus nauseosus (Pallas *ex* Pursh) Britt.				X
Cirsium undulatum (Nutt.) Spreng.				X
Glycyrrhiza lepidota Pursh			X	X
Grindelia squarrosa (Pursh) Dunal				X
Solidago missouriensis Nutt.				X
Tragopogon dubius				X
Cactaceae				
Opuntia polycantha				X
Cyperaceae				
Carex rostrata Stokes *ex* With.		X		
Carex sp.		X		
Scirpus acutus Muhl. *ex* Bigl.		X		
Fabaceae				
Melilotus officinalis (L.) Pallas			X	X
Trifolium hybridum L.				X
Haloragaceae				
Myriophyllum spicatum L.	X			
Iridaceae				
Iris missouriensis			X	X
Juncaceae				
Juncus balticus Willd.		X		
Onagraceae				
Epilobium ciliatum Raf.		X		
Poaceae				
Agrostis stolonifera L.		X	X	X
Bromus inermis Leyss.				X
Bromus tectorum L.				X
Hordeum jubatum L.				X
Leymus cinereus (Scribn. & Merr.) Love				X
Pascopyrum smithii (Rydb.) Love				X
Phleum pratense L.			X	X
Poa pratensis L.				X
Stipa comata Trin. & Rupr.				X
Potamogetonaceae				
Potamogeton friesii Rupr.	X			
Potamogeton richardsonii (Bennett) Rydb.	X			
Rosaceae				
Rosa woosii Lindl.			X	X

Table 1. (con't)

Family *Species*	Zones OWA	 SLA	 SLT	 TRL
Salicaceae				
Salix planifolia		X		
Typhaceae				
Typha latifolia L.		X		

METHODS

Movements of salamanders across a drift fence enclosing a breeding pond northwest of Mammoth in Yellowstone National Park were recorded from April to October, 1993, and surveys of seven permanent ponds in the northern part of the Park were made between May and July, 1993.

Migration Studies

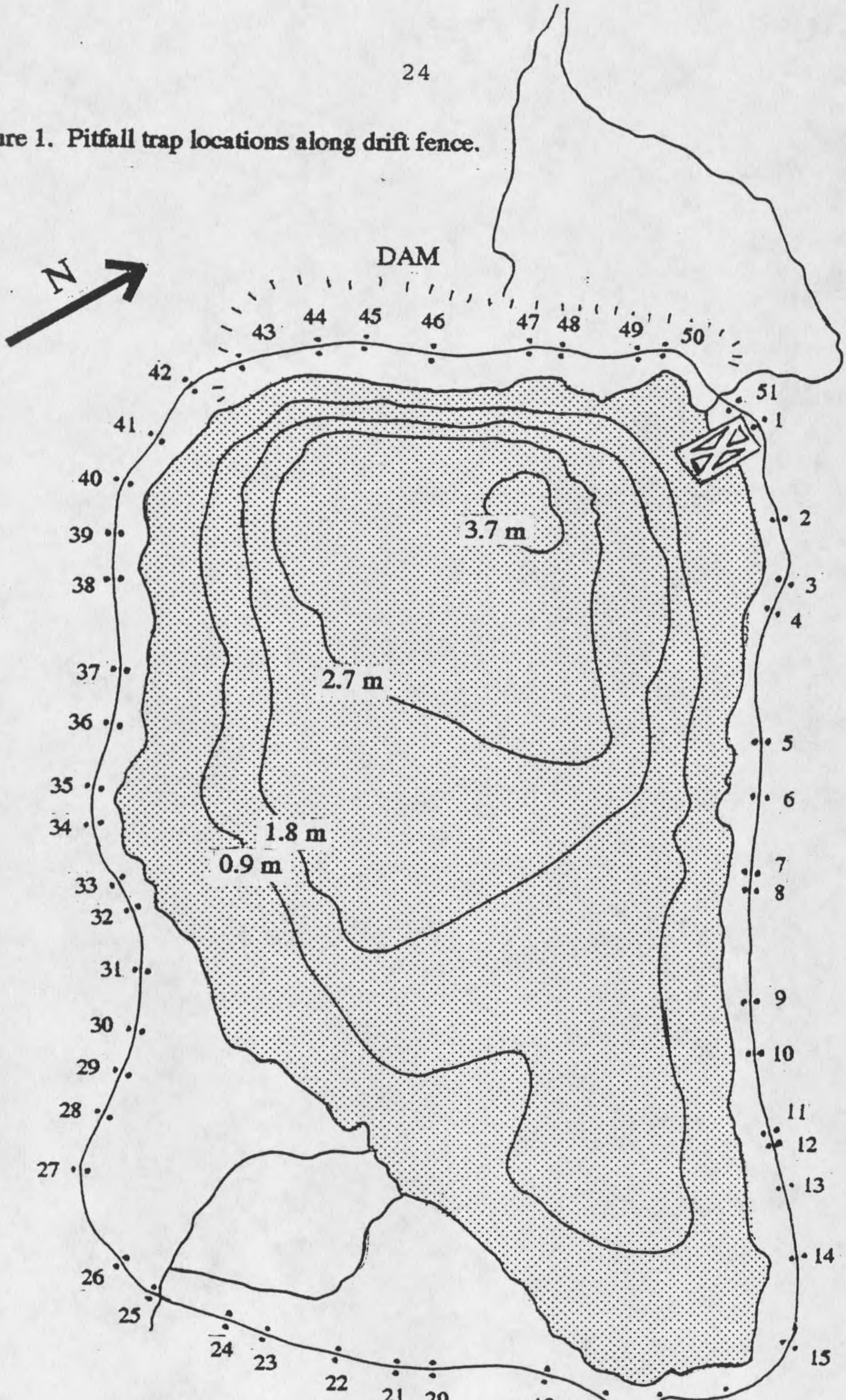
A drift fence and pitfall array were constructed around the entire periphery of Ice Lake Reservoir in late March and early April, 1993 to intercept *A. tigrinum* moving to and from the lake. The time of construction coincided with the breakup of winter ice on the lake. The fence, 543.6 meters in length, was placed as close as possible to the water's edge, but this distance varied from half a meter to five meters, as dictated by the nature of the shoreline. The fence was constructed of 35.6 cm high aluminum. It was buried in a trench three to six centimeters deep and stapled or wired to wooden stakes placed approximately one meter apart. Hardware cloth (0.6 cm mesh) spanned the inlet and surface water outlet and, when connected to the fencing, blocked salamander travel through these routes. Vegetation within approximately 50 cm of both sides of the fence was kept clipped.

The pitfall traps consisted of double-deep number ten cans, so that the resulting trap was 15.5 cm in diameter and 36 cm deep. They were buried so that the rims were flush with the ground and against the fence. The bottoms of most of the cans were punctured to allow water to drain out, thereby reducing the mortality rate of mammalian captives. Fifty-one pairs of traps, with one of each pair on either side of the fence, were placed around the lake following a simple Latin square plus one design (Munholland and Borkowski 1993). Under this design, the length of fence was divided into 2,500 0.217 meter segments arranged in a 50 by 50 matrix. A simple Latin square sample of size 50 was randomly chosen without replacement from among these 2500 units so that exactly one unit was selected from every row and column, thus ensuring good coverage. Then from the remaining 2450 units one additional unit was selected at random. Once the 51 units were selected, a random point was chosen on the fence from which to start measuring in order to locate each of the 51 units. For example, the first unit chosen in the simple Latin square sample was at the intersection of row one and column 32. I therefore measured 6.94 meters (32 X 0.217 m) in a counter-clockwise direction from the random point on the fence, and placed a pair of pitfall traps. The second unit chosen in the simple Latin square sample was at the intersection of row 2 and column 38. This unit was therefore 56 units from the first, and thus the second pair of pitfall traps was placed 12.15 meters (56 X 0.217 m) from the first pair. This pattern was continued for the 49 other units selected (Figure 1).

The pitfall traps were checked daily within an hour of sunrise and within an hour of sunset from 9 April to 26 April. Subsequently the traps were checked within an hour of sunrise, unless a precipitation event occurred since the last check or was likely to occur before the next check, in which case the traps were checked within an hour of sunset as well. This was done on a daily or near daily basis (27 days were missed) until the study ended on 10 October 1993. In addition, the traps outside the fence were closed during periods of low immigration activity (22 June to 26 July, 19 August to 20 August, 30 August to 13 September, 16 September to 19 September, and 22 September to 6 October). The vegetation along the fence was kept trimmed so that any salamanders moving along the fence would have been detected. No salamanders were detected during these periods. Instances when they were reopened coincided with times when immigration was likely to occur, such as prior to a precipitation event or following a major emigration event.

Each salamander captured in a pitfall trap was marked, sexed, weighed, measured and released onto the opposite

Figure 1. Pitfall trap locations along drift fence.



side of the fence. The location of the pitfall trap where the individual was captured was also recorded. Salamanders were sexed by examining the cloacal lips (Stebbins 1951). The salamanders were weighed in the field by placing each individual in a mesh bag of known weight and suspending it from an Ohaus dial spring scale. I measured the snout-vent length (SVL) of each individual by placing it in a clear plastic box, holding the box above my head, and spanning this length with a mechanical drawing divider. The total length of each individual was then measured to the nearest 0.5 mm with a ruler. Recaptured salamanders were also sexed, weighed, measured, scored for toe clip number and pitfall trap designation, and released to the opposite side of the fence. To facilitate analysis, calendar dates were converted to a consecutive numbering system, beginning with 9 April.

The salamanders were marked by toe clipping. The digits on the left hind limb represented the units, the digits on the right front limb represented the 10's, those on the left front represented the 100's, and the digits on the right rear limb represented the 1000's. An attempt was made to take no more than one digit per limb to reduce the impact on mobility. In addition, the middle toe on the right rear limb of each individual was removed to be used in a skeletochronolgical analysis separate from this paper. Therefore a maximum of 749 individuals could be marked in this study. Removal of this toe meant that the 157 individuals that received a mark of 1000 or higher had to have two toes removed from the right rear limb. Excised toes from each salamander were placed in individually labeled vials containing 10% formalin.

The only exception to the procedure of releasing captured individuals on the opposite side of the fence was for those recaptured in an outer trap within 24 hours of a capture in an inner trap. These individuals were returned to the outside of the fence, thus imposing a one day minimum stay in the terrestrial environment (Beneski et al. 1986). This procedure was established to reduce the possibility of excessive movement resulting from the effects of trapping and handling. A one day minimum stay in the aquatic environment was not imposed because an individual was much less likely to attempt to emigrate on the day following an immigration event.

Five minnow traps were set in the lake for the purpose of capturing larvae, as well as to provide information on the number of unmarked metamorphs in the lake. Five pitfall trap locations were randomly chosen, and one minnow trap was set from the shoreline at each of these points. The minnow traps were set approximately six meters from shore and were tethered by a length of nylon twine. These traps were checked each time that the pitfall traps were checked. If the period between checking the traps was to be greater than 24 hours, the minnow traps were pulled so that an individual could not be held captive for longer than this time. The traps were initially set out on 20 April, 1993. The minnow traps were only set for 12 hour periods between 16 June and 12 August to prevent death of metamorphs due to drowning. After 12 August the normal pattern was resumed.

Metamorphs captured in minnow traps were processed just as if they had been captured in a pitfall trap, and then released back into the lake. Larvae captured in the traps received variable treatment. Of the 97 larvae captured, 29 were measured, marked and released, 48 were measured and released, and 21 were collected for assessment of reproductive maturity.

Some environmental parameters were measured and recorded at the study site. These data included water temperature, air temperature, and soil temperature at the time the site was visited, and minimum and maximum air temperature and precipitation since the last visit to the site. Water and soil temperatures were measured with a laboratory grade hand-held thermometer. Water temperature was measured from the shoreline and at approximately two cm depth. Soil temperature was measured by placing the thermometer into an approximately two cm deep hole excavated each time in bare, shaded soil. The current air temperature was read from a Taylor Minimum-Maximum thermometer, which was also used to record the minimum and maximum temperatures since the last visit.

A Taylor rain gauge was used to record the amount of precipitation in millimeters since the last visit. The rain gauge and the minimum-maximum thermometer were attached approximately four feet off the ground to a wooden structure located on site. A record of daily minimum and maximum air temperatures and amount of precipitation was obtained from a National Park Service weather station located in Mammoth, Wyoming (elevation 1,902 meters), approximately 6.5 kilometers from Ice Lake Reservoir. In addition, a measure of seasonality was established by dividing the 185 days of the study into 37 five-day periods to allow for the inclusion of this variable in the statistical analysis.

Larval survey

Seven permanent lakes in the northern range of Yellowstone National Park were surveyed in 1993 to determine if paedomorphosis exists in the Park. The lakes were sampled with an aquatic box trap that measured 91.4 cm high, 45.7 cm wide, and 45.7 cm deep. The trap consisted of a frame constructed of wood covered with hardware cloth (0.6 cm mesh). One side of the trap was modified to produce a funnel-shaped entrance (61 cm by 2.5 cm). An access door was constructed on the side opposite the entry way and held closed with wire. Salamanders were directed to the funnel by a weir (1 m by 6.7 m), one end of which was attached to the trap at the entry way and the other end of which was anchored to shore with a stake. The weir, constructed of fiberglass screening, had styrofoam floats attached to the top edge for buoyancy and jack chain attached to the bottom edge to hold it to the substrate.

The seven lakes chosen to be sampled, all of which were known to contain *A. tigrinum* (USFWS Fishery and Aquatic Management Program in Yellowstone National Park - Technical Reports for Calendar Years 1964-1982; personal observation), were Floating Island Lake, Foster Lake, Slide Lake, Ice Lake Reservoir, Rainbow Lake (middle), and two unnamed lakes on Mount Everts (USFWS designates these as SONYEW #0899 and #0897). The trap was set in each lake for three consecutive 24-hour periods and was moved at the end of each period. Three random points on the shore of each lake were located by estimating the circumference of the lake in meters and then randomly choosing three integers from those less than the estimated circumference. The point at which the lake was first approached was treated as the starting point, and each of the chosen random locations were found by measuring from there with a 30 meter measuring tape. The weir was anchored to the shore and kept perpendicular to the shoreline as the trap was pulled into the water. The trap was set down onto the substrate when the weir was drawn tight or the trap was in one meter of water, whichever was achieved first. A small airspace was maintained at the top of the trap to prevent the drowning of metamorphs or anurans. Captured salamanders were measured and weighed using the same techniques described above.

Collected larvae were killed in a solution of 3-aminobenzoic acid ethyl ester (Sigma Chemicals) and fixed in 10% formalin. Several months later they were transferred to 50% ethyl alcohol. Each collected larva was dissected under laboratory conditions and its stage of reproductive readiness was assessed using the criteria developed for *A. tigrinum* by Collins (1981) (Table 2).

Statistics

Statistical analyses in this study employed the two sided t-test (Neter et al. 1988) and least squares regression (Lotus 1-2-3, version 2.3).

Table 2. Criteria used to classify salamanders into stages of breeding readiness, from Collins (1981). Individuals in stages III, IV or V are reproductively mature. Numerals in parentheses refer to diameter (mm).

Stage I: male and female.
Gonadal tissue primarily white and flaccid; Wolffian ducts or oviducts narrow, with few folds; cloacal margins not swollen; peritoneum largely unpigmented.

Stage II: female.
Oviducts enlarged (0.5-1), white, weakly convoluted; ova small (<1), mostly white-cream colored; dorsal third of peritoneum light gray; cloacal margins not swollen.

Stage II: male.
Duct enlarged (0.5-1), convoluted, but not distended in coils; testes small, flaccid; peritoneum black; cloacal margins swollen, with gray to gray-black borders, especially posterior.

Stage III: female.
Oviducts large (3-4), convoluted, white; ova small and white, medium (1-1.5) and cream or cream-tan or black, with some perhaps large (1.5-2) and bipolar cream and tan; at least dorsal two-thirds of peritoneum gray to black; cloacal margins swollen, bulbous with interior margins light gray to black and rugose.

Stage III: male.
Duct large (>1), convoluted, cream colored with localized black pigment; testes turgid; cloacal margins swollen, gray to gray-black, rugose borders, especially posterior; peritoneum black, especially densely pigmented dorsally.

Stage IV: female.
Oviducts large, convoluted, white, distended in coils; ova small and white or large and bipolar cream and tan; peritoneum and cloaca same as III.

Stage IV: male.
Duct large, convoluted, cream colored with scattered black pigment spots, distended in coils; testes turgid, enlarged; cloaca and peritoneum same as III.

Stage V: female.
All characters same as III except most ova small and white with a few darkly pigmented.

RESULTS AND DISCUSSION

Population Demographics

Trapping for 185 days with pitfalls and 84 days with minnow traps at Ice Lake Reservoir during the 1993 field season yielded 306 individual salamanders (metamorphs and larvae) that were marked and released. Of these 306 captured individuals, 205 metamorphs were sexually mature and presumably present in the pond during the spring (prior to 12 June) breeding season of 1993. Six sexually mature larvae were also captured and are thus counted as part of the breeding population. These six larvae were not marked. Females outnumbered males in the breeding population 111 to 100, producing a sex ratio of 1.00M:1.11F. This contrasts with the findings of Rose (1976) who observed 1.3M:1.0F and 2.27M:1.0F ratios in two surveys of an *A. tigrinum* population.

The mean snout-vent length of males (101.5 mm) intercepted while immigrating into Ice Lake Reservoir was significantly greater than the mean snout-vent length of immigrating females (97.8 mm)(two sided t-test, $p<0.05$, $n_{male}=98$, $n_{female}=111$). This differed from findings by Botts (1978) and Peckham and Dineen (1955) in Georgia and Indiana, respectively, that snout-vent lengths of male and female *A. tigrinum* did not differ significantly.

The mean weight of immigrating females was greater than the mean weight of immigrating males (male:28.8 g; female:29.8 g) at Ice Lake Reservoir, but, due to small sample sizes and the apparent lack of constant variance, this hypothesis cannot be statistically tested ($F_{(63,107)}=0.53$, $p>0.10$). Botts (1978) and Peckham and Dineen (1955) found that female *A. tigrinum* were heavier than males during immigration.

It was not possible to determine the date that egg masses were first deposited in Ice Lake Reservoir due to the turbidity of the water. However, female salamanders attached egg masses to the nylon twine that tethered the minnow traps on 11 occasions, the first on day 15 (23 April). Thus, the first eggs were detected in the site 14 days after the first immigrating male salamander was captured, and eight days after the first immigrating female was captured on day 7. The last observation of an egg mass attached to a minnow trap line occurred on day 34 (12 May). Approximately 920 eggs were observed on the 11 occasions. For six of the eleven oviposition events it was possible to determine that four egg masses were deposited at night, while two egg masses were deposited during the day.

Two size classes of larvae, determined to belong to cohorts representing two years, existed in the lake in 1993 (Figure 2). The first larva was captured on day 13.