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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Master of Science

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Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 1995

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
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Robert S Moore
Chairperson, Graduate Committee

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24 May 1995
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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.

ACKNOWLEDGMENTS

The study was supported by the National Park Service, Yellowstone National Park. The Department of Biology, Montana State University, also provided funding.

I thank Dr. R.E. Moore, M.S.U. Department of Biology, for his patience throughout this project, assistance with funding and thorough review. Dr. L. Irby, Dr. C. Kaya, and Dr. H. Picton, M.S.U. Department of Biology, provided critical review during the study. Dr. P. Munholland, M.S.U. Department of Mathematical Sciences, provided valuable statistical assistance. The direction of this project was greatly influenced by both Dr. C. Peterson, Idaho State University, and John Varley, Yellowstone National Park.

The quality of the project was enhanced by assistance in the field from my wife, Sharon, and son, Jacob.

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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

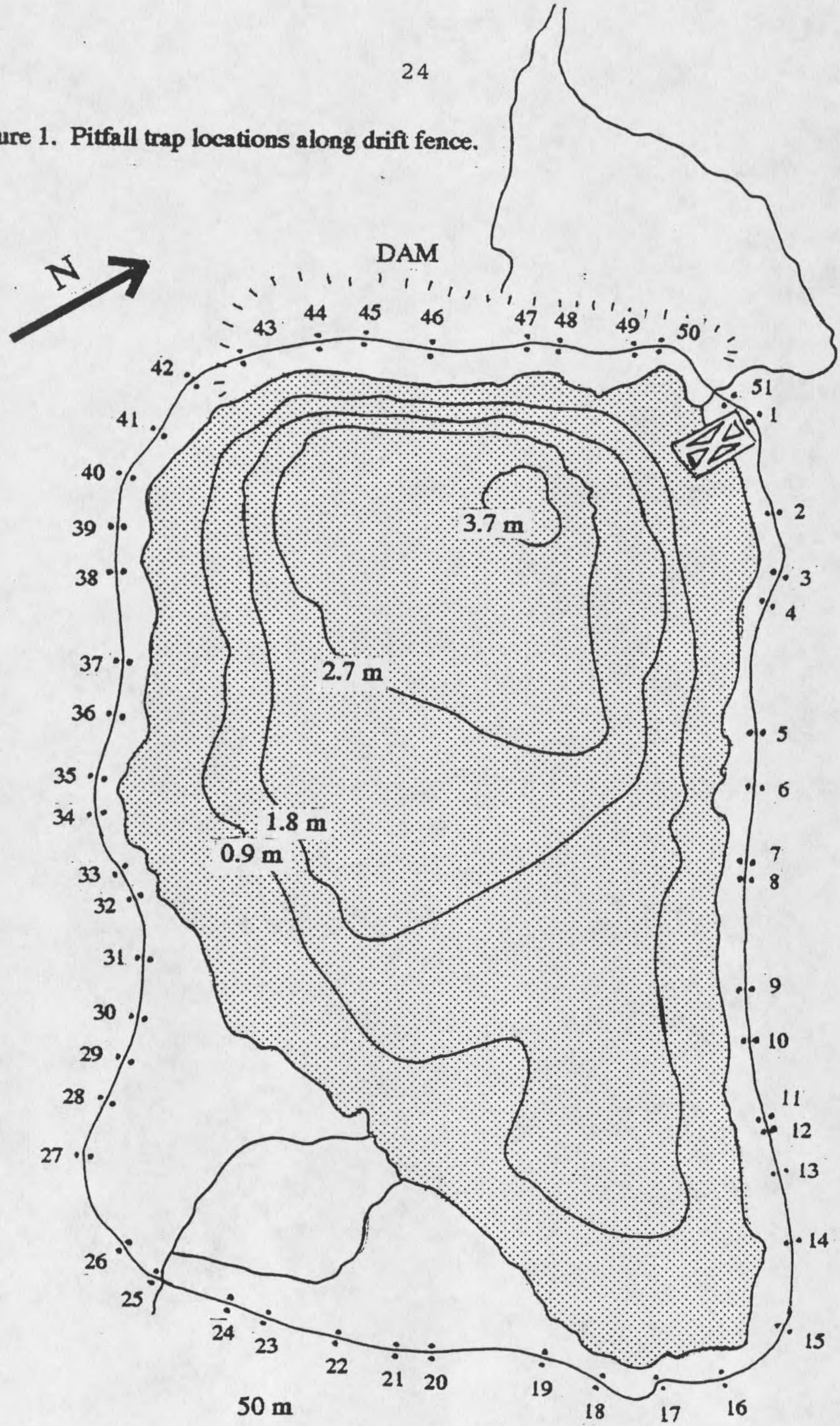
A drift fence and pitfall array were constructed around the entire periphery of Ice Lake Reservoir in late March and early April, 1993 to intercept *A. tigrinum* moving to and from the lake. The time of construction coincided with the breakup of winter ice on the lake. The fence, 543.6 meters in length, 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).

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

<u>Stage II: female.</u>
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.

<u>Stage II: male.</u>
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.

<u>Stage III: female.</u>
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.

<u>Stage III: male.</u>
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.

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

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

<u>Stage V: female.</u>
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.

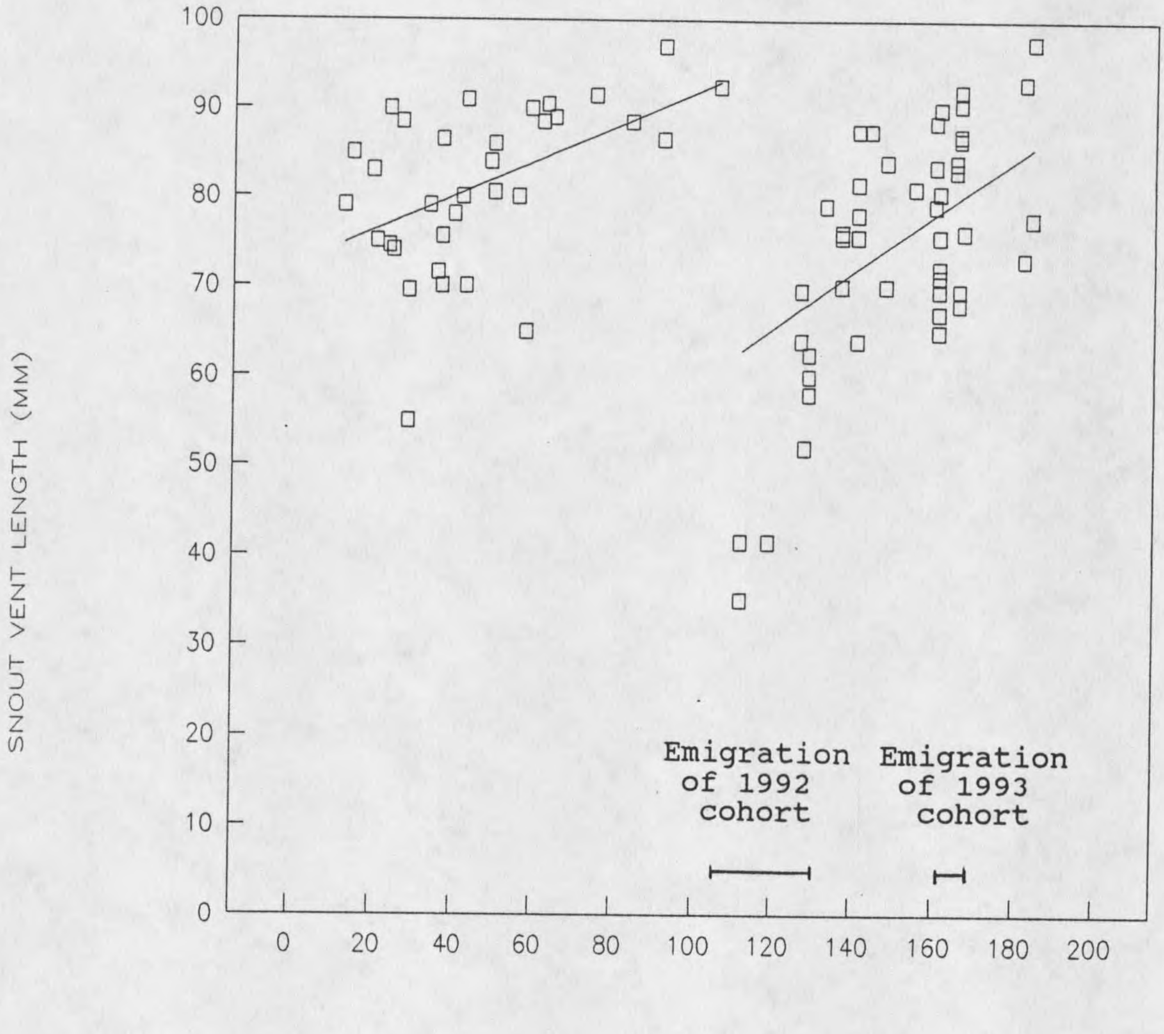
The mean snout-vent length of males (101.5 mm) intercepted while immigrating into Ice Lake Reservoir was significantly greater than the mean snout-vent length of immigrating females (97.8 mm)(two sided t-test, $p<0.05$, $n_{male}=98$, $n_{female}=111$). This differed from findings by Botts (1978) and 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.

Figure 2. Growth of 1992 and 1993 larval cohorts in Ice Lake Reservoir, 1993.



$n_{(1992)}=34$ $n_{(1993)}=48$

Due to its size (SVL 79.0mm, 20g) and, because it was captured only seven days after the arrival of the first female, I believe that this larva hatched in 1992 and overwintered in the lake. I marked and released 22 members of this 1992 cohort by day 106, the last day a larva of this cohort was captured.

On day 112 (29 July) I captured the first two of 48 larvae belonging to a smaller size class of larvae believed to have hatched in 1993. The SVL of newly hatched *A. tigrinum* has been found to range from 6mm (Webb and Roueche 1971) to 17mm (Hassinger et al. 1970), and thus the SVL of these individuals (41.5mm, 35.0mm) indicate that they hatched sometime before day 112. *A. tigrinum* in Utah require approximately 20-25 days to attain this size from a hatching snout-vent length of about 10mm (Tanner et al. 1971). Extrapolation using the growth rate curve for larvae in Utah thus suggests that the larvae at Ice Lake Reservoir hatched sometime between day 87 (4 July) and day 92 (9 July), 53-58 days after the last observed oviposition event. The results of a study by Hassinger et al. (1970), who recorded an incubation period of between 40 and 50 days for *A. tigrinum* in New Jersey, support this finding.

During the period from day 106 (23 July) to day 128 (14 August), 45 recently metamorphosed individuals (determined by the presence of gill stubs) were intercepted while emigrating. The SVL of these individuals suggest that they belonged to the 1992 cohort. In addition, three of the emigrants were individuals that had been marked as larvae.

Three recently metamorphosed individuals were intercepted while emigrating during the period between day 161 (16 September) to day 166 (21 September), and, based on their SVL's, I believe that they were from the 1993 cohort. The mean SVL of these three individuals (79.8 mm) was significantly different from the mean SVL of the 45 recent metamorphs (99.7 mm) from the 1992 cohort (two sided t-test, $p<0.05$). Since no more recent metamorphs belonging to either cohort were intercepted before the end of the study on day 185, it is presumed that most of the 1993 cohort overwintered as larvae. Thus, most larvae in Ice Lake Reservoir postpone metamorphosis until the second summer following oviposition, but limited metamorphosis does occur during the first summer.

Brandon and Bremer (1967) observed a two year larval period for *A. tigrinum* in southern Illinois, as did Whitford and Vinegar (1966) for *A. maculatum* in cool, spring-fed ponds in Rhode Island. Bizer (1978) and Sexton and Bizer (1978) found two immature larval size classes in certain high elevation permanent sites in Colorado, with metamorphosis occurring during the second warm season. Turner (1951, 1955) suggested that two summers are normally required before *A. tigrinum* will metamorphose in Yellowstone National Park. Semlitsch et al. (1988) suggest that postponing metamorphosis in favor of attaining a larger body size can result in reproduction at an earlier age.

The size at metamorphosis for larvae from the 1992 cohort in Ice Lake Reservoir was much greater than that found by Bizer (1978) for *A. tigrinum* in Colorado. Extrapolation of Bizer's data shows that the SVL of larvae metamorphosing during their second summer was between 66 mm and 75 mm, while the SVL of larvae metamorphosing during their first summer was between 55 mm and 62 mm. The larger size at metamorphosis observed in Ice Lake Reservoir may be attributed to the fact that the Colorado sites of Bizer (1978) are 1,500 to 2,000 meters higher in elevation.

It appears that early larval growth in the 1993 cohort is nonlinear. Therefore I dropped the first three data points of the 1993 cohort to fit a line to the remaining data points. The resulting slopes of the least squares lines for growth of the 1992 and 1993 cohorts of larvae were significantly different (two sided t-test, $p<0.05$), indicating that first year larvae grow at a faster rate than do second year larvae (Figure 2).

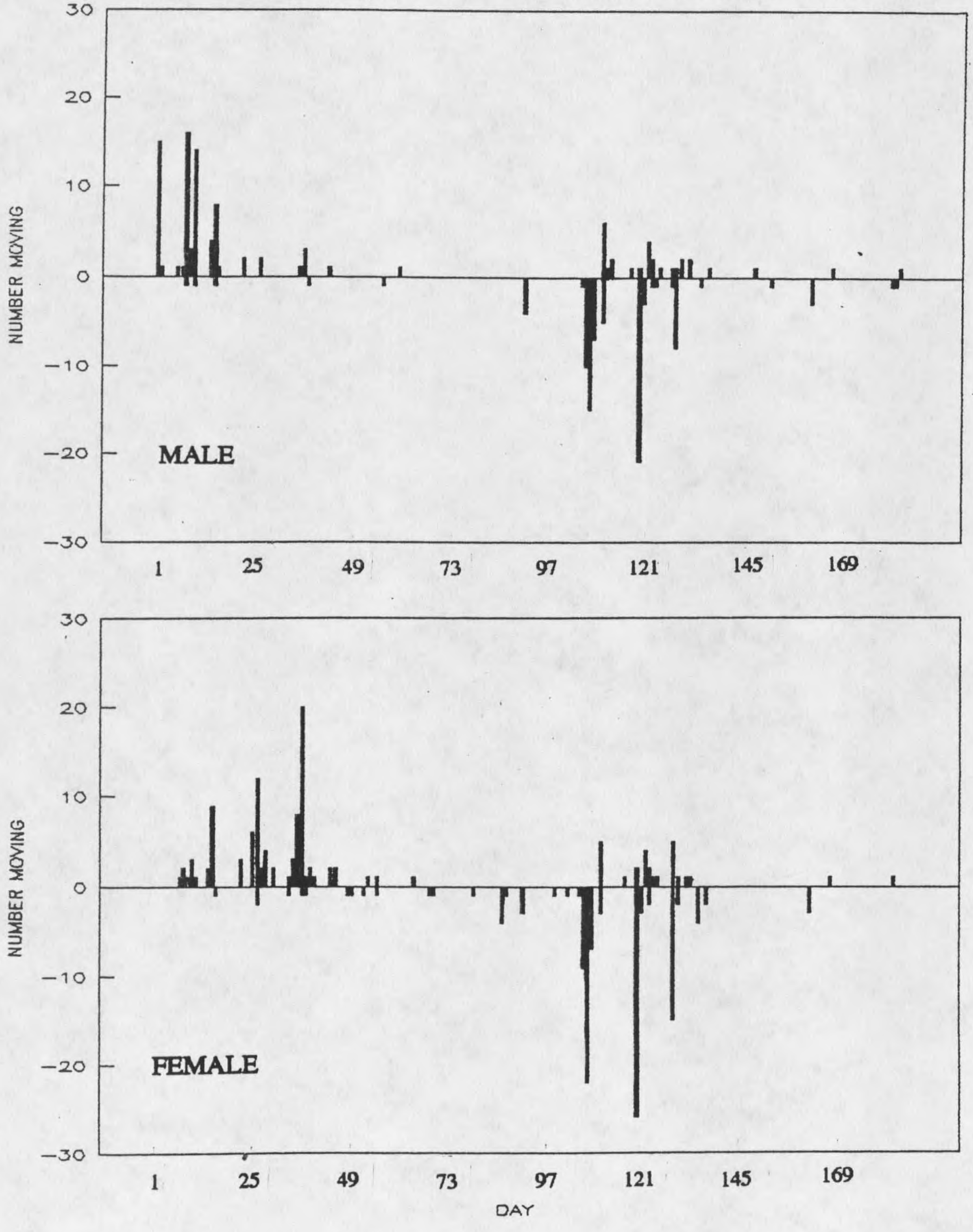
General Movement Patterns

The 465 migratory movements recorded in 1993 by interception of individuals at the drift fence occurred on 75 of the 185 days that the study was in progress. Two hundred eighty metamorphs were responsible for the 465 movements observed. Some movement of these individuals, either in or out of the lake, was recorded during each month from April through October (Figure 3).

Two hundred-ten individuals were responsible for the 241 immigrations observed in 1993 while 190 individuals were responsible for the 224 emigrations. One hundred thirty individuals were intercepted immigrating to the pond and subsequently emigrating from the pond.

Immigration to the pond had probably begun before trapping was initiated, since 15 immigrants were captured on day 1. Also, 22 unmarked adult metamorphs were first captured in minnow traps and 26 unmarked adult metamorphs (excluding recently metamorphosed individuals) were first captured while emigrating from the lake. These individuals could have immigrated to the lake prior to the initiation of the study. There are three other possible explanations for these unmarked individuals. Some or all may have either: 1) "trespassed" (i.e., passed across the fence undetected), 2) overwintered in the lake, or 3)

Figure 3. Migratory movements. Movement in positive direction indicates immigration, movement in negative direction indicates emigration.



emerged from burrows that were inside the fence periphery. Although I could not ascertain whether these latter two occurred, trespassing of marked salamanders was recorded on 21 occasions. Gibbons and Bennett (1974), Gibbons and Semlitsch (1981), and Semlitsch (1983b) recommend the drift fence method for studying movements of amphibians to and away from an aquatic site as few species are capable of climbing such a fence. However, problems arose in Yellowstone due to the presence of large herbivores and high winds. The fence was damaged 20 times (13 by animal, 7 by wind or other). Burrowing beneath the fence by salamanders was not thought to be a major problem due to the overall hard-packed nature of the soil around the fence. It is possible, though, that salamanders were able to pass beneath the fence by utilizing the tunnel networks of small mammals.

The 241 immigrations intercepted at the drift fence occurred in two distinct time periods. The first period started day 1 (9 April) and continued through day 64 (11 June), during which 177 immigrations were recorded. Most individuals that participated in the 1993 breeding season entered the lake during this period; however, first time captures of adult immigrants still occurred as late as day 136. Major immigration peaks (n>10) occurred on days 1, 8, 10, 15, 26, and 37 (Figure 3).

The second period of immigration began on day 110 and continued until the completion of the study. The immigrations in this period were usually made by individuals that had emigrated a few days earlier. Fifty-nine of the 64 immigration events recorded during this period occurred during the first 27 days of the period. The only major immigration peak (n>10) occurred on day 110.

The first emigrant was captured on day 8, but this individual attempted to re-immigrate on the following day. Such behavior was quite common, and it seemed as though these individuals were merely "wandering" into the terrestrial environment during favorable conditions. The first concerted emigration effort (7 individuals) occurred on day 91 (8 July), and emigration peaks (n>10) occurred on days 106, 107, 108, 119, and 128 (14 August). The emigration peaks on days 119 and 128 contained a large number of recently metamorphosed individuals (45% and 48% of the total emigration, respectively), whereas the peaks on days 106, 107, and 108 were composed of fewer recently metamorphosed individuals (11%, 13%, and 29% of the total emigration, respectively). Sporadic, low level migration continued into the fall, with a few salamanders still actively migrating as of day 183 (8 October). Migrations may have continued past the conclusion of the study on day 185. The low level of migratory movement observed at this time of year and the approach of winter suggest that few individuals would have moved after day 185, however.

Arrival and Duration of Stay

Male *A. tigrinum* entered Ice Lake Reservoir earlier than females in 1993 (Figure 3). The mean arrival date for males (n=72) first captured while immigrating was day 13 (21 April), while the mean arrival date for females (n=90) first captured while immigrating was day 32 (10 May). The arrival of males was significantly earlier than the arrival date of females (two sided t-test, $P<0.05$). This is congruent with the findings of Beneski et al. (1986), Botts (1978), Douglas (1979), McClure (1943), Sexton et al. (1990), and Williams (1970) for ambystomids.

Males were captured on day 1 of the study and some may have migrated prior to this day, but the first female was not captured until day 7. In addition, the first three immigration peaks (n>10, occurring on days 1, 8, and 10) were composed primarily of males while the fifth and sixth peaks (days 26 and 37) were composed primarily of females (Figure 3). The immigration peaks on days 15 and 110 contained approximately equal numbers of males and females. These data agree with Semlitsch (1985a) who found that male *A. talpoideum* dominated the first month of migration, while females dominated the second month. Botts (1978) observed that males dominated the first month of immigration, equal numbers of males and females were involved in the second month of immigration, and the third month was dominated by female immigrants.

Males also remained in the lake for a significantly longer period of time than did the females (two sided t-test, $P<0.05$). The mean duration of stay for males that were first captured while immigrating and last captured while emigrating ($n=34$) was 98.0 days, whereas the mean duration of stay for females ($n=54$) was 73.6 days. This is four times longer than the duration of stay for *A. macrodactylum* in Idaho (Beneski et al. 1986) and three times longer than the duration of stay for *A. jeffersonianum* in Indiana (Williams 1970). However, the longest stay by a male was similar in length to the longest stay by a female, 159 days and 153 days, respectively.

The mean date of emigration for females ($n=96$) was day 110 (27 July), while the mean date of emigration for males ($n=62$) was day 115 (1 August). The mean dates of emigration were not significantly different between male and females (two sample t-test, $p=0.32$). Therefore, the observed difference between the sexes in the duration of stay in the lake was primarily due to the earlier immigration by males. Beneski et al. (1986) observed both an earlier arrival and a later departure by male *A. macrodactylum*.

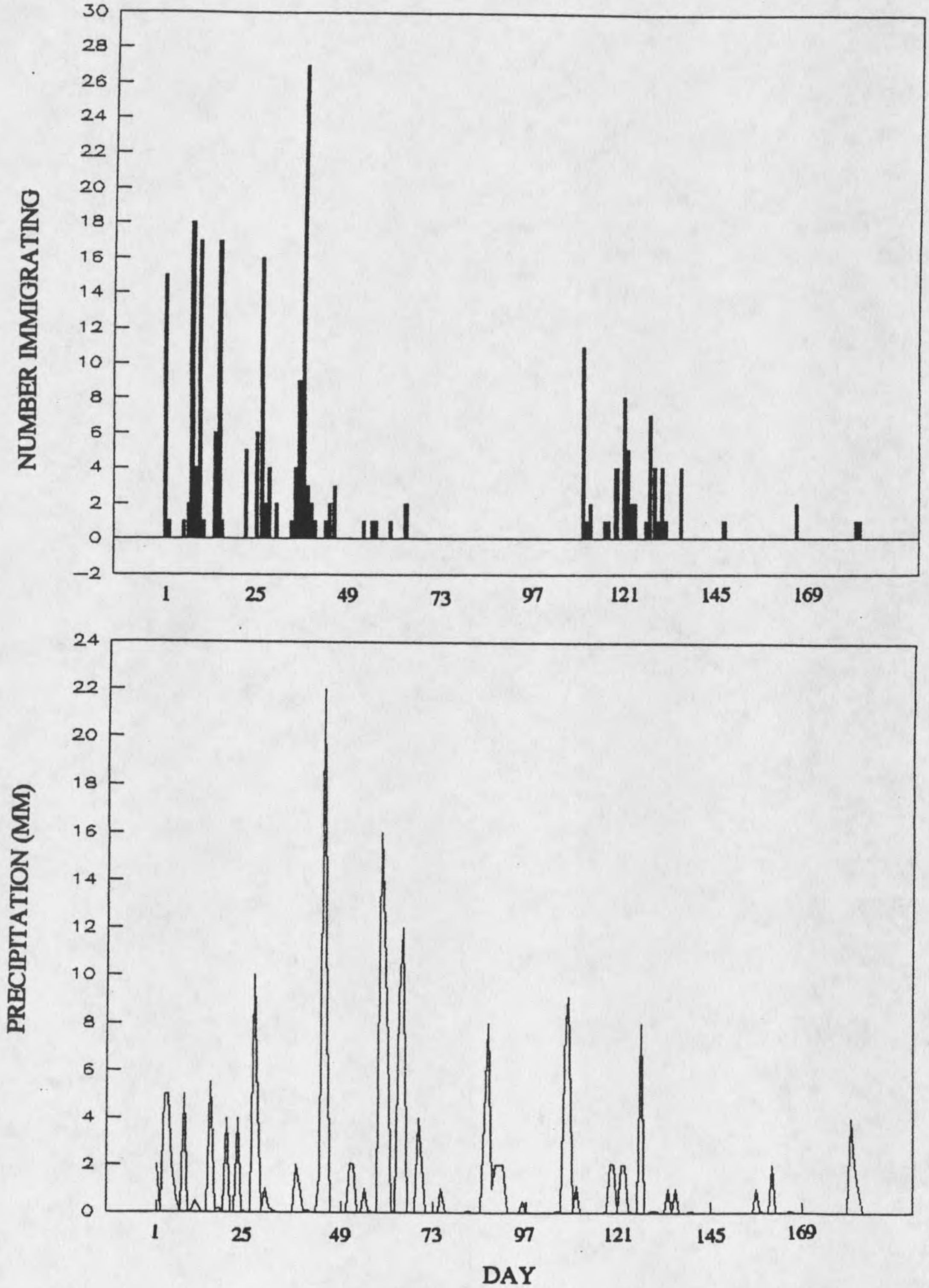
Diel Movement Patterns

I determined the diel pattern for 340 movements and found 336 (98.8%) to be nocturnal. Two hundred eighty-one (82.6%) of these movements occurred within 12 hours following a precipitation event. Many ambystomids have been found to prefer nocturnal movement to diurnal movement (Blanchard 1930, Botts 1978, McClure 1943, Semlitsch 1981, 1983b and 1985a, Sexton et al. 1990, and Williams 1970). Semlitsch and Pechmann (1985) noted that *A. tigrinum* and *A. talpoideum* preferred nocturnal migration even during periods when the rainfall regime was the same for both day and night. They suggest that avoidance of water loss and visual predators effects an avoidance of diurnal migration in ambystomids.

Environmental Effects on Immigration

Linearly regressing the number immigrating on minimum daily air temperature, daily precipitation, and seasonality observations is not significant ($p>0.05$, $df=181$). A comparison of the number immigrating per day and daily precipitation for the 24 hour period previous to the morning of any immigration captures (Figure 4) shows that the majority of immigrations occurred on days when there was a precipitation event. Salamander movement

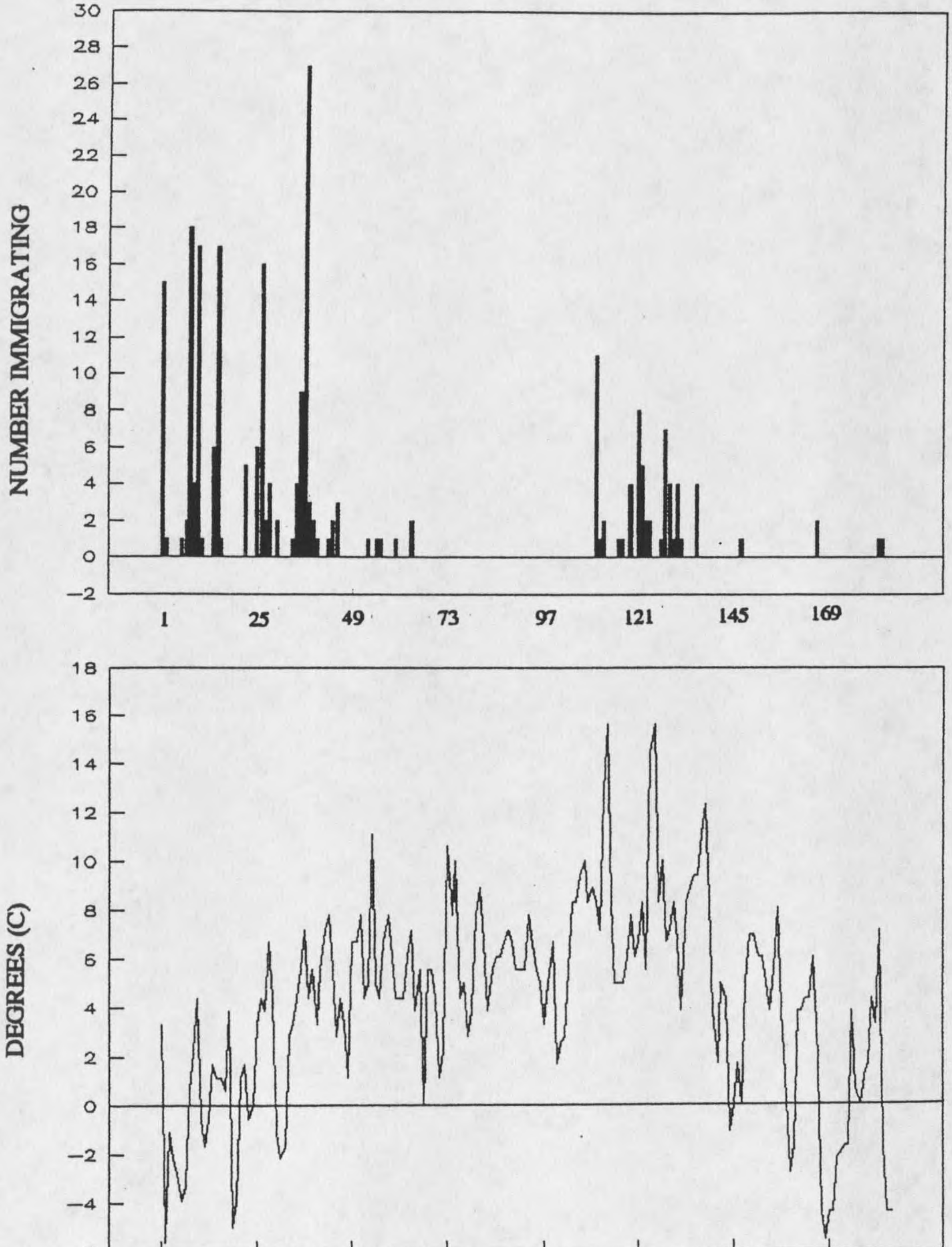
Figure 4. Daily immigration versus daily precipitation.



occurred in fresh snow on four occasions. Precipitation occurred on only 39.5% of the study days, yet 83% of the recorded immigrations (201 of the 241 immigrations recorded for the study) occurred within 24 hours of these precipitation events. The mean amount of precipitation that fell during the 24 hours prior to any immigration captures (2.1 mm, n=53) was greater than the mean amount of precipitation that fell during the 24 hours prior to days with no captures (0.8 mm, n=132), but, due to small sample sizes and the apparent lack of constant variance, this hypothesis cannot be statistically tested ($F_{(52,131)}=2.98$, $p>0.10$) . Thus precipitation may be important as a predictor of the daily occurrence of immigration but not as a predictor of magnitude of migrations. Semlitsch (1985a) reached the same conclusion for *A. talpoideum* in the southeast U.S. His study on the effects of rainfall and temperature on migration left 45-83% of the variation in migratory magnitude unexplained. However, Semlitsch (1983b) found that the magnitude of *A. talpoideum* migrations was correlated to the amount of precipitation.

Immigrations rarely occurred when the minimum daily temperature was less than 0 C (Figure 5). The minimum daily temperature fell below 0 C on 16% of the days of the study, but only 3.7% of the immigrations occurred on these days. Overall, 96% of immigrations occurred on days when

Figure 5. Daily immigration versus minimum daily air temperature.



the minimum air temperature was in the range between 0 C and 15.6 C. However, the mean daily minimum air temperature for days on which immigrations occurred (4.5 C) was not significantly different from the mean daily minimum air temperature for days on which there were no immigrations (4.3 C) (two-sided t-test, p=0.75). The minimum daily air temperature was below 0 C on seven occasions that immigration occurred, though only nine movements were intercepted on these days. The lowest temperature recorded for a day on which migration events occurred was -5.6 C.

There was no significant difference between the mean daily maximum air temperature of the 24 hour periods prior to immigration captures (20.5 C) and the mean daily maximum air temperature of the 24-hour periods prior to no captures (20.8 C) (two sided t-test, p=0.79).

I was not able to determine whether there was a threshold soil temperature above which immigration was initiated, as suggested by Sexton et al. (1990). Immigrations were intercepted on the first day of the study. The mean surface soil temperature taken within one hour of sunrise was not different for days on which immigrants were captured (7.2 C) and days on which immigrants were not captured (7.2 C) during the first 64 days of the study, but, due to small sample sizes and the apparent lack of constant variance, this hypothesis cannot be statistically tested ($F_{(23,27)}$=0.40, p>0.10).

Environmental Effects on Emigration

Linearly regressing the number emigrating on minimum daily air temperature, daily precipitation, and seasonality observations is not significant (p>0.05, df=181). The majority of the emigration occurred on days when there were precipitation events (Figure 6). Precipitation occurred on only 39.5% of the study days, yet 95% of the recorded emigrations (212 of the 224 emigration captures recorded for the study) occurred within 24 hours of these precipitation events. In addition, the mean amount of precipitation that fell during the 24 hours prior to any emigration (2.3 mm) was significantly greater than the mean amount of precipitation that fell during the 24 hours prior to days with no captures (0.9 mm)(two sided t-test, p<0.05). Precipitation was important as a predictor of the daily occurrence of emigration but not as a predictor of magnitude of emigration.

Emigration did not occur when the minimum daily temperature was less than 0 C (Figure 7). All emigration occurred on days when the minimum daily air temperature was in the range between 0 C and 15.6 C. The mean minimum daily air temperature for days on which emigration occurred (5.7 C) was significantly different from the mean

Figure 6. Daily emigration versus daily precipitation.

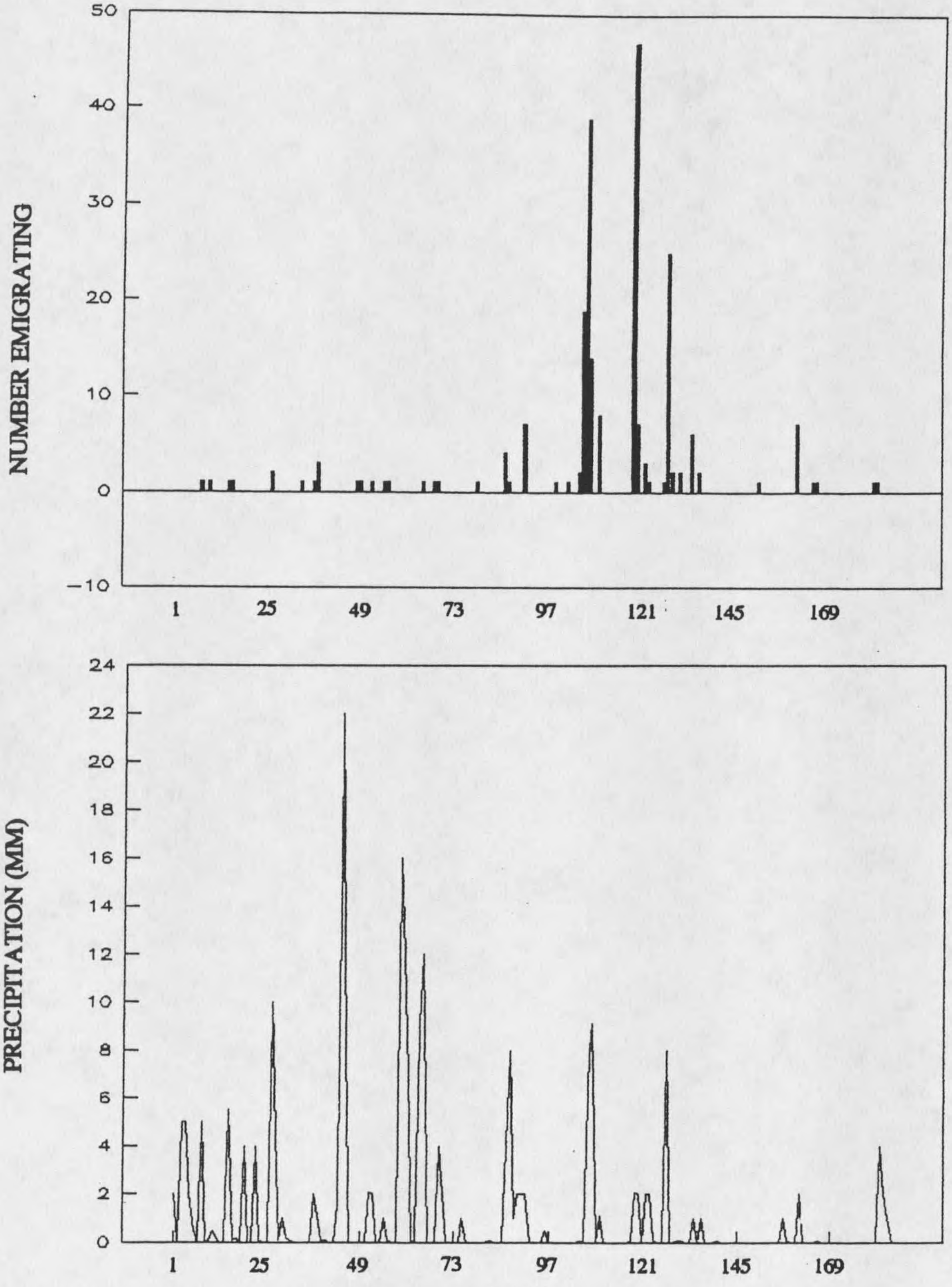
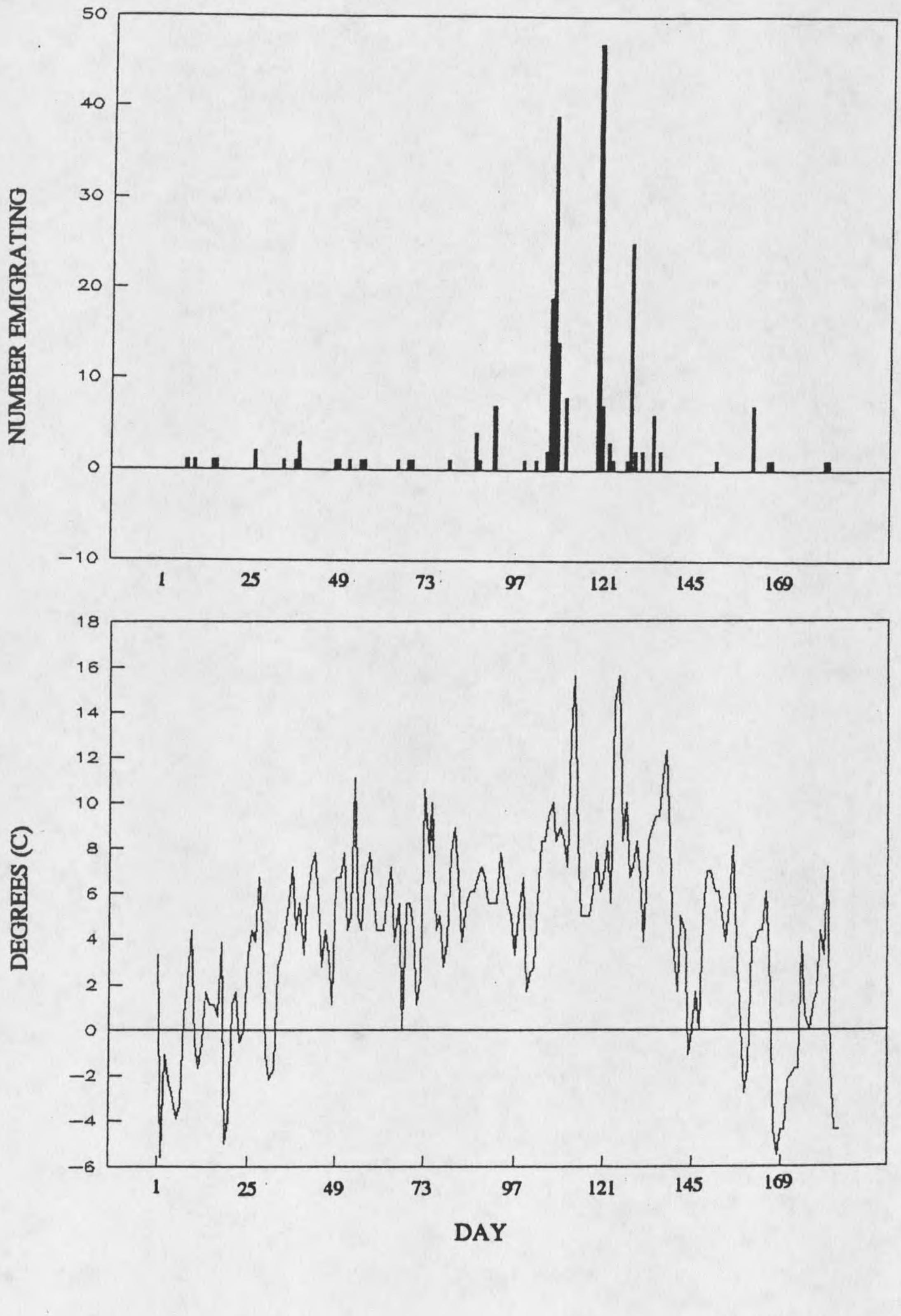


Figure 7. Daily emigration versus minimum daily air temperature.



daily minimum air temperature for days on which there was no emigration (3.8 C)(two sided t-test, $p<0.05$). There was no significant difference between the mean maximum daily air temperature of the 24 hours prior to emigration captures (22.2 C) and the mean maximum daily air temperature of the 24 hour periods prior to no captures (20.1 C), but, due to small sample sizes and the apparent lack of constant variance, this hypothesis cannot be statistically tested ($F_{(42,114)}=0.58$, $p>0.10$).

Emigration from Ice Lake Reservoir did not immediately follow oviposition despite the presence of optimal temperature and precipitation events (Figures 8, 9). Emigration was observed soon after oviposition in *A. tigrinum* (Botts 1978) and *A. macrodactylum* (Beneski et al. 1986).

The stomach contents of five metamorphosed *A. tigrinum* from Ice Lake Reservoir and elsewhere in the northern part of Yellowstone National Park contained aquatic invertebrates. Thus, it may be beneficial for these salamanders to remain in the breeding pond after oviposition to feed. Analysis of the stomach contents of emigrating *A. tigrinum* by Botts (1978) revealed that only 35% had been feeding inside the drift fence, and that their food consisted mainly of terrestrial invertebrates presumably taken on the shore.

Scatter and residual plots for percent of initial body weight gained versus the duration of stay in the aquatic environment for 80 individuals that were first captured while immigrating and last captured while emigrating indicate a possible nonlinear regression relationship exists, thus suggesting high variability in weight gain patterns (Figure 8). Perhaps a threshold weight must be attained before emigration can occur. The mean weight gained by males (n=20) during time spent in the lake was 10.3 grams and the mean weight gained by females (n=80) was 13.6 grams.

Mean water temperature measured within one hour of sunrise was not found to be significantly different on days that emigrants were captured and days that emigrants were not captured during the period from day 45 to day 185 (two sided t-test, p=0.31). Therefore, it seems likely that, in addition to air temperature, precipitation and possibly weight gain, emigration may be influenced by other factors.

The onset of emigration by *A. tigrinum* in this study corresponds with the initial decrease in day length (Figure 9). Day length has been shown to effect migratory disposition in many species of birds (Welty and Baptista 1988) as well as fish (Orr 1970) by causing an increase in the activity of the thyroid gland. Day length may influence migration in *A. tigrinum* as well (Taylor 1972, Taylor and Adler 1978, Wolstenholme and Knight 1970,

Figure 8. Scatter plot of weight gain versus duration of stay in lake.

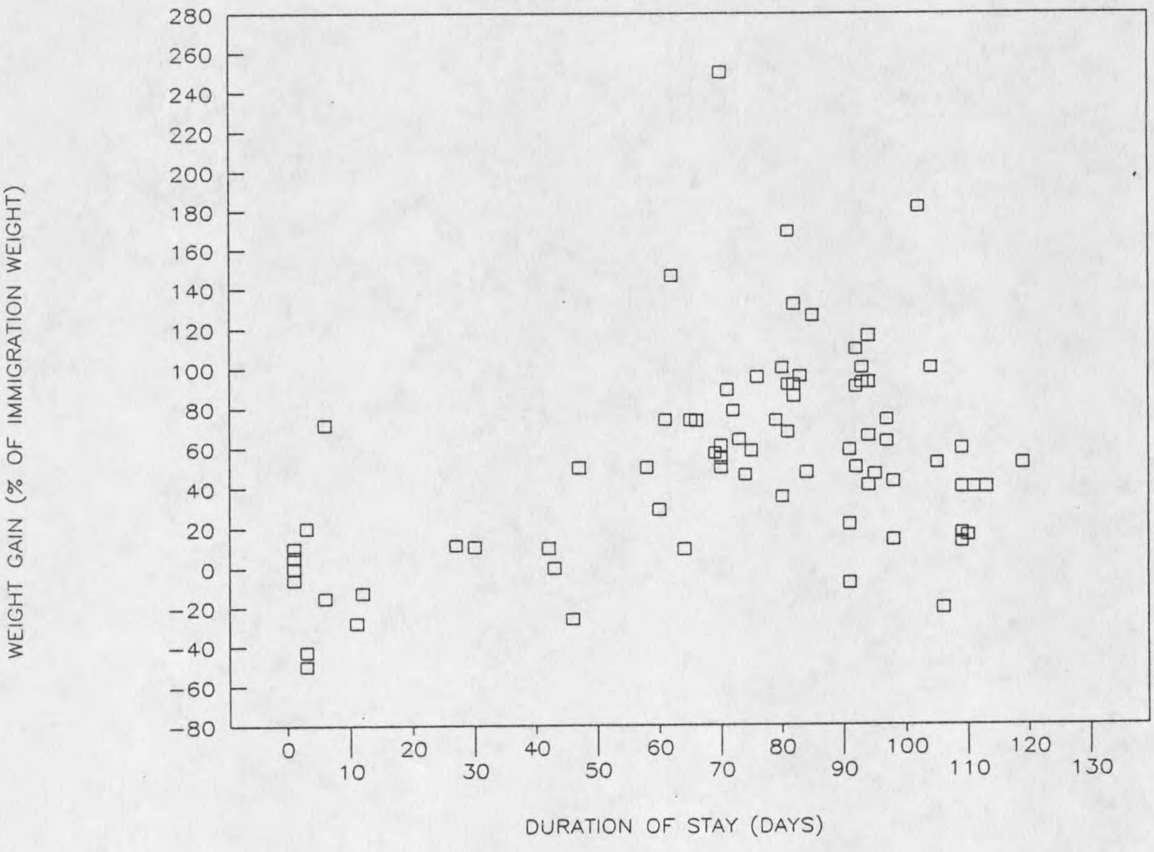
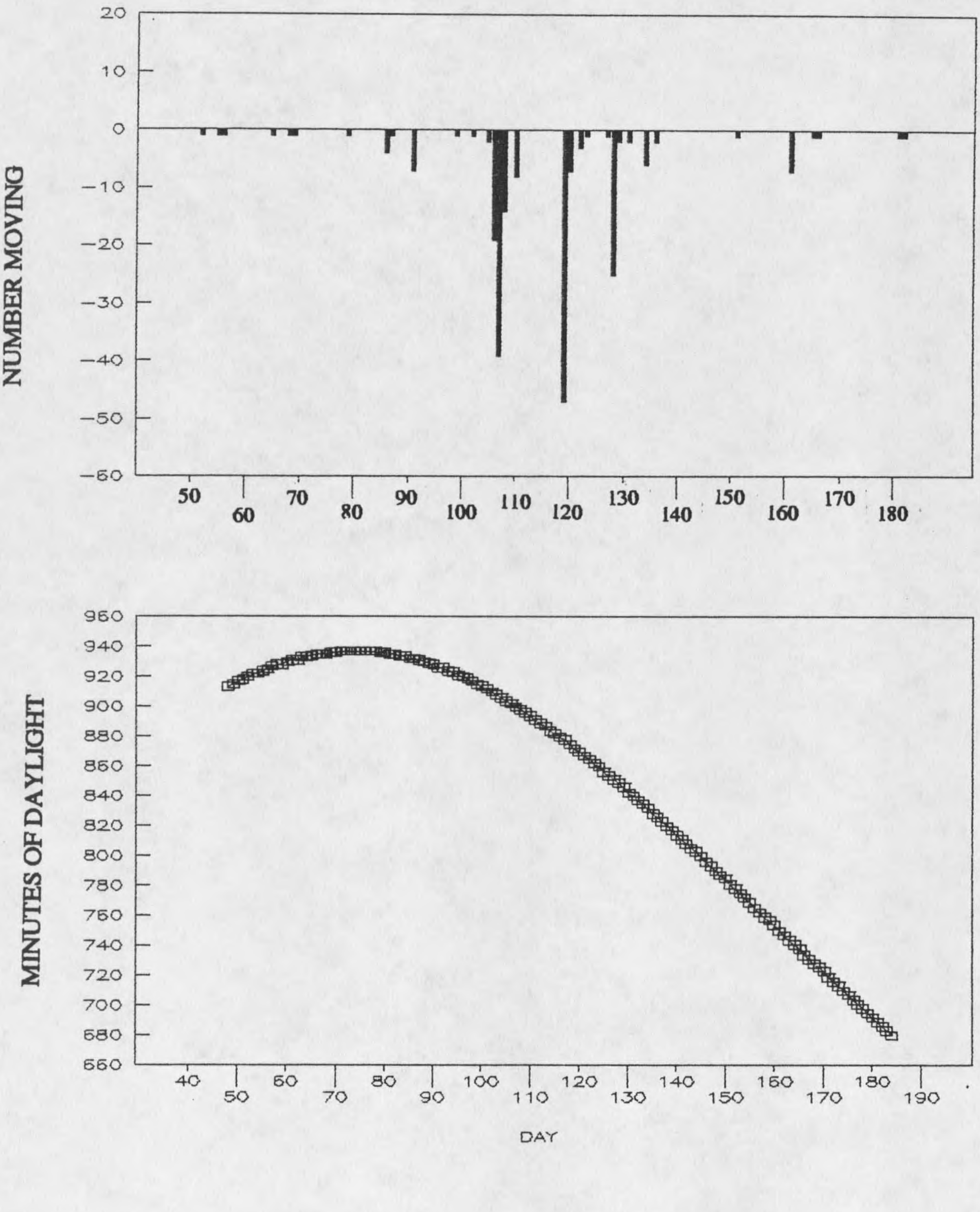


Figure 9. Movement versus day length.

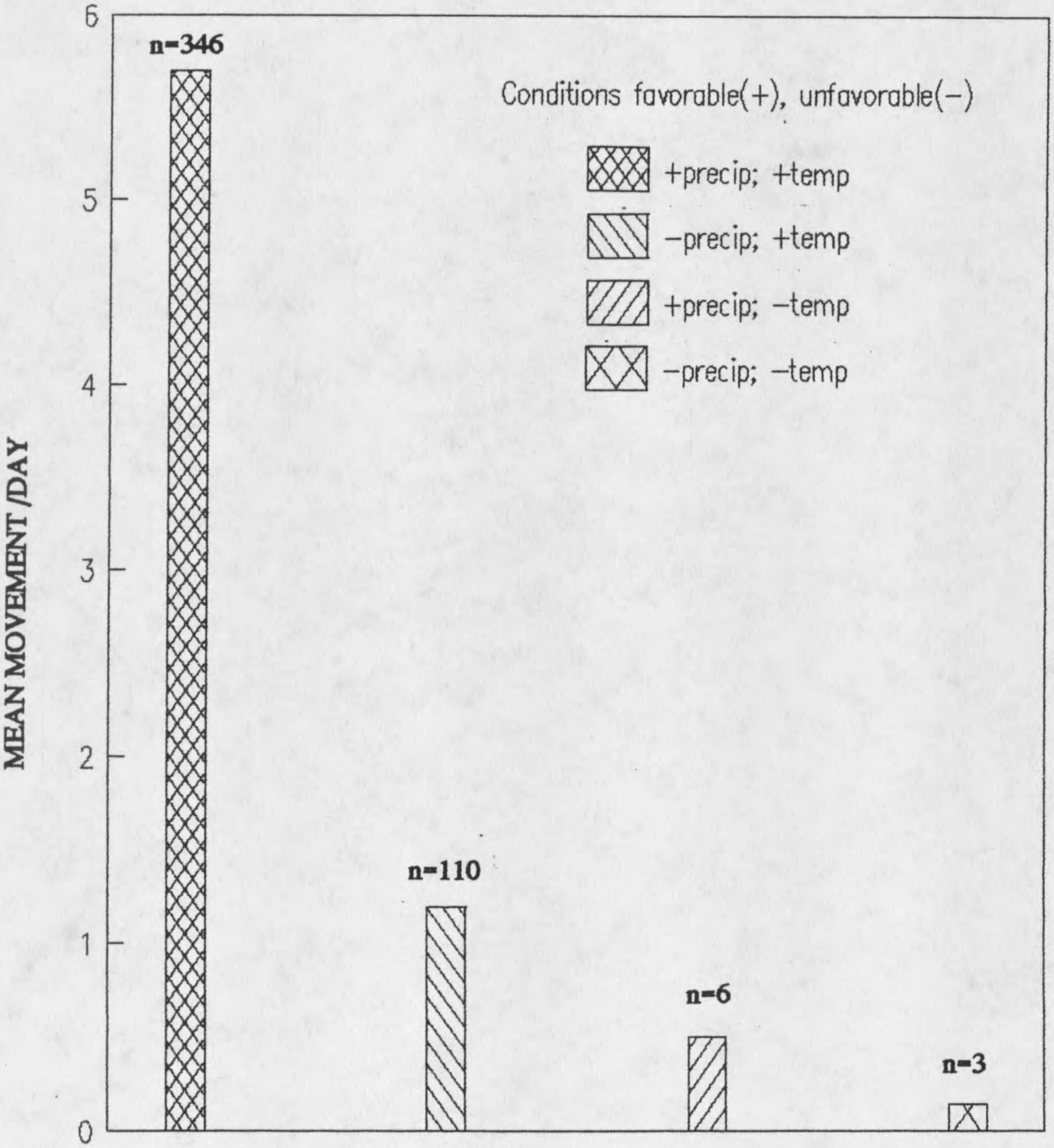


Adler 1969, Welty and Baptista 1988, Gern et al. 1986, Tamarkin et al. 1985, and Duvall and Norris 1978, 1980).

As with other studies (Beneski et al. 1986) there is a broad overlap in this study between favorable precipitation events (>0 mm) and favorable air temperatures (≥0 C), thus making it difficult to determine which characteristic has a greater influence on the migratory movements of these salamanders. At Ice Lake Reservoir an average of 5.7 movements occurred on each day that both precipitation and daily minimum air temperature were favorable. When temperature was favorable but precipitation was not, 1.2 movements per day occurred. When precipitation was favorable but temperature was not, 0.5 movements per day occurred. When neither was favorable, only 0.14 movements per day occurred. Thus, daily minimum air temperature is a better predictor of the daily occurrence of migratory movement than precipitation. Nonetheless, much more movement is likely to occur when both are favorable (Figure 10).

Beneski et al. (1986) obtained similar results with *A. macrodactylum*, noting that favorable precipitation and temperature resulted in the most movements per day but that favorable temperature alone resulted in more movements per day than did favorable precipitation alone. Temperature was more likely to be limiting on some days early in the study, which may have resulted in larger

Figure 10. Mean temperature per day when precipitation and temperature are favorable (+) and unfavorable (-).



movements per day on days when temperature was favorable simply because there were fewer of these days. Beneski et al. (1986) suggest that *A. macrodactylum* may prefer to migrate on the first few days of favorable temperature to avoid predators such as garter snakes and shrews. The first garter snake was observed at Ice Lake Reservoir on day 48, though shrews were captured as early as day 2.

Paedomorphosis

Salamanders captured with the aquatic box trap were classified as either metamorphs or larvae (Table 3). Larvae were only captured in two sites (Slide Lake, n=13 and Ice Lake Reservoir, n=4). Only two larvae, captured in Ice Lake Reservoir on 13 July, possessed the cloacal characteristics and snout-vent lengths that indicated they might be paedomorphic and thus were collected. The reproductive maturity of these two larvae was assessed using the criteria set forth by Collins (1981) (Table 2), where stages I and II are considered to be immature while stages III, IV and V are considered reproductively mature. These larvae, captured on 13 July, were found to be immature (Table 4).

The five minnow traps placed in Ice Lake Reservoir provided information regarding the frequency of paedomorphs in that lake. Four hundred twenty minnow-trap-nights in Ice Lake Reservoir resulted in the

Table 3. Numbers of *A. tigrinum* larvae and metamorphs captured during lake survey with aquatic box trap.

Site	Dates	#Larv	SVL, range	#Metamorphs	SVL, range
Float. Isl.	5/13-5/15	0	---	9	97.2mm 79.5,109.5
Foster	6/15-6/17	0	---	2	110.3mm 107.5,113.0
Everts 0899	6/22-6/24	0	---	2	114.3mm 98.0,130.5
Everts 0897	6/29-7/1	0	---	0	---
Slide	7/7-7/9	13	33.3mm 24.0,40.0	3	107.3mm 106.5,108.0
Ice	7/13-7/15	4	93.5mm 79.0,100.0	2	102.0mm 91.0,113.0
Rain-bow	8/3-8/5	0	---	0	---

Table 4. Trap type, capture date, sex, body measurements, and stage of breeding readiness of dissected larvae from Ice Lake Reservoir. The sex designation may be inaccurate for those larvae belonging to stage I as the gonadal tissue tends to be rather androgynous at this stage.

Trap	Cap. Date	Sex	SVL(mm)	Weight (g)	Stage
minnow	8-13-93	F	64.0	14	I
minnow	8-13-93	F	69.5	14	I
minnow	5-07-93	M	69.5	32	I
minnow	5-14-93	F	71.5	14	I
minnow	5-03-93	M	74.0	20	I
minnow	5-02-93	--	74.5	17	I
minnow	5-15-93	M	77.0	16	I
minnow	4-21-93	--	79.0	11	I
minnow	5-12-93	F	79.0	20	I
minnow	4-28-93	M	83.0	18	I
minnow	4-23-93	--	85.0	14	I
minnow	5-05-93	F	88.5	37	I
minnow	5-02-93	F	90.0	39	I
minnow	5-30-93	F	92.0	71	II
box	7-13-93	M	97.0	54	II
box	7-13-93	F	100.0	55	II
minnow	5-03-93	F	111.0	84	II
minnow	5-10-93	F	120.0	105	III
minnow	8-27-93	F	123.5	--	III
minnow	5-05-93	F	112.5	99	IV
minnow	4-29-93	M	117.5	74	IV
minnow	4-29-93	M	125.5	85	IV
minnow	5-02-93	M	142.0	117	IV

capture of 97 larvae. Twenty-one of these larvae, ranging in SVL from 64.0 mm to 142.0 mm, were sacrificed for dissection. Six of these larvae (3 males, 3 females) were found to be reproductively mature (Table 4). These larvae tended to be larger than the reproductively mature metamorphs at the site. The mean snout-vent length of the paedomorphs was 123.5 mm, while the mean snout vent length of the six largest metamorphs captured at the site was 118.8 mm. Due to small sample sizes and the apparent lack of constant variance, this hypothesis cannot be statistically tested ($F_{(5,5)}=17.58$, $p>0.10$). However, the mean weight of the five paedomorphs (96 g) for which weight was available was significantly greater than the mean weight of the five heaviest metamorphs (66 g) captured at the site (two sided t-test, $p<0.05$).

Turner (1951, 1955) stated that paedomorphosis was known to occur in certain beaver lakes in the northern part of Yellowstone National Park, but no documentation exists for this claim (F.B. Turner, pers. comm.). My study demonstrated that paedomorphosis occurs in at least one site in Yellowstone National Park. Further intensive study would be required to determine if other permanent lakes in the Park contain paedomorphs. I believe that aquatic box traps can be effective devices for sampling larvae in Yellowstone National Park, but traps need to be left for an extended period of time in each lake to be sampled and checked daily.

CONCLUSIONS

Immigration by *A. tigrinum* at Ice Lake Reservoir in Yellowstone National Park in 1993 began in April. The major period of immigration ended in June. Ninty-six percent of the immigrations occurred when the minimum daily temperature was 0 C or greater, while 83% occurred within 24 hours of a precipitation.

The major emigration period began in July and continued through August. All emigrations occurred when the minimum daily temperature was 0 C or greater, while 95% occurred within 24 hours of a precipitation event.

Ninty-nine percent of all migrations were nocturnal. More migrations occurred when both temperature and precipitation were favorable than when only one or none was favorable.

Males arrived earlier at the lake than females, but males and females tended to emigrate at about the same time. Females outnumbered males in the breeding population 111 to 100. Mean SVL of males was greater than that of females, but the mean weight of females was greater than that of males.

Eggs were deposited in Ice Lake Reservoir in April and May, usually at night. The eggs probably hatched in early July, 53-58 days after the last observed oviposition event. Two size classes of larvae, belonging to cohorts representing two years, existed in the lake in 1993. Emigration of newly metamorphosed individuals from the 1992 cohort occurred in July and August. Most of the 1993 cohort likely overwintered in the lake.

Six larvae captured in Ice Lake Reservoir were found to be reproductively mature, thus demonstrating that paedomorphosis occurs in at least one lake in Yellowstone National Park. Further intensive study is recommended to determine if other permanent lakes in the Park contain paedomorphs.

REFERENCES CITED

Adler, K. 1969. Extraoptic phase shifting of circadian locomotor rhythm in salamanders. Science 164:1290-1291.

Anderson, J.D. 1967. A comparison of life histories of coastal and montane populations of *Ambystoma macrodactylum* in California. American Midland Naturalist 77:323-355.

Baldauf, R.J. 1952. Climatic factors influencing the breeding migration of the spotted salamander, *Ambystoma maculatum*. Copeia 1952:178-181.

Beneski, J.T. Jr., E.J. Zalisko, and J.H. Larsen Jr. 1986. Demography and migratory patterns of the eastern long-toed salamander, *Ambystoma macrodactylum columbianum*. Copeia 1986:398-408.

Bizer, J.R. 1977. Life history phenomena of *Ambystoma tigrinum* in montane Colorado. PhD Dissertation, Washington University. 211pp.

__________. 1978. Growth rates and size at metamorphosis of high elevation populations of *A. tigrinum*. Oecologia 34:175-184.

Blanchard, F.N. 1930. The stimulus to the breeding season of the spotted salamander, *Ambystoma maculatum* (Shaw). American Naturalist 64:154-167.

Blaustein, A.R., P.D. Hoffman, D.G. Hokit, J.M. Kiesecker, S.C. Walls, and J.B. Hays. 1994. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? Proceedings of the National Academy of Science 91:1791-1795.

Botts, D.A. 1978. Life history and movement of *Ambystoma tigrinum* and associated vertebrates around a semi-permanent pond. M.S. Thesis, Auburn University, Auburn, Alabama. 105pp.

Brandon, R.A. and D.J. Bremer. 1967. Overwintering of larval tiger salamanders in southern Illinois. Herpetologica 23:67-68.

Chadwick, C.S. 1940. Identity of prolactin with water drive factor in *Triturus viridescens*. Proceedings of the Society for Experimental Biology and Medicine. 45:665-337.

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

Collins, J.T. 1990. Standard common and current scientific names for North American amphibians and reptiles, third edition. Herpetological Circular No. 9. Society for the Study of Amphibians and Reptiles, Department of Biology, St Louis University, St. Louis, Missouri. 41pp.

Douglas, M.E. 1979. Migration and sexual selection in *Ambystoma jeffersonianum*. Canadian Journal of Zoology 57:2303-2310.

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

Duvall, D. and D.O. Norris. 1978. Stimulation of land-drive behavior in adult salamanders (*Ambystoma tigrinum*) by thyroxine (T_4). American Zoologist 18:589.

__________ and __________. 1980. Stimulation of terrestrial-substrate preferences and locomotor activity in newly transformed tiger salamanders (*Ambystoma tigrinum*) by exogenous or endogenous thyroxine. Animal Behavior 28:116-123.

Eagleson, G.W. 1976. A comparison of the life histories and growth patterns of the salamander *Ambystoma gracile* (Baird) from permanent low altitude and montane lakes. Canadian Journal of Zoology 54:2098-2128.

Gentry, G. 1968. Notes on the availability of eggs of the *Ambystoma* species of salamanders in Tennessee. Journal of the Tennessee Academy of Science 43:53.

Gern, W.A., D. Duvall, and J.M. Nervina. 1986. Melatonin: a discussion of its evolution and actions in vertebrates. American Zoologist 26:985-996.

Gibbons, J.W. and D.H. Bennett. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:236-242.

__________, and R.D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 7:1-16.

Gould, S.J. 1977. Ontogeny and Phylogeny. The Belknap Press of Harvard University Press, Cambridge, Mass. 501pp.

Grant, W.C. and J.A. Grant. 1958. Water drive studies on hypophysectomized efts of *Diemectylus viridescens*. Part I. The role of the lactogenic hormone. Biological Bulletin 114:1-9.

Gruberg, E.R. and R.V. Stirling. 1972. Observations on the burrowing habits of the tiger salamander (*Ambystoma tigrinum*). Herpetological Review 4:85-87.

Harris, R.N. 1987. Density dependent paedomorphosis in the salamander *Notophthalamus viridescens dorsalis*. Ecology 68:705-712.

__________. 1989. Ontogenetic changes in size and shape of the facultatively paedomorphic salamander *Notophthalamus viridescens*. Copeia 1989:35-42.

__________, R.D. Semlitsch, and H.M. Wilbur. 1990. Local variation in the genetic basis of paedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 44:1588-1603.

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.

Hoy, P.R. 1871. The development of *Ambystoma lurida* Sager. American Naturalist 5:578-579.

Koch, E.D. and C.R. Peterson. 1989. A preliminary survey of the distribution of amphibians and reptiles in Yellowstone National Park. *In* Clark, T.W. and A.H. Harvey, eds. Rare, sensitive, and threatened species of the Greater Yellowstone Ecosystem. Northern Rockies Conservation Cooperative. Pp. 47-49.

Martin, G. 1990. Froggy bottom. Discover 11:36-37.

McClure, H.E. 1943. Salamanders and snow. Ecology 24:265-266.

Milstein, M. 1990. Unlikely harbingers; the sudden, worldwide disappearance of amphibians alerts scientists to ecological breakdown. National Parks July-August, 1990:18-24.

Munholland, P.L., and J.J. Borkowski. 1993. Simple Latin square sampling + 1: a spatial design using quadrats. Technical Report #10-13-93, Department of Mathematical Sciences, Montana State University, Bozeman, Montana. 20pp.

Neter, J., W. Wasserman, and G.A. Whitmore. 1988. Applied Statistics. Third edition. Allyn and Bacon, Inc., Boston, MA. 1006pp.

Orr, R.T. 1970. Animals in migration. The Macmillan Company, New York. 303pp.

Packer, W.C. 1960. Bioclimatic influences on the breeding migration of *Taricha rivularis*. Ecology 41:509-517.

Peckham, R.S. and C.F. Dineen. 1955. Spring migration of salamanders. Indiana Academy of Science, Proceedings 64:278-280.

Peters, J.A. 1964. Dictionary of Herpetology. Hafner Publishing Company, New York. 392pp.

Pierce, K.L. 1979. History and dynamics of glaciation in the northern Yellowstone National Park area. Department of the Interior, United States Geological Survey, professional paper No. 729-F.

Pough, F.H. 1983. Amphibians and reptiles as low-energy systems. *In* W.P. Asprey amd S.I. Lustick, eds. Behavioral Energetics. Ohio State University Press, Columbus. Pp. 141-188.

Rogers, K.L. 1985. Facultative metamorphosis in a series of high altitude fossil populations of *Ambystoma tigrinum* (Irvingtonian: Alamosa County, Colorado). Copeia 1985:926-932.

Rose, F.L. 1976. Sex ratios of larval and transformed *Ambystoma tigrinum* inhabiting the Llano Estacado of west Texas. Copeia 1976:455-461.

__________ and D. Armentrout. 1976. Adaptive strategies of *Ambystoma tigrinum* Green inhabiting the Llano Estacado of west Texas. Journal of Animal Ecology 45:713-729.

Ross, D.A. 1991. Amphibians and reptiles in the diets of North American raptors. Wisconsin Endangered Resources Report 59. Wisconsin Department of Natural Resources, Madison, Wisconsin. 33pp.

Salthe, S.N. and J.S. Mecham. 1974. Reproductive and courtship patterns. Pp. 310-473 *in* B. Lafts, ed., Physiology of the Amphibia, vol. II. Academic Press, New York.

Semlitsch, R.D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology 59:315-322.

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

__________. 1983b. Structure and dynamics of two breeding populations of the eastern tiger salamander *Ambystoma tigrinum*. Copiea 1983:608-616.

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

__________. 1985a. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. Copeia 1985:477-489.

__________. 1985b. Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. Oecologia 65:305-313.

__________. 1987a. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. Ecology 68:994-1002.

__________. 1987b. Density dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. Ecology 68:1003-1008.

__________. 1987c. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61-69.

__________ and J.W. Gibbons. 1985. Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. Ecology 66:1123-1130.

__________, R.N. Harris, and H.M. Wilbur. 1990. Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. Evolution 44:1604-1613.

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

__________, D.E. Scott, and J.H.K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184-192.

__________ and H.M Wilbur. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 43:105-112.

Sever, D.M. and C.F. Dineen. 1977. 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.R. Bizer. 1978. Life history patterns of *Ambystoma tigrinum* in montane Colorado. American Midland Naturalist 99:101-118.

__________, C.P. Phillips, and J.E. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). Copeia 1990:781-787.

Shaffer, H.B. 1984. Evolution in a paedomorphic lineage. Allometry and form in the Mexican ambystomid salamanders. Evolution 38:1207-1218.

Snyder, R.C. 1956. Comparative features of the life histories of *Ambystoma gracile* (Baird) from populations of low and high altitudes. Copeia 1956:41-50.

Sprules, W.G. 1974a. The adaptive significance of paedogenesis in North American species of *Ambystoma* (Amphibia:Caudata): an hypothesis. Canadian Journal of Zoology 52:393-400.

__________. 1974b. Environmental factors and the incidence of neoteny in *Ambystoma gracile* (Baird) (Amphibia:Caudata). Canadian Journal of Zoology 52:1545-1552.

Stebbins, R.C. 1951. Amphibians of western North America. University of California Press, Berkely and Los Angeles. 539pp.

__________. 1985. Western Reptiles and Amphibians. Houghton Mifflin Company, Boston. 336pp.

Tamarkin, L., C.J. Baird, and O.F.X. Almeida. 1985. Melatonin: a coordinating signal for mammalian reproduction? Science 227:714-720.

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.

Taylor, D.H. 1972. Extra-optic photoreception and compass orientation in larval and adult salamanders (*Ambystoma tigrinum*). Animal Behavior 20:233-236.

__________ and K. Adler. 1978. The pineal body: site of extraocular perception of celestial cues for orientation in the tiger salamander (*Ambystoma tigrinum*). Journal of Comparative Physiology A 124:357-361.

Turner, F.B. 1951. A check-list of the reptiles and amphibians of Yellowstone National Park with incidental notes. Unpublished paper from the Yellowstone National Park Library, Mammoth, Wyoming. 18pp.

__________. 1955. Reptiles and amphibians of Yellowstone National Park. Yellowstone Interpretive Series No.5. Yellowstone Library and Museum Association, Mammoth, Wyoming.

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

Wake, D.B. 1991. Declining amphibian populations. Science 253:860.

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

Welty, J.C. and L. Baptista. 1988. The life of Birds. Saunders College Publishing, New York. 581pp.

Whiteman, H.H. and S.A. Wissinger. 1990. Ecological correlates of paedomorphosis in high elevation populations of *Ambystoma tigrinum nebulosum*. American Zoologist 30:A86.

Whitford, W.G. and A. Vinegar. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. Copeia 1966:515-519.

Williams, P.K. 1970. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. Dissertation, Indiana University, Bloomington, Indiana. 47pp.

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.

__________, __________, and S.C. Horn. 1990. Dietary and habitat differences among morphs in a sub-alpine population of salamanders. American Zoologist 30:86A

Wolstenholme, G.E.W. and J. Knight, eds. 1970. The pineal gland. A Ciba Foundation symposium, London. Science 175:618-619.