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An Analysis of Migratory Behavior Physiological Condition and Life History Strategy in the Salamanders *Ambystoma Mabeei* and *A. Opacum* in Southeastern Virginia

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AN ANALYSIS OF MIGRATORY BEHAVIOR, PHYSIOLOGICAL CONDITION, AND LIFE HISTORY STRATEGY IN THE SALAMANDERS *AMBYSTOMA MABEEI* AND *A. OPACUM* IN SOUTHEASTERN VIRGINIA

by

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B.S. May 1996, Old Dominion University

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ABSTRACT

AN ANALYSIS OF MIGRATORY BEHAVIOR, PHYSIOLOGICAL CONDITION AND LIFE HISTORY STRATEGY IN THE SALAMANDERS *AMBYSTOMA MABEEI* AND *A. OPACUM* IN SOUTHEASTERN

Michael W. McCoy
Old Dominion University, 2000
Director: Dr. Alan H. Savitzky

Ambystoma mabeei is listed as threatened in Virginia due to its rarity and susceptibility to urbanization and poor forestry practices. The goal of this study was to identify factors that may affect the persistence of *A. mabeei* in Virginia by studying the life history and ecology of *A. mabeei* and its syntopic congener *A. opacum*. This information will contribute to the knowledge of life history variation within Ambystomatidae and will be critical for the development of a comprehensive management plan for *A. mabeei*. Population sizes of the two species and the proximate factors responsible for initiating breeding migrations were determined by a mark-recapture study. Salamanders were captured using drift fence and pitfall trap arrays installed in three independent sections encompassing approximately 65% of the pond's perimeter. Analyses of covariance (ANCOVA) were used to compare mass relative to snout-vent length as an index of physiological condition. An analysis of gut contents indicated that *A. mabeei* consume a variety of prey and individuals from Virginia harbor high loads of gastric parasites.

The results of this study support the hypothesis that environmental conditions influence the breeding migrations of *Ambystoma mabeei* and *A. opacum*. The intensity and timing of each migration event are influenced by weather conditions prior to the onset of the breeding season. Adult condition and reproductive success are influenced by annual climatic patterns as well. A model is proposed that explains the migratory patterns observed during this study. This model incorporates both a heritable migration cue and seasonal variation in adult condition. The presence of a genetic determinant for breeding migration provides a mechanism by which adaptation to changes in local environmental conditions can occur. Before we can understand the true status and fate of *Ambystoma mabeei* in Virginia, additional research into several major areas of the species life history is needed. These studies should address the community ecology, landscape ecology, parasitology and physiological ecology of both the larvae and adults.

This thesis is dedicated to my mother and father for their unyielding guidance and support through out my life. They taught me to appreciate and respect nature and to pursue my dreams. I would also like to dedicate this thesis to my wife Krista for her love, support and motivation.

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TABLE OF CONTENTS

Page

Section

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Ambystomatid salamanders exhibit a diverse array of life history patterns, encompassing many of the strategies seen in the urodeles in general. This makes the genus *Ambystoma* a model group for studying the evolution of life history patterns and reproductive strategies seen in the salamanders as a whole (Petranka, 1990). Ambystomatid salamanders are moderate to large, stout-bodied animals reaching total lengths of 100 - 350 mm (Petranka, 1998). They are characterized by having small heads and elongate bodies with prominent costal grooves. With the exception of some paedomorphic populations, they are terrestrial throughout their adult lives, but little is known of their activities during this time. They return to the water only to breed. In most species of ambystomatids, courtship and oviposition occur in ephemeral ponds, streams, or other bodies of water that do not support populations of predatory fishes. Two species (*A. opacum* and *A. cingulatum*) deposit their eggs terrestrially in the fall, within dried ephemeral pond beds. Fall and winter rains fill the ponds and submerge the eggs, which triggers hatching. In addition, female *A. opacum* excavate a nest chamber and guard their eggs, providing moisture and protection from predators. In most species, however, breeding occurs during the spring.

The first studies of the behavioral ecology of ambystomatid salamanders focused primarily on courtship behavior and egg deposition and included descriptions of spermatophores and egg masses. (For a review of courtship and oviposition behaviors, see Petranka, 1998.) More recent studies have focused on their reproductive biology, population dynamics, ecological interactions and the events that initiate immigration to

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The Journal of Herpetology was used as a model for the format and style of this thesis.

breeding ponds. However, the reproductive biology, courtship behavior, age at maturity, migratory behavior, growth rate, survivorship, interspecific interactions, feeding behavior and ecological preferences of *Ambystoma mabeei* remain unknown (Hardy and Anderson, 1970; Pague and Mitchell, 1991; Petranka, 1998).

Ambystoma mabeei was described by Bishop (1928) and was originally believed to be restricted to the coastal plain of the Carolinas until its discovery in southeastern Virginia in 1979 (Mitchell and Hedges, 1980). Despite this extension of its known range, the species remains relatively restricted geographically when compared to most other species of ambystomatids. In Virginia, *A. mabeei* has been documented at only seven locations in Gloucester, Isle of Wight, Southampton, and York counties and the cities of Hampton, Newport News and Suffolk. It was documented in the Grafton Ponds Sinkhole Complex (York County) in 1983 (Ensley and Cross, 1984), which is believed to sustain the largest population of the species in the state (Clark, 1998). Many of the other Virginia populations have been extirpated or are represented by only one or a few individuals (Roble, 1998). Due to its rarity and sensitivity to urbanization and forestry practices, *A. mabeei* is listed as State Threatened in Virginia (Pague and Mitchell, 1991; Roble 1998). The goal of this study was to elucidate various aspects of the life history and ecology of *Ambystoma mabeei,* including its diet, migratory and reproductive behaviors, population size and status, and to identify the variables that may affect its survival in southeastern Virginia in the future. This information will be critical for Virginia to develop a comprehensive management plan for this species and will contribute to the knowledge of life history variation within Ambystomatidae. Although this study focuses primarily on the life history and ecology of *Ambystoma mabeei,* I also report data collected on its syntopic congener, *A. opacum.*

Because little information is available for *Ambystoma mabeei,* I provide a background against which the current study can be viewed by reviewing the literature concerning ambystomatids in general. First I review the literature concerning the terrestrial ecology and migratory behavior of *Ambystoma.* Then I review the literature on the population dynamics and reproductive biology of this group, followed by their diets and foraging behaviors. Finally, I summarize the literature available on *A. mabeei.*

Terrestrial Ecology and Migration Behavior

The migratory behavior of ambystomatid salamanders has been well studied over the past 50 years, producing a wealth of literature. In most species immigration to breeding ponds is cued by environmental variables, such as temperature and precipitation. Due to the expansive literature on this subject, I limit my review to only the most extensively studied species.

Blanchard (1930) was one of the first researchers to look at the climatic parameters associated with initiating the migration of ambystomatid salamanders to breeding ponds. He studied a population of *Ambystoma maculatum* in Michigan in which migration occurred during the first warm days of spring, when the temperature first rose above freezing. However, the maximum and minimum temperatures had little to do with the migrations and the arrival of adult salamanders was more strongly correlated with the incidence of rainfall. These insights were supported by several subsequent studies. Bishop (1941) also concluded that precipitation was a primary factor initiating the migration of *A. maculatum* to breeding sites and observed that migrations may also be initiated by the runoff of snowmelt following a rapid rise in temperature. Bishop also observed immigration of *A. jeffersonianum* under the same conditions. More recent studies have re-examined the influence of temperature on the migration of *A. maculatum* to breeding ponds. Baldauf (1952) observed salamanders migrating on warm, foggy nights and concluded that temperature and humidity were the most important factors contributing to the spring migration of these salamanders. Whitford and Vinegar (1966) also observed salamanders migrating in the absence of rain on warm, humid nights. In a Missouri population of *A. maculatum*, migrations occurred at a minimum mean three-day air temperature of 5.5° C and were more closely related to temperature than to daily precipitation (Sexton et al., 1990). Furthermore, the mean three-day air temperature was closely tied to soil temperature at 30 cm deep, which the authors believed to be the most accurate predictor of migration, with precipitation or moisture serving a threshold function.

Similar studies on migration in other species of *Ambystoma* have produced results that at least partially agree with those seen in *A. maculatum*. However, breeding migrations in a South Carolina population of the mole salamander (*A. talpoideum*) were not correlated with either temperature or precipitation (Semlitsch, 1985). In fact, the initiation of breeding migrations in this species "always occur during the coldest but not necessarily the wettest months of each year" (Semlitsch, 1985). However, cumulative total rainfall for the period of immigration was significantly correlated with the size of the breeding population. The breeding migrations of *A. californiense* (Loredo and Van Vuren, 1996) are also related to the onset of early spring rains.

Ambystomatid salamanders exhibit diverse life histories. First, there is a high level of variability in the duration of the breeding period within and among populations. For example, the breeding season in a North Carolina population of *A. maculatum* can last 56-73 days (Stenhouse, 1985), whereas populations in Ohio may breed for only 3-5 days (Brodman, 1995). Second, the timing of immigration to a particular pond may vary as well. Brodman (1995) notes that breeding migrations in Ohio are synchronized. However, Baldauf (1952), Husting (1965) and Harris (1980) reported that the breeding migrations of *A. maculatum* were intermittent within a single season. Harris (1980) also found that the timing of migration in a North Carolina population was highly variable among individuals. Migrations occurred in a series of three groups, with the last bout of breeding occurring two months after the initial burst. This may account for extended breeding seasons in some populations. Third, Husting (1965) found that some female *A. maculatum* might not breed during consecutive years and this behavior has been documented in *A. opacum* and *A. talpoideum* as well (Semlitsch, 1981; Pechmann et al., 1991; current study).

Despite these asynchronous chronological patterns of migration, salamanders often exhibit strong similarity in spatial patterns from year to year when migrating to and from traditional breeding sites. Douglas (1981) found significant patterns of orientation in migrating *Ambystoma maculatum, A. opacum*, and *A. jeffersonianum*. The entry of salamanders into and out of breeding ponds was significantly nonrandom for all three species, and the angles of approach to and departure from the pond were similar. In addition, Phillips and Stenhouse (1989) found that 35% of individuals entered the pond within 5 m of their entry point from the previous year, and 45% of marked animals exited the pond within 5 m of their entry point. In a population in northern Michigan, entry and exit patterns for *A. maculatum* were bimodal, indicating a possible preference for particular dispersal corridors (Kleeberger and Werner, 1983). In addition, Stenhouse (1985) determined that adult *A. maculatum* and *A. opacum* arrive at the breeding site in the same chronological order from year to year, which "suggests that the animals are coming from the same retreat yearly." Thus, the differences in the timing of entry among salamanders may be a result of the time it takes to migrate from retreats that are located at different distances from the breeding site (Stenhouse, 1985). The establishment of a home range has also been conclusively supported for *A. talpoideum* (Semlitsch, 1981), and there is evidence for the establishment of home ranges in *A. opacum* and *A. maculatum* as well (Semlitsch, 1983; Stenhouse, 1985; Ducey, 1989; Ducey and Heuer, 1991).

Population Dynamics

A decline in the number of individuals in a particular population of amphibians is often considered to be a harbinger of local extinction. However, studies have shown that not all fluctuations in the number of individuals in a population indicate a negative trend (Pechman et al., 1991). Amphibian breeding populations fluctuate dramatically due to natural processes such as climatological anomalies, predation, competition, and the synergistic effects of these processes (Pechman et al., 1991; Semlitsch et al., 1996). For example, many amphibians use temporary ponds for some aspect of their life cycle, most commonly for breeding and larval development. Therefore, the size and persistence of their populations may be limited by the duration and timing of the hydroperiod of the pond or by intrinsic characteristics such as "genetic intolerance for local adaptation," resistance to desiccation, or other physiological stressors (Semlitsch et al., 1996).

The density of breeding amphibians fluctuates both among ponds within the same year (Stenhouse et al., 1983; Stenhouse 1985) and within ponds between different years (Husting, 1965; Shoop, 1974; Stenhouse, 1985; Pechman et al., 1991; Semlitsch et al., 1996). In a 16-year study by Semlitsch, et al. (1996), the total number of breeding adults of 13 species of amphibians varied by at least two orders of magnitude during the study period, and the interannual differences may have resulted either from the effects of climatological anomalies or demographic factors. Breeding populations of *Ambystoma talpoideum*, *A. opacum*, and *Bufo terrestris* were all positively correlated with rainfall during the breeding season, whereas the size of breeding populations of *A. opacum, A tigrinum*, *Eurycea quadridigitata*, *Pseudacris nigrita*, and *P. ornata* were positively correlated with the number of metamorphs produced in previous years. Semlitsch, et al. (1996) concluded from these data that some adults may use cumulative rainfall as a predictive measure of hydroperiod. This would allow females to skip breeding in years when breeding ponds are dry or are likely to dry before larvae can develop and metamorphose. This hypothesis was supported by the observation that in drought years most species did not breed (Semlitsch et al., 1996).

Furthermore, competitive, predator/prey, or other intra- and interspecific interactions can influence community structure within amphibian assemblages (Wilbur, 1980; Morin, 1981; Semlitsch et al., 1996). Salamander larvae are predatory and feed on both anuran and other salamander larvae and on a variety of invertebrate prey, which makes them an important component in shaping vernal pond communities (Wilbur, 1972;

Morin, 1981; Morin, 1983a; Morin, 1983b; Sih et al., 1985; Taylor et al., 1988; Semlitsch et al., 1996). At very high densities their roles as predator and competitor can be an important stressor on sympatric congeners (Stenhouse et al., 1983; Stenhouse, 1985; Sih et al., 1985; Stenhouse, 1987; Cortwright, 1988). Many studies have focused on the interactions between *Ambystoma opacum* and syntopic congeners (Stenhouse et al., 1983; Sih et al., 1985; Stenhouse, 1985; Stenhouse, 1987; Cortwright, 1988). Because they breed in the autumn, their larvae reach a comparatively large size earlier in the spring than the larvae of spring-breeding species, which makes *A. opacum* a formidable predator on other *Ambystoma* larvae (Stenhouse et al., 1983; Sih et al., 1985; Stenhouse, 1985; Stenhouse, 1987; Cortwright, 1988). *A. opacum* larvae have been shown to reduce premetamorphic survival of *A. maculatum* to less than 1% in ponds in North Carolina (Stenhouse, 1987). Cortwright (1988) also noted that the presence of *A. opacum* significantly decreased the survival of *A. jeffersonianum* in cage experiments.

The relative effect of predatory salamanders on syntopic species varies with density of the predator, density of salamander prey, and the diversity of other taxa (Wilbur, 1972; Sih, et al., 1985; Cortwright, 1988; Semlitsch et al., 1996). Variation in the densities of predators or prey within ponds from year to year allows predators, competitors, and prey to coexist (Wilbur, 1972; Morin, 1981; Morin, 1983a; Morin, 1983b; Sih et al., 1985; Stenhouse, 1985). Stenhouse (1985) found that the inclusion of additional prey taxa and increased spatial heterogeneity increased the survival of *A. maculatum* in the presence of *A. opacum* in laboratory experiments. Morin (1981; 1983b) and Wilbur (1972) found that the addition of preferred prey species greatly improved the survivorship of other species that would otherwise have been extirpated when introduced to predatory salamanders independently. However, the interactions among congeners are still more complex. Predatory and prey ambystomatid larvae tend to have a high level of resource overlap, making the prey species an important competitor as well. The growth rate of *A. opacum* (predator) has been shown to decrease in the presence of a high density of *A. maculatum* (prey); the growth rate of the prey species also decreased (Stenhouse et al., 1983). This dual inhibition of growth presumably reflects competition between the predatory and prey salamander species (Stenhouse, et al. 1983).

Reproductive Biology

Although this study does not address reproductive biology specifically, it is important to understand the reproductive characteristics this group. The size and fitness of hatchlings within a population of ambystomatid salamanders (Kaplan, 1980) can influence their interactions. These characteristics have traditionally been attributed to the positive fitness benefit of greater parental investment (Kaplan, 1980). However, parental investment (primarily pre-paritive investment) varies both within a population of salamanders (Kaplan, 1980) and within individual females (Kaplan and Cooper, 1984). Parental investment in salamanders is determined by the size of the ovum, but because they are relatively small animals, with limited abdominal space, a trade-off exists between the size of each ovum produced and the total number of ova. Current theory predicts that (1) increased ovum size results in larger hatchlings, which are more competitive and less susceptible to predation, and (2) more ova of smaller size produce offspring that are more susceptible to predation, although there is a smaller chance that all of the offspring will die before metamorphosis.

Kaplan (1980) examined intrapopulational variation in parental investment in *Ambystoma opacum*, *A. tigrinum*, and *A. maculatum* to determine the effects of such variation on total fitness. He found that egg size does not affect the growth rate of embryos during the early stages of development (Kaplan, 1980), but that egg volume nonetheless is strongly correlated with hatchling size (Kaplan, 1980; Walls and Altig, 1986). Small larvae produced from small ova also take longer to reach the stage of first feeding compared to large larvae produced from large eggs. This is especially important because after feeding has begun, larval growth rate increases (Walls and Altig, 1985), amplifying the size differences (Kaplan, 1980). Kaplan (1980) concludes that, although larger eggs often instill an advantage over smaller ones in competitive or predator-rich environments, females producing smaller eggs may be equally successful in a complex environment. Furthermore, several studies have shown a positive correlation between clutch size and female snout-vent length (Petranka and Petranka, 1980; Woodward, 1982; Petranka, 1990; Walls and Altig, 1986). This correlation between body size and clutch size is presumably a result of the ability of larger individuals to allocate more energy to reproduction than to growth (Walls and Altig, 1985), allowing a larger female to make a greater investment in total reproductive effort (Walls and Altig, 1985, Kaplan and Salthe, 1979).

Diet and Foraging Behavior

Ambystomatid larvae are generalist predators, consuming copepods, isopods, amphipods, ostracods, cladocerans, insects, other amphibian larvae, and a variety of other items ranging from plant seeds to unicellular algae to snails (Stewart, 1956; Hassinger et al., 1970; Licht, 1975; Petranka and Petranka, 1980; Smith and Petranka, 1987; Taylor et al., 1988; for a review of the diet of ambystomatids see Petranka, 1998). The larvae primarily consume zooplankton during all stages of the larval period (Hassinger et al., 1970; Licht, 1975; Petranka and Petranka, 1980; Taylor et al., 1988). However, larger items (usually chironomids or ephemeropterans) may be taken as the larvae grow, because gape limitations decrease and energy demands increase (Hassinger et al., 1970; Licht, 1975; Petranka and Petranka, 1980; Taylor et al., 1988).

Spatial stratification of larvae has been observed when competitive/predatory congeners occur syntopically (Anderson and Graham, 1967; Hassinger et al., 1970; Petranka and Petranka, 1980). Larvae typically remain hidden in the leaf litter during the day and stratify in the water column to feed during the evening (Anderson and Graham, 1967; Hassinger et al., 1970; Petranka and Petranka, 1980). Vertical stratification in these animals is correlated with the stratification of prey items (Anderson and Graham, 1967; Hassinger et al., 1970; Petranka and Petranka, 1980) and the partitioning of resources (Taylor et al., 1988). Although *Ambystoma* larvae feed throughout the day and night (Petranka and Petranka, 1980), diurnal feeding occurs in the leaf litter. This behavior serves as a mechanism for avian and other predators, and it places them in proximity to prey species, which also concentrate in substrate during the day (Petranka and Petranka, 1980). In the evening invertebrates tend to move upward into the water column and stratify, triggering larvae to disperse into the water column as well. Thus, stratification behavior in larval salamanders maximizes the number of prey items that are encountered throughout the day and night and reduces exposure to potential predators (Petranka and Petranka, 1980).

Previous Studies of *Ambystoma mabeei*

Ambystoma mabeei is one of the least studied species of ambystomatid salamanders in the United States. It is known to inhabit lowlands (Bishop, 1928), tupelo-cypress bottoms (Mosiman and Rabb, 1948), sinkhole ponds (Ensely and Cross, 1984), vernal pools, and pine flatwoods (Petranka, 1998). In a North Carolina population eggs were found between February and March, with larvae first appearing in early February. Metamorphosis occurred between May and June (Hardy, 1969). The breeding sites were ephemeral wetlands of various sizes, with the pH in all tested locations consistently about 4.5 (Hardy, 1969). There was a bimodal size distribution in the larvae of *A. mabeei,* which may have signified two hatching dates and hence two bouts of breeding activity (Hardy, 1969). Hardy (1969) also observed both Siren intermedia and larval A. tigrinum feeding on larval *A. mabeei*. *A. mabeei* are also known to migrate long distances. On one occasion 91 *A. mabeei* metamorphs were found under a single board approximately one kilometer from any known breeding locality. This may indicate a tendency for *A. mabeei* to transform and migrate from their natal ponds in groups (Hardy, 1969). Large numbers of adult *A. mabeei* also have been seen moving on the ground surface on warm rainy nights during the breeding season (Hardy, 1969).

Objectives

The objectives of this study were: (1) to determine the proximate factors responsible for initiating breeding migrations in *Ambystoma mabeei* and *A. opacum*; (2) to determine whether the size of the active breeding population is correlated with climatological or other variables, such as demographics; (3) to compare the diet of larval *A. mabeei* from different geographic regions, to determine whether they consume different prey types; (4) to determine the size and status of the Grafton Ponds population of *A. mabeei*; (5) to explore the potential impact that changes in the vegetative community have had on *A. mabeei* in the Grafton Plains sinkhole pond complex and to make recommendations to conserve existing populations of *A. mabeei* in Virginia.

MATERIALS AND METHODS

Diet

Analysis of stomach content.---To determine diet I removed the stomach contents of preserved adult and larval *Ambystoma mabeei* from museum collections. For each specimen, snout-vent length, total length, and pre- and post-dissection masses were recorded. Specimens from localities throughout the range of the species were examined (for a list of localities and sample sizes for specimens examined see Table 1). Virginia populations were represented by a much smaller sample than were the more southern populations, because of the threatened status of *A. mabeei* in Virginia.

There was no *a priori* reason to believe that the diet of Virginia salamanders would differ sufficiently to warrant additional terminal collection.

Mass was determined with a top-loading electronic balance (Fisher Scientific) and recorded to two significant digits. Before being weighed, each animal was blotted dry using a dust-free paper wipes. Snout-vent and tail lengths were measured (in mm) using digital calipers (Masimoto) to two significant digits.

To remove stomach contents from larvae, I made a ventrolateral incision from the first to the last costal groove, to expose the stomach. A second incision was made through the stomach wall, and from the base of the esophagus to the pylorus, and all contents were removed with forceps. Intestinal and esophageal contents were not removed. The stomach contents were identified to the lowest taxonomic level possible under a Wild M3 dissecting scope, at 40X magnification.

Adult specimens were opened with a midventral incision from the sternal elements to the pelvic region. A second perpendicular incision was then made from the

Table 1. List of museum specimens examined for diet.

Location Collected	**Date Collected**	**Museum Collection**	**Number Dissected**	**Size range (SVL) mm**
Bladen Co., NC	25 April 1958	NCSM	15	29.0 - 33.5
Scottland Co., NC	23 May 1968	NCSM	5	26.0 - 32.0
Scottland Co., NC	29 April 1972	NCSM	5	24.0 - 25.5
Sampson Co., NC	13 April 1974	NCSM	5	19.0 - 21.0
Carteret Co., NC	25 March 1975	NCSM	5	10.0 - 13.5
Columbus Co., NC	21 March 1976	NCSM	10	16.5 - 31.5
Columbus Co., NC	2 May 1977	NCSM	10	19.0 - 29.0
Robeson Co., NC	26 March 1987	NCSM	10	17.5 - 24.5
Berkley Co., SC	3 March 1990	USNM	1	14.5
York Co. VA	19 May 1999	VMNH	9	31.0 - 33.5

midventral cut through the lateral body wall. The stomach was opened and its contents were removed with forceps. Stomach content data are presented as the percentage of the total number of stomachs dissected.

Population Dynamics and Migration Behavior

Study Site.---The field portion of this study was conducted on the Grafton Ponds Natural Area Preserve and surrounding Newport News Watershed property. The Preserve and Watershed are located in an area known as the Grafton Plain (Johnson, 1972), which extends from the northern border of the City of Hampton, west to the Lee Hall scarp in the City of Newport News and north to the York River in York County. The dominant vegetative structure of the site consists of a mixed pine and hardwood forest canopy, with scattered ericaceus understory shrubs. The area is characterized by the presence of more than 200 seasonally flooded depression ponds. The dissolution of carbonate-rich marine sands with abundant fossil shells and clays, comprising the Yorktown formation, forms these depression or sinkhole wetlands through a process similar to cave formation in karst regions. Ponds on the Grafton Plain (which I will refer to collectively as the Grafton Ponds) range in size from only a few meters to more than 90 m in diameter, and from less than 1 meter to more than 2 m in depth. (Johnson, 1972).

Reproducing populations of *Ambystoma mabeei* have been documented at 15 of the Grafton Ponds, and in 10 of these *A. mabeei* occurs sympatrically with *A. opacum*. This study was conducted at Mabeei Pond (designated N105-7 in the inventory of the Virginia Division of Natural Heritage), in which both species occur. Mabeei Pond is located within the boundaries of the Grafton Ponds Natural Area Preserve, 0.4 km north of Virginia Route 105, and 2.4 km west of Virginia Route 17. This pond has a somewhat hourglass shape and has reached a maximum recorded depth of 148 cm.

Mark-Recapture Study.---To determine the size and status of the Mabeei Pond population of *Ambystoma mabeei* and *A. opacum* and to determine the proximate factors responsible for initiating breeding migrations of both species, I conducted a mark-recapture study. Salamanders were captured using drift fence and pitfall trap arrays installed in three independent sections encompassing approximately 65% of the pond perimeter (Table 2; Heyer et al., 1994). The drift fences consisted of 0.5 m sheet metal recessed into the ground approximately 5-10 cm so that approximately 40-45 cm of fence stood vertically (Gibbons and Semlitsch, 1981; Heyer et al., 1994). Eleven-liter plastic containers, used for pitfall traps, were placed in pairs, one on each side of the fence, at approximately 3 m intervals (Gibbons and Semlitsch, 1984; Heyer et al., 1994). Trapping was initiated during March of 1995 and ended in August 1999. However, not all fences and traps were in operation for the same duration (Table 2).

Upon capture, snout-vent length, tail length, and mass were recorded, and each individual was assigned a unique mark. Salamanders were marked by removing their toes in unique combinations (Waichmann, 1992; Heyer et al., 1994) using surgical scissors sterilized in 70 % EtOH. The toes were clipped near their base, which slowed regrowth and caused malformation in regenerated toes, assuring that marks could be positively identified. After measurement marking, each animal was released on the opposite side of the fence from which it was caught (Gibbons and Semlitsch, 1984; Heyer et al., 1994).

Table 2. Installation and removal dates for drift fences and pitfall traps.

Approx. Length of Fence in meters	Percent of Pond Encircled	No. Paired Pitfall Traps	Date Installed	Date Removed
175	45	23	March /1996	August /1999
30	10	5	January /1997	August /1999
30	10	5	February / 1997	August /1999

Meteorological data for the study period were obtained from the National Climatological Data Collection Service for the Newport News/Williamsburg Waterworks climatic data-recording station. This station is located less than 6 km from the field site and thus should accurately reflect the climatic conditions at Mabeei Pond. These data were used to determine whether the size of the active breeding population and the initiation of immigration to breeding ponds are correlated with rainfall.

Population Estimates.---The population sizes for both *Ambystoma mabeei* and *A. opacum* were estimated using the two-sample Lincoln-Peterson estimator for closed populations. Although this model makes underlying assumptions that cannot be tested with two samples, it nonethelesss is a useful and intuitive method for estimating population density when only incomplete samples are obtained, or when short study duration precludes the use of more complex and less biased methods (Heyer et al., 1998). Assumptions of the model include: (1) the population is closed; (2) all animals in the population have an equal probability of being captured; and (3) marks are neither lost nor incorrectly recorded (Wilson et al., 1999). I estimated the population size for both species using the animals captured immigrating to the pond as my first sample and animals captured emigrating from the pond as the second. Thus, I reduced the probability that the assumptions of the model were violated, because it is unlikely (for these salamanders) those individuals immigrated into the population or that new individuals were added through reproduction between immigration and emigration events. In addition, I tested for nonrandom patterns of movement into and out of the pond by the salamander. However, unlike the populations studied by Stenhouse (1989) and Kleeberger and Werner (1983) (discussed previously) no patterns were present.

Therefore, all animals are assumed to have been equally catchable. Finally, to reduce the chance of violating the third assumption, data for multiple years were reviewed to ensure consistency of marks.

Migration Behavior.—I used cumulative annual precipitation as an index against which the movement patterns of both species of salamanders were analyzed. For my purposes, annual precipitation was calculated from 1 August to 31 July for *Ambystoma mabeei* and from 1 July through 30 June for *A. opacum*. These time periods were determined based on the month in which all activity for a given species ceased following a breeding event.

Physiological Condition.—To measure and compare physiological condition, I conducted analyses of covariance (ANCOVA), using snout-vent length as the covariate. This allowed me to get an index of mass (or condition) relative to snout-vent length for the population of each species. For this analysis each year of data collected from pitfall trapping was treated as an independent sample (replicate) of the population of each species. To prevent violating the assumptions of the ANCOVA, and to ensure that my data were independent, I conducted separate analyses of covariance on data collected from animals that were captured in multiple years and on animals that were not recaptured. In both cases the variance was similar and the results of the ANCOVA were also similar, indicating that the indices of condition that I used for comparison were independent.

The data were analyzed using SAS for Windows, Version 8.0. Comparisons of Least Squares Means were calculated by Student's t-tests. Sequential Bonferonni's Correction was used to adjust estimates of the alpha to avoid erroneous significance values, which may have resulted from conducting multiple analyses on the same data set. Graphs were generated using Sigma Plot, version 4.0.

RESULTS

Diet

Ninety-eight percent of all *Ambystoma mabeei* larvae dissected contained food items (Table 3). However, the stomach contents of Virginia specimens were different than those of conspecifics from more southern locations. The most frequent food items of salamanders from the Carolinas were Cladocera (92.4%), Copepoda (80.3%), Diptera (43.9%), and Hemiptera (mostly Corixidae; 43.9 %). In Virginia specimens, the most frequent food items were Isopoda (88.9%) Amphipoda (77.8 %), Odonata (11.1%), Cladocera (11.1%), and Copepoda (11.1%). There was also an important difference in the frequency of occurrence of gastric parasites. Nearly all Virginia *A. mabeei* larvae dissected (88.9%) contained large loads of parasitic nematodes in the stomachs, whereas only one individual (1.5%) from the Carolina populations had parasites in its stomach. Of the 15 adult *A. mabeei* that were dissected and analyzed for stomach contents, only one contained food.

Population Estimates

During this study, population estimates indicate that *Ambystoma opacum* outnumbered *A. mabeei* by nearly a thousand individuals at Mabeei Pond (Fig. 1). The estimated population sizes of both species indicated that neither species was decreasing or increasing in size throughout the four years in which they were monitored (Fig. 1). However, *A. opacum* exhibited greater reproductive success than *A. mabeei* (Fig. 2). In 1996, 54 *A. opacum* metamorphic individuals were trapped when emigrating from the pond, compared to only six *A. mabeei*. Recruitment was similar for *A. opacum* and *A. mabeei* in 1997, with 44 and 53 metamorphs, respectively, trapped when leaving the pond. However, recruitment of *A. mabeei* was reduced to only a few individuals in 1998, and in 1999 there apparently was a complete lack of recruitment. *A. opacum* was again successful during the 1998 season, but their success also was restricted to only a few individuals during 1999 (Fig. 2).

Migration Behavior of *Ambystoma mabeei*

Breeding migrations of adult *Ambystoma mabeei* occurred each year between 15 January and 15 March. Metamorphs emerged from the pond during June. Immigration to the pond occurred when temperatures were above freezing, and there seemed to be a relationship between seasonal cumulative rainfall and the initiation of movements.

During the 1997 and 1998 seasons total cumulative precipitation was relatively high, reaching almost 1400 mm each year. However, during the 1997 season the total precipitation prior to January (indicated by the initial levels of precipitation in Fig. 3) was much higher than the 1996, 1998, and 1999 seasons (Fig. 3). Climatological conditions for 1996 and 1999 were quite different from those in 1997 and 1998. The total cumulative precipitation for both 1996 and 1999 was low (approx. 1100 mm) compared to 1997 and 1998, and the amount of precipitation accumulated prior to January during the 1996 and 1999 seasons, was similar to the level at the beginning of the 1998 season. Thus, the 1997 season was characterized by having above average precipitation conditions during the fall and winter prior to the activity season, whereas the 1996,1998, and 1999 seasons (Fig 3) were similar to each other, exhibiting relatively dry conditions prior to the beginning of the activity season of *Ambystoma mabeei* in January.

Table 3. List of stomach contents of *Ambystoma mabeei*, expressed as a percentage of the number of stomachs in which they were found.

Taxon (North Carolina) N=66	**(%) of Stomachs**	**Taxon (Virginia) N=9**	**(%) of Stomachs**
Animal Matter	**98.6**	**Animal Matter**	**88.9**
Insecta		Insecta	
Odonata		Odonata	
Anisoptera	7.6	Anisoptera	11.1
Zygoptera	4.6	Zygoptera	0
Diptera	43.9	Diptera	0
Ephemeroptera	18.2	Ephemeroptera	0
Hemiptera		Hemiptera	
Corixidae	40.9	Corixidae	0
Notonectidae	3.0	Notonectidae	0
Coleoptera		Coleoptera	
Dytiscidae	6.1	Dytiscidae	0
Isopoda	19.7	Isopoda	88.9
Amphipoda	21.2	Amphipoda	77.8
Ostracoda	21.2	Ostracoda	0
Copepoda	80.3	Copepoda	11.1
Decapoda	1.5	Decapoda	0
Cladocera	92.4	Cladocera	11.1
Hydracarina		Hydracarina	
Orbiculae	24.2	Orbiculae	0
Nematoda		Nematoda	
Non-parasitic	6.1	Non-parasitic	0
Parasitic	1.5	Parasitic	88.9
Plant Matter	**16.7**	**Plant Matter**	**11.1**
Seeds	6.1	Seeds	0
UID Plant	12.1	UID Plant	11.1

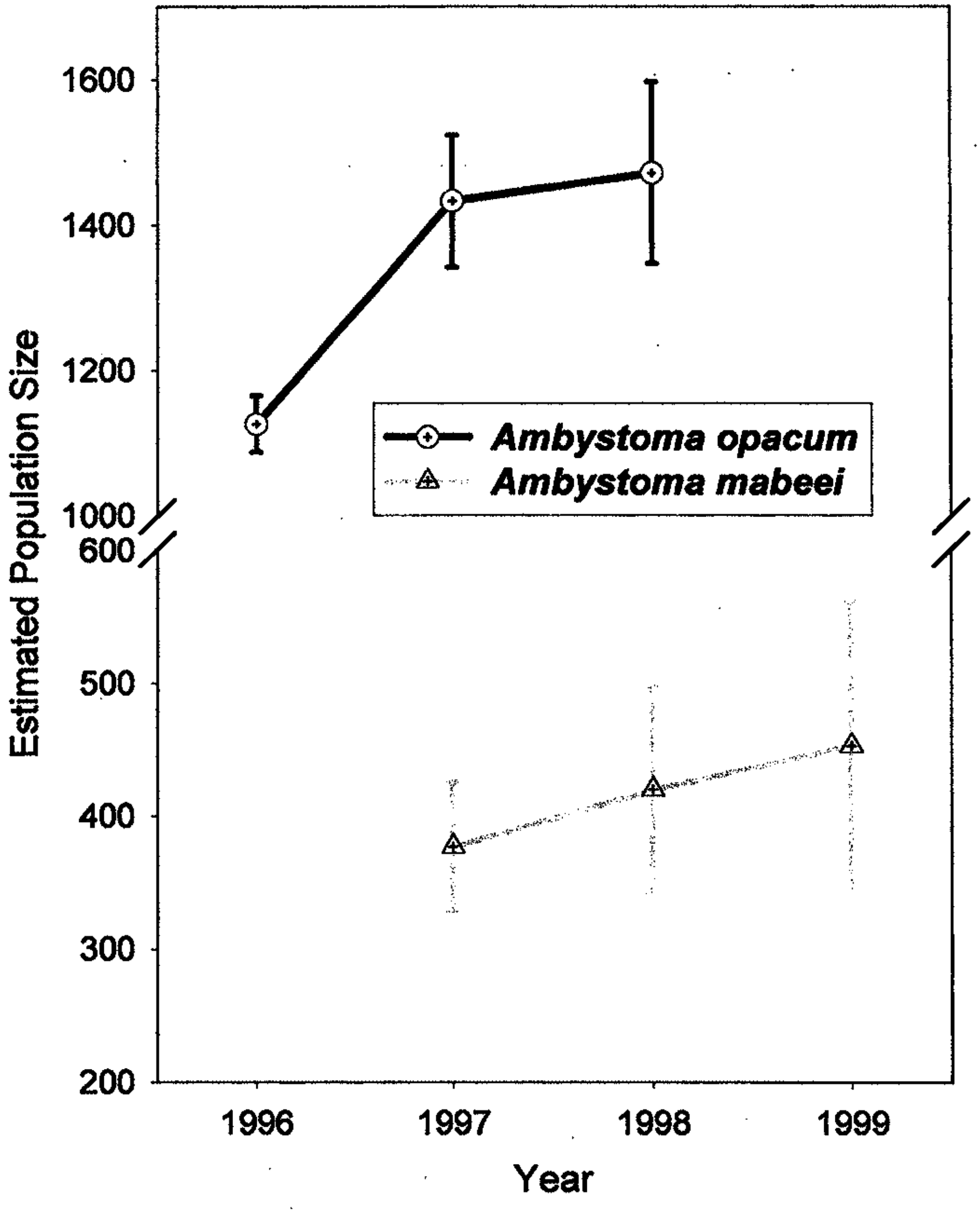

FIG. 1. Population estimates for *Ambystoma mabeei* and *A. opacum* at Mabeei Pond calculated using two-sample Lincoln-Peterson Estimate. Estimates are offset, reflecting the differences in breeding phenology and the timing of trap installation.

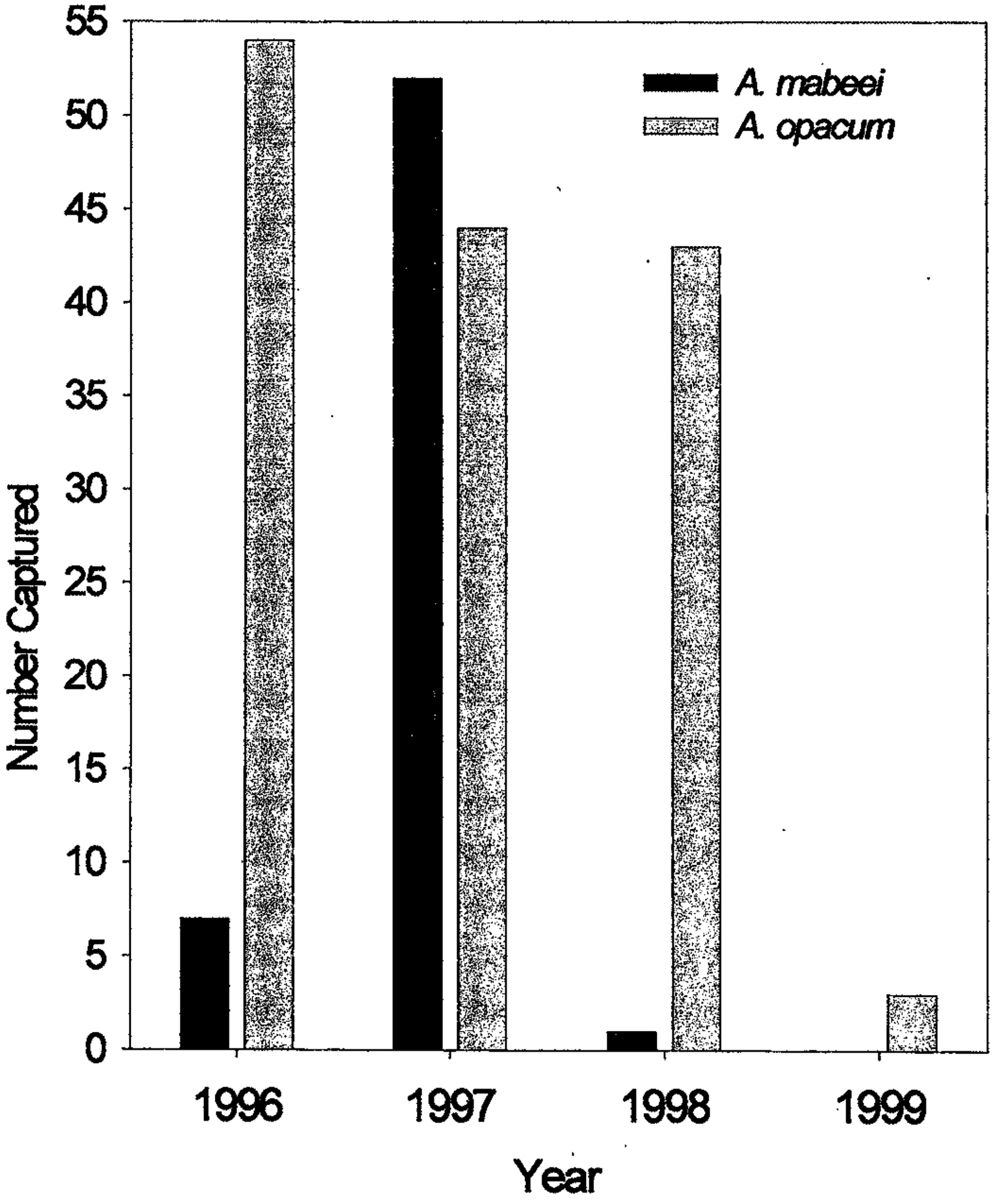

FIG. 2. Number of emerging *Ambystoma mabeei* and *A. opacum* captured at the drift fence. No *A. mabeei* were captured emerging from the pond during 1999.

I captured similar numbers of *Ambystoma mabeei* during each year of the study. However, the timing and intensity of migrations varied between years (no inferences can be made about the 1996 sample year because the traps were installed during the activity period). Immigration during the 1997 season appeared to be rather consistent in migration rate throughout the period of 15 January through 5 March (Fig. 3). In 1998, migration was more condensed temporally, with an intense pulse of migration occurring during the end of January and beginning of February (Fig. 3). Immigration during the 1999 season is strongly bimodal, with a burst of activity occurring during January, followed by a pause in activity throughout February and early March. A second and larger burst of activity occurred around 15 March, after a rapid increase (>100 mm) in cumulative precipitation (Fig. 3). Both the precipitation and temperature conditions during February 1999 were similar to the 20-year average for that month (NCDC 1999); therefore, short-term climatological conditions cannot explain the break in migratory activity (Fig. 3).

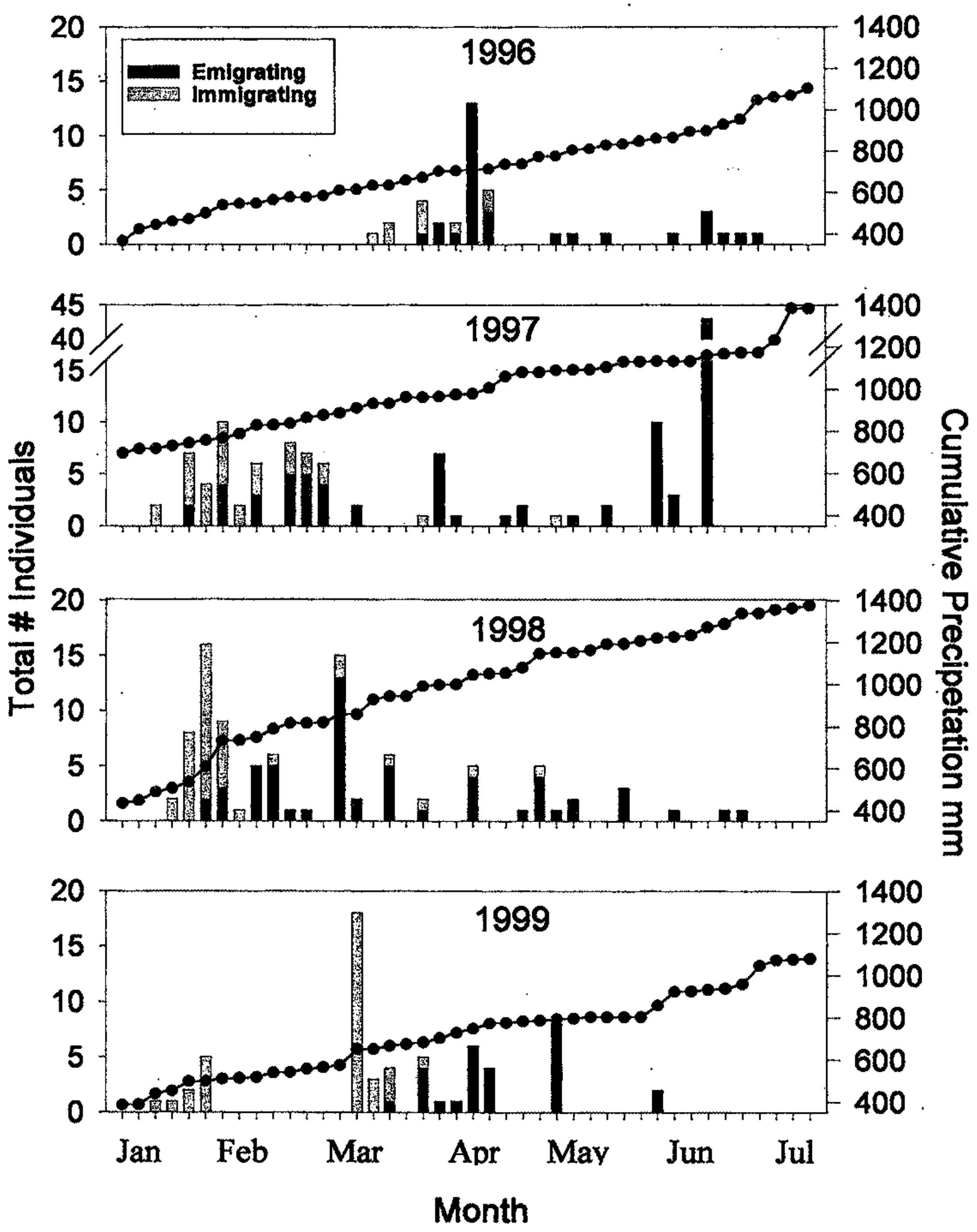

FIG. 3. Movement patterns of *Ambystoma mabeei* and cumulative precipitation, plotted in five-day intervals. Precipitation was calculated on the salamander's activity year, which was defined as 1 August to 31 July. Only data for the period after January 1 are illustrated.

Migration Behavior of *Ambystoma opacum*

Breeding migrations of adult *Ambystoma opacum* began during late September and continued through early November (Fig. 4). However, individuals were sporadically captured leaving the pond through February and March. Many of these late season movements can be attributed to local movements and not to breeding activity. Most activity, both immigration and emigration occurred during the period between 20 September and the end of October.

The 1996-1997 and 1997-1998 seasons both had similar total amounts of precipitation (approx. 1200 mm), but the total precipitation accumulated by the beginning of September was higher in 1996 than in 1997 or 1998 (Fig. 4). The relatively even migration in 1996 over a period of several weeks seems to have been associated with a higher level of precipitation at the start of the breeding season (Fig. 4). However in 1997-1998, as in *Ambystoma mabeei*, a bimodal pattern of activity, with a short pause during the first two weeks of October was observed. That break in activity was followed once again by a large burst of activity after a considerable increase in precipitation (Fig. 4).

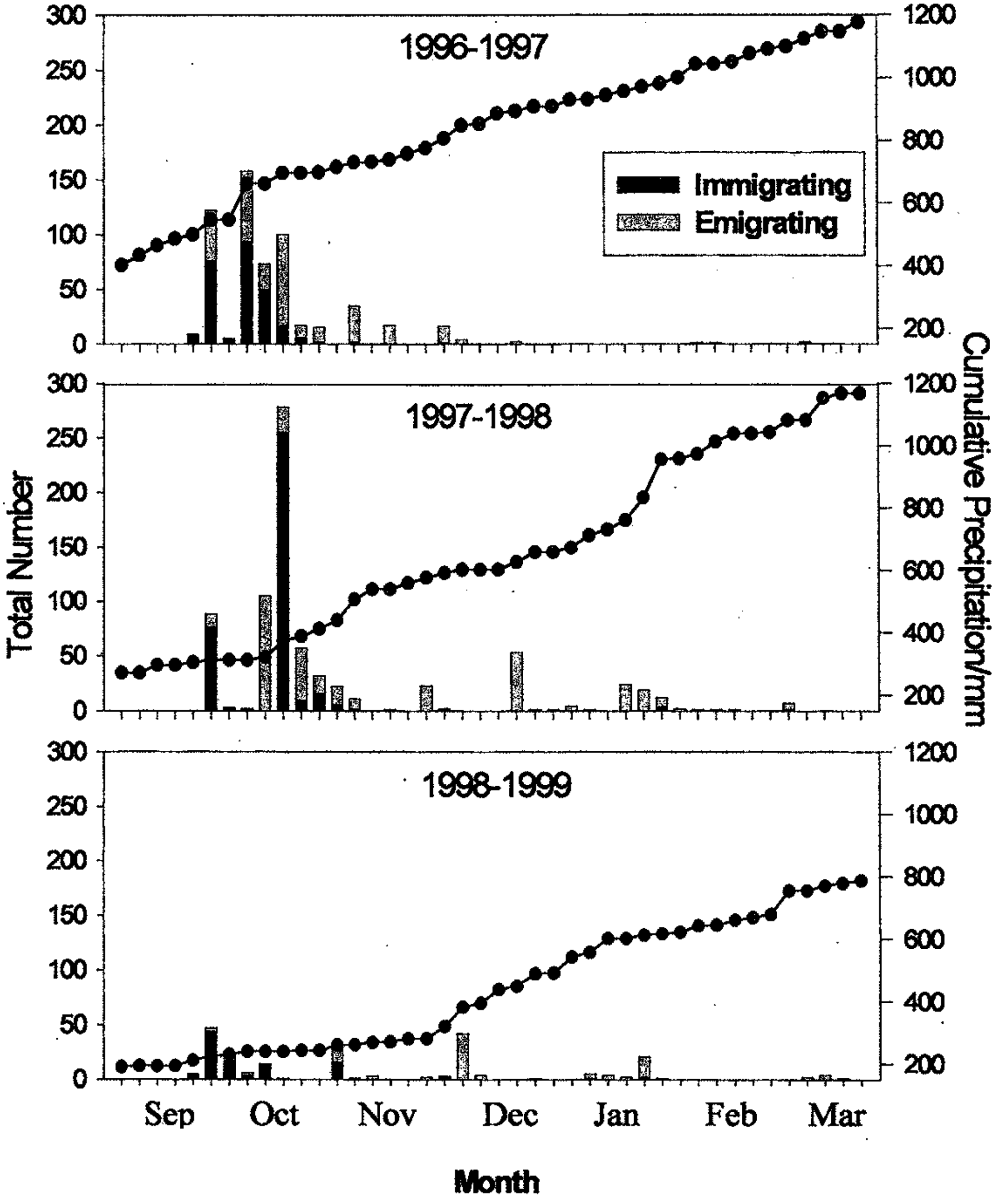

FIG. 4. Movement patterns of *Ambystoma opacum*, and cumulative precipitation plotted in five-day intervals. Precipitation calculated on the salamander's activity year, which was defined as from 1 July to 30 June. Only data for the period after to September 1 are illustrated.

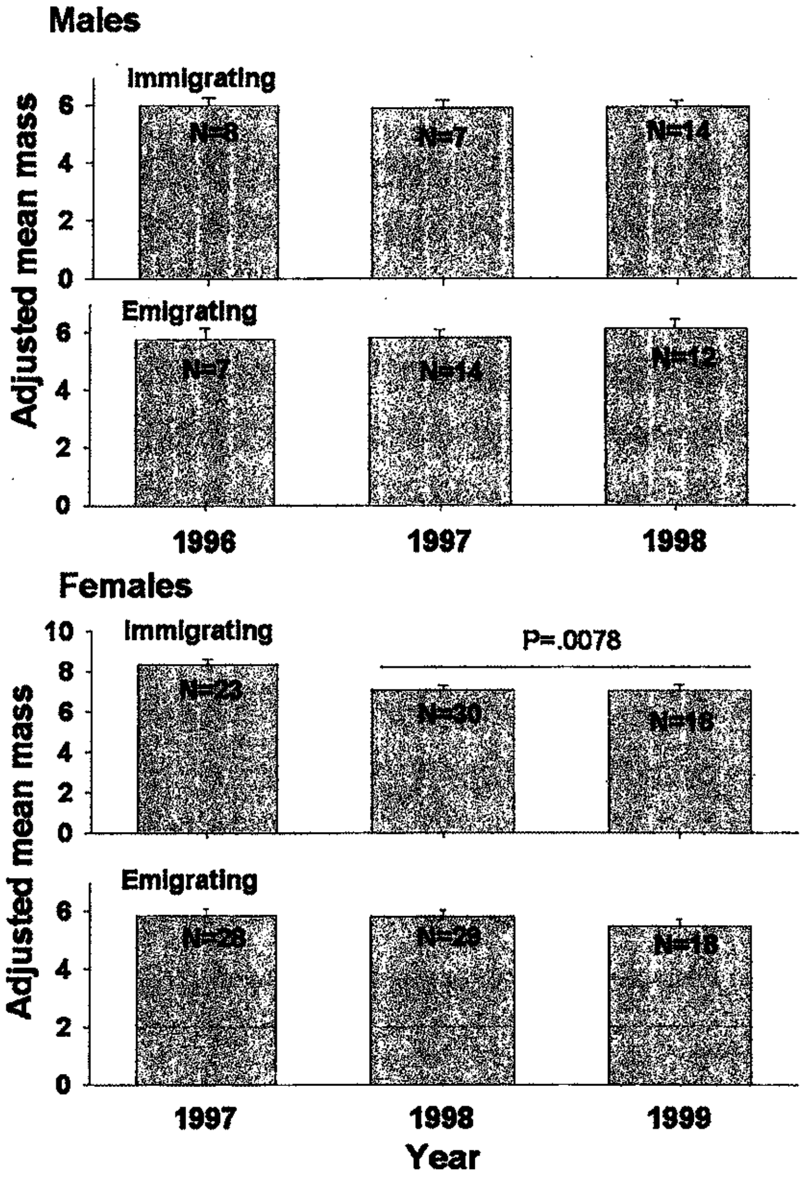

Fig. 5. The physiological condition (mean adjusted mass) of immigrating and emigrating *Ambystoma mabeei*. The condition of immigrating females during 1999 was significantly lower than in the previous two years as represented by the p value and horizontal bar. The horizontal bar overlaps columns that are not significantly different.

Physiological Condition of *Ambystoma opacum*

The condition of immigrating and emigrating male *Ambystoma opacum* was significantly different between years (F=18.06, P< 0.0001, df = 2 for males; F=15.98, P<0.0001, df=3 for females). Emigrating male *A. opacum* were significantly heavier during the 1996-1997 and 1997-1998 seasons than they were during the 1998-1999 season (P=0.0006, df=86; Fig. 6). Immigrating males were also significantly heavier during the 1996-1997 and 1997-1998 seasons than during the 1998-1999 season (P = 0.0012, v= 92; Fig. 6).

For female *Ambystoma opacum* there was a significant interaction between year and snout-vent length for immigrating (F = 8.97, P_{int} = 0.0002, df = 2; Fig. 6) and emigrating (F = 3.78, P_{int} = 0.0250, df = 2; Fig. 7) individuals. The mean adjusted mass, and thus the physiological condition, of immigrating male and female *A. opacum*, were not compared using significance tests because they exhibited different slopes between years in the relationship between mass and snout-vent length (Ott, 1992; Zar, 1996). However, the overall trend in the data is the same as that seen for males (Fig. 6). The mean mass of female *A. opacum* was greater during the 1996-1997 and 1997-1998 seasons than during the 1998-1999 season, both while immigrating and emigrating.

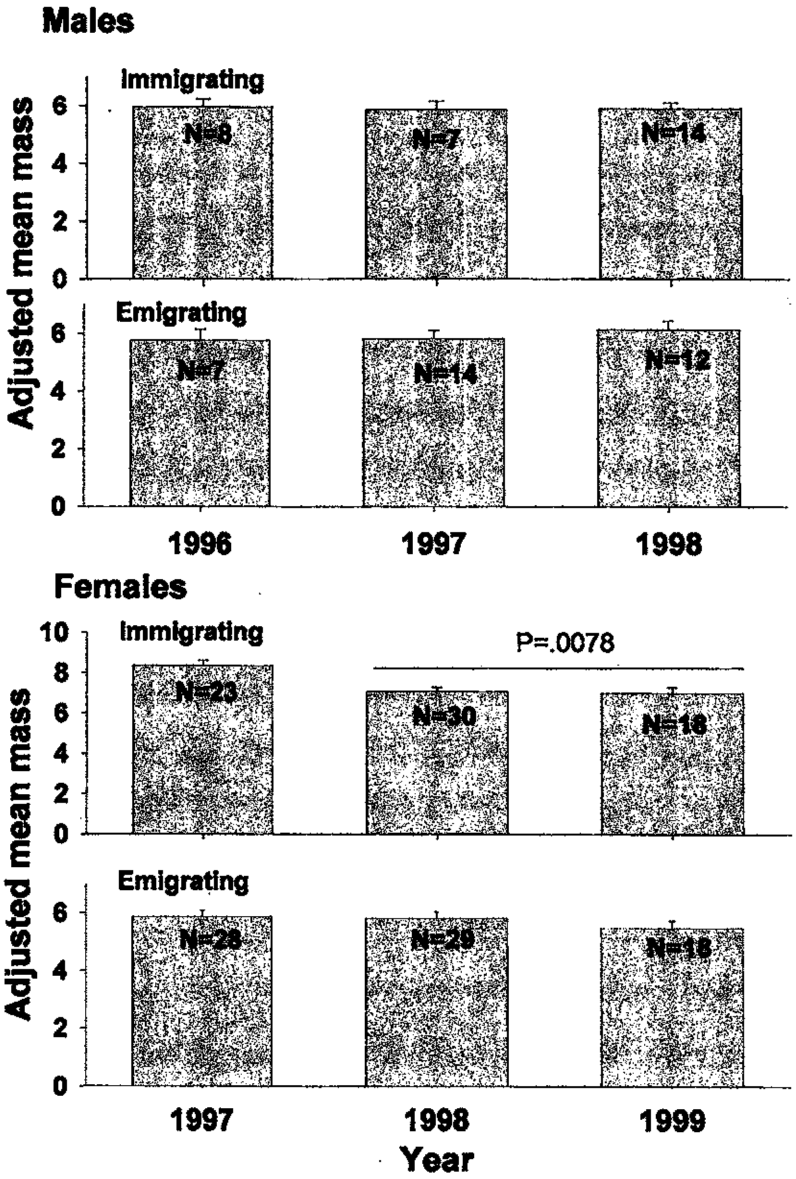

Fig. 6. The physiological condition (mean adjusted mass) of immigrating and emigrating *Ambystoma opacum*. The horizontal bar overlaps columns that are not significantly different. For females significance test were not conducted. However, the trend in the data is the same as that of the previous two graphs.

DISCUSSION AND CONCLUSIONS

Weather Conditions and Migration

The results of this study support the hypothesis that environmental conditions influence the timing of breeding migrations of adult *Ambystoma mabeei* and *A. opacum* (Blanchard, 1930; Bishop, 1941; Baldauf, 1952; Spotila and Beumer, 1970; Semlitsch, 1985; 1987; Semlitsch et al., 1993; Sexton et al., 1990; Pechmann et al., 1991; Loredo and Van Vuren, 1996). In addition, reproductive success in both species is strongly tied to climatological patterns. However, patterns of precipitation affected the two species in different ways, and these differences may reflect differences in reproductive and life history strategies of each species. Moreover, duration of the breeding season differed from that seen in studies of other ambystomatid species. Semlitsch (1985) found that environmental conditions were the best proximate predictors of migration in *A. talpoideum*. In addition, Pechman et al. (1991) reported that the size of the breeding population was correlated with cumulative precipitation during the breeding season, and Semlitsch (1987) concluded that the duration of breeding migration becomes truncated during wet years and protracted during dry years.

The size of the breeding population of *Ambystoma mabeei* was similar during each year of the study, but the pattern and timing of breeding migrations were considerably different between years. Migration of *A. mabeei* appears to be initiated in response to cumulative seasonal precipitation, and thus the intensity and timing of migration are influenced by conditions prior to the onset of the breeding season. Above average precipitation during late summer and fall has a much greater influence on the onset and success of mating than does precipitation during other seasons (Table 4a).

Breeding activity in *Ambystoma opacum* was truncated during the 1996-1997 season, when precipitation was the highest, and more protracted during the 1997-1998 and 1998-1999 seasons, when cumulative precipitation during the breeding period was low (Table 4a). In addition, the size of the breeding population during the 1998-1999 season was much smaller than in the two previous seasons. This demographic difference may be in response to dry conditions during the breeding period (Pechmann et al., 1991) or the result of low cumulative precipitation prior to the breeding season (Table 4b).

Because these salamanders are dependent on ephemeral ponds that function on an annual hydrologic cycle, selection is expected to favor salamanders that synchronize their breeding activity to coincide with conditions that optimize their reproductive potential (Semlitsch et al., 1993). This type of reproductive synchrony should have a genetic component, which links favorable environmental conditions to the onset of reproductive events. Semlitsch et al. (1993) proposed a model containing such a genetic element. However, they concluded that most phenotypic variation in arrival time of breeding salamanders was related to annual variation in climatic conditions, and that stabilizing selection may have eliminated most of the genetic variance in migratory behavior. They proposed that genetic differences may have little influence on the timing of breeding migration, but "differing selective pressures between the sexes may contribute to the maintenance of differential amounts of genetic variation" in males and females (Semlitsch et al., 1993). Presumably, the reduction of genetic

Table 4. Summary of the relationship between reproductive success, physiological condition, and seasonal precipitation during this study. A. *Ambystoma mabeei*, B. *A. opacum*.

A.

	Precipitation				***Ambystoma mabeei***	
	JUL-SEP	**OCT-DEC**	**JAN-MAR**	**APR-JUN**	**Mass Immigration**	**Metamorph Recruitment**
1996-1997	++	++	-	-	↑	**High**
1997-1998	-	+	+	+	↓	Low
1998-1999	—	-	+	-	↓	None

B.

	Precipitation				***Ambystoma opacum***	
	JUL-SEP	**OCT-DEC**	**JAN-MAR**	**APR-JUN**	**Mass Immigration**	**Metamorph Recruitment**
1996-1997	++	++	-	-	↑	**High**
1997-1998	-	+	+	+	↑	High
1998-1999	—	-	+	-	↓	None

variability results from stabilizing selection resulting from strong associations between environmental conditions and reproductive success (Semlitsch et al., 1993).

However, genetic variability can be maintained by mixed evolutionary stable strategies (ESS) based on differential arrival times of individuals (Parker and Courtney, 1983; Parker, 1985; cited in Semlitsch et al., 1993:334). Ephemeral ponds are transient and unpredictable aquatic habitats; so stabilizing selection can be counteracted by directional and diversifying selection pressures (Fig. 8). This is because stabilizing selection occurs during years when conditions are optimal for all breeding strategies (defined below) and directional and diversifying selection occurs when environmental conditions are suitable for only small subsets of the population (Fig. 8). For example, because ambystomatid salamanders are long-lived and have low larval recruitment (Duellman and Trueb, 1986), any subset of a population (e.g., early or late breeders) may experience a reproductive advantage in response to environmental conditions during any given year. However, the small subset of the population that experiences high reproductive success would not greatly alter the timing of migration for the population as a whole. Thus, the variable conditions of local breeding ponds (i.e., dynamic filling and drying cycles) can result in a mixed ESS and thereby maintain variable arrival time (and cues that initiate migration) to the breeding site.

Semlitsch, et al. (1993) concluded that phenotypic variation in migratory behavior among years was more closely tied to annual climatic conditions than to genetic variation within the population because the arrival time of individuals lacked

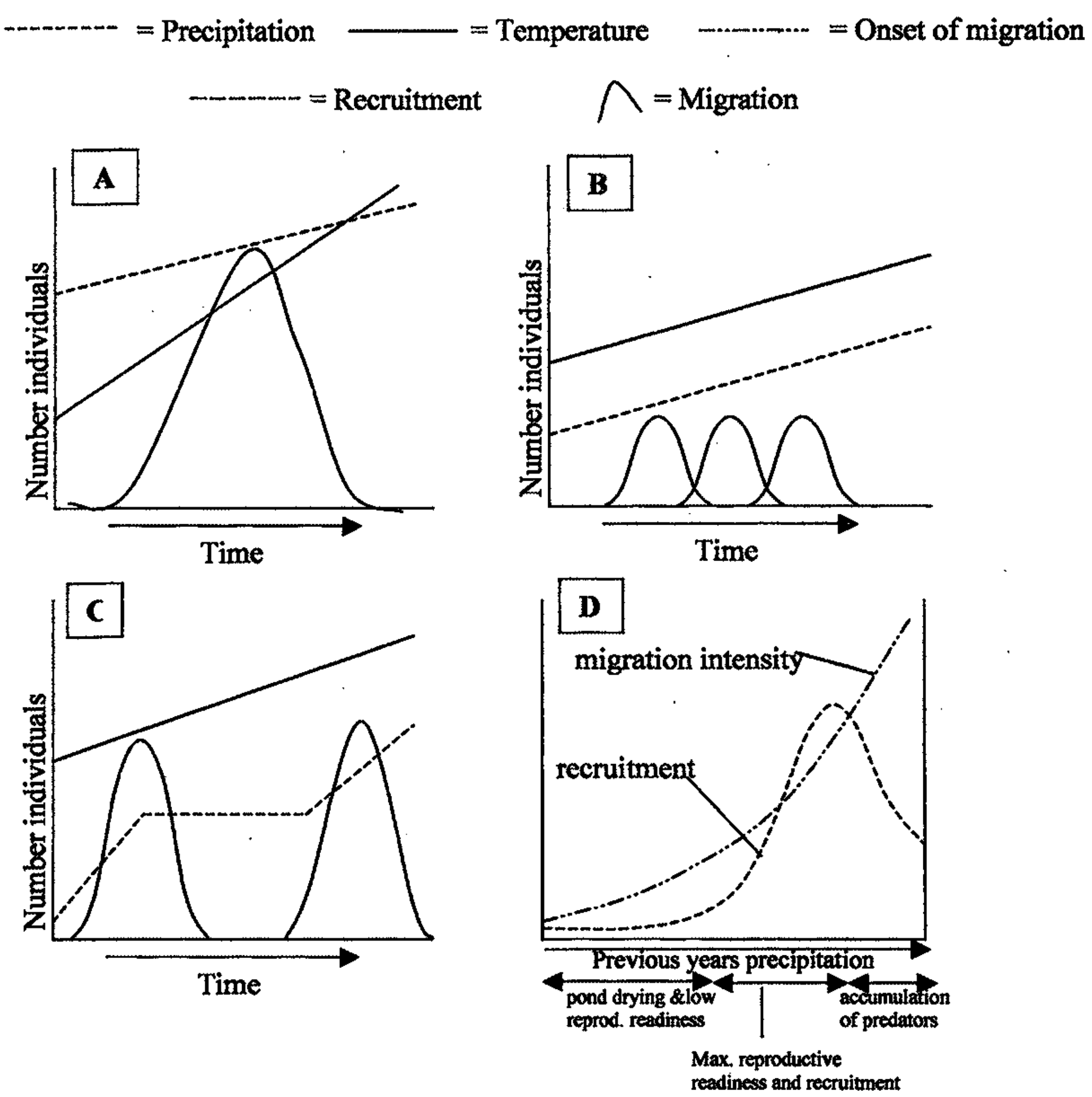

FIG. 8. Model of evolutionary stable strategy and the relationship of precipitation, physiological condition and recruitment. A. Stabilizing selection. High precipitation at the onset of the breeding season transfers the threshold for migration to temperature causing a mass migration when the temperature reaches a threshold value. B. Diversifying selection. Average increases in precipitation results in small consistent migrations the cumulative precipitation levels exceed the threshold levels for different portions or the population. C. Directional selection. Sporadic precipitation patterns result in highly divided timing in migration in which the one sector of the population will have an advantage depending on the post breeding climatic conditions. D. The relationship between the onset of breeding migrations, physiological condition, precipitation and recruitment.

high repeatability between years. However, the "decision" to migrate and breed may also be influenced by the nutritional condition of an individual (Fraser, 1980). Thus, "the effects of physiological condition can shift the average breeding date away from the optimum" (Semlitsch et al., 1993:338). Therefore, the lack of repeatability between years and the strong association with annual climatic conditions does not necessarily imply a lack of genetic variability. On the contrary, I submit that a strong association with annual environmental conditions (Savage, 1935; Hurlbert, 1969; Semlitsch, 1985; Semlitsch et al., 1993) as opposed to shorter-term climatic events (such as daily or weekly weather patterns; Semlitsch, 1987; Pechmann, 1991) supports a genetic component to breeding behavior.

I propose a model that includes a genetically determined cue for migration and allows for seasonal variation in adult condition to explain the patterns observed during this study and the patterns of ambystomatid migration in general. The presence of a genetic determinant for breeding behavior gives the population or species a mechanism by which adaptation to changes in local climatic conditions can occur. It also provides a process by which a colonizing population may synchronize breeding behavior according to the hydrological conditions of the new breeding site.

Salamanders that migrate and breed when environmental conditions are favorable for their young will experience higher fitness relative to those that migrate at less favorable times. Thus, their migration cue is expected to be associated with conditions that optimize reproductive output, such as pond hydroperiod. Pond hydroperiod is closely associated with seasonal trends in precipitation (Semlitsch et al., 1993). Therefore, cumulative precipitation could function as a cue for migration that is correlated with optimal hydroperiod that will reduce mass mortality of offspring as a result of pond drying (Semlitsch, 1987; Semlitsch et al., 1993).

Asynchrony in the time of arrival of individuals at a pond can instill a reproductive advantage or disadvantage on individuals during a particular set of weather conditions. Individuals that respond to lower levels of precipitation will migrate to ponds and breed earlier than those whose migration is triggered by higher cumulative levels of precipitation. Therefore, early migration will give a selective advantage if conditions turn out to be wet. Breeding early will allow offspring to grow more quickly (in the absence of conspecific competitors) and to grow to a size that is less susceptible to competition and predation by other species (Heyer, 1979; Harris, 1980). Alternatively, premature drying of ponds early in the breeding season will result in a complete loss of reproduction for early breeders during that season (Semlitsch, 1987; Pechmann et al., 1991). Conversely, individuals that have higher precipitation thresholds will be more successful in dry years because they will have waited until the threat of premature drying has passed. However, in wet years late breeders will be at a disadvantage to their early-breeding conspecifics because the early breeders offspring will be larger and more competitive (Alford and Wilbur, 1985; Wilbur, 1987). In addition if weather conditions are severe (i.e., severe drought) all individuals in the population (early and late breeders) may forego breeding (Semlitsch et al., 1996).

In wet years breeding migrations may be induced in response to favorable thermal conditions, because all individuals already will have reached the threshold amount of precipitation required to initiate migration. During these wet years migration is truncated into a burst (Fig. 8A) and the local population will approach panmixis, thus maintaining genetic variability and resisting directional selection. During years of average and uniformly distributed precipitation, migration will be highly protracted in duration, with numerous small bursts of activity occurring regularly as portions of the population reach or exceed their threshold levels of precipitation (Fig. 8B). During years in which precipitation patterns are highly variable or erratic, migration may be condensed into two or more large bursts of activity. If those bursts are separated by a sufficient amount of time, contact between breeding adults with different precipitation optima will be prevented, and directional selection can occur (Fig. 8C). In addition, variable weather patterns will influence the physiological condition of the adults and consequently also will affect reproductive readiness and migration time (Fig. 8D). The association between migration, reproductive readiness and condition is discussed further below.

The activity patterns observed for both *Ambystoma mabeei* and *A. opacum* correspond to the predictions of the proposed model. Breeding migrations of *A. mabeei* during 1997 were continuous and consistent in magnitude, whereas in 1998 immigration was somewhat truncated; in 1999 migration was bimodal, with immigration events condensed into two brief bursts of activity. These differences are associated with the cumulative level of precipitation experienced prior to the onset of the breeding season. Cumulative precipitation levels were much higher at the beginning of the breeding season during 1997, and thus temperature rather than precipitation may have served as the threshold factor for initiating migration. Conversely, during the 1998 and 1999 seasons, bouts of activity were more closely tied to rapid increases in precipitation. During the later years most immigration occurred after cumulative annual precipitation reached 600 mm. The tendency of *Ambystoma mabeei* to migrate in response to a precipitation threshold becomes clear upon close inspection of Figure 3. In all years the number of *A. mabeei* migrating during any given period was associated with the accumulated precipitation. For example, during March 1999 a large burst of immigration occurred following an increase in precipitation of more than 100 mm, pushing the annual total beyond the 600 mm threshold. Previous studies have suggested that the number of individuals participating in a particular migration event or breeding season is related to the amount of precipitation that occurs during the migration event (Pechmann et al., 1991). If migration is cued by environmental conditions during the breeding season (e.g., Pechmann et al., 1991; Baldauf, 1952; Bishop, 1941; Semlitsch, 1987), then the lack of migration during February and early March of 1999 could not be explained by temperature or rainfall, because the climatological conditions during this time period did not differ from the 20-year average. However, the lack of migration during February and early March may have been inhibited by low cumulative precipitation prior to the onset of breeding.

Weather, Reproductive Condition and Recruitment

The relative reproductive success (i.e., recruitment) of *Ambystoma mabeei* and *A. opacum* exhibits annual variation, as does the condition (i.e., mass corrected for snout-vent length) of the reproductively active adults immigrating to the pond. Recruitment of *A. mabeei* metamorphs was high only during the 1997 season, but was very low during the 1998 season and no recruitment occurred in 1999. Likewise, immigrating female *A. mabeei* were heavier during the1997 season than during the 1998 and 1999 seasons. *A. opacum,* on the other hand, experienced high recruitment during both the 1996-1997 season and 1997-1998 season, but had very low reproductive success during the 1998-

1999 season. Immigrating male and female *A. opacum* also were heavier during the two seasons in which recruitment was high and lighter during the season when reproductive success was low.

In addition to the timing of migration, the association between adult condition and reproductive success appears to be related to annual climatological patterns, with high relative mass of reproductive adults occurring in years when precipitation was high. For *Ambystoma mabeei*, high reproductive success occurred when above average precipitation fell during the late summer and fall. In contrast, *A. opacum* exhibited high adult mass and high recruitment of metamorphic salamanders when conditions were abnormally wet during the fall and early winter or were normal during the late winter and spring (Table 4a,b). The only season in which *A. opacum* was unsuccessful was 1998-1999, when conditions were extremely dry throughout the fall and winter.

Reproductive output (i.e., the number and size of eggs produced) is expected to reflect the size and physiological condition of the female (Duellman and Trueb, 1986; Fraser, 1980; Ims, 1990), and it has been well established that egg number and egg size are positively correlated with body size in amphibians (Kaplan, 1979; Kaplan and Salthe, 1979; Duellman and Trueb, 1986; Walls and Altig, 1986). Thus, closely related species that are the same size and are exposed to the same environmental conditions might be expected to allocate the same amount of energy to reproduction (Duellman and Trueb, 1986). In addition, physiological condition can affect the timing of breeding, as well as the relative reproductive effort of vertebrates (Price et al., 1988; Ims, 1990). For example, Fraser (1980) found that factors such as past reproductive history and recent food intake and nutrition contribute to reproductive condition. Therefore, foraging success and nutritional quality of the food consumed can have a major influence on the reproductive output of females and the relative success of their offspring (Semlitsch et al., 1993).

The association between adult condition, recruitment, and climatic patterns raises two questions concerning the ecology of *Ambystoma mabeei* and *A. opacum*. First, how does cumulative seasonal precipitation, beyond its effects upon pond drying or other adverse aquatic conditions, affect the reproductive success of a population of adult ambystomatid salamanders? Second, why do these species react differently to the same environmental conditions?

The intra- and interannual differences in the timing of migration and in the relative reproductive success of *Ambystoma mabeei* and *A. opacum* may be influenced by moisture and foraging conditions in the terrestrial environment. Moisture and foraging success in conjunction with reproductive history can influence gonadal development and fat storage. Therefore, weather patterns and adult physiological condition can be important in determining an individual's reproductive readiness and time of arrival at the breeding site (Semlitsch et al., 1993).

Ambystoma mabeei appears to be more sensitive to environmental variables than *A. opacum*, as indicated by the lack of reproductive success for *A. mabeei* during the 1996 and 1998 seasons. This may reflect lower physiological tolerance to drought conditions in *A. mabeei*, given that their condition is diminished during years with low precipitation. This intolerance may result from competitive interactions during the nonbreeding season and/or their occurrence in suboptimal habitat. Because *A. opacum* far outnumbers *A. mabeei* at this pond, with an estimated difference of nearly one thousand adult individuals, *A. opacum* may exert a significant impact on the behavior and survival of adult *A. mabeei* in several ways.

I propose four hypotheses that may explain this pattern. First, the overwhelming number of *Ambystoma opacum* may saturate the best terrestrial refuges, and consequently exclude *A. mabeei* from the most suitable ranges during non-breeding season. Second, *A. opacum* might aggressively defend home ranges during the nonbreeding season and force *A. mabeei* to use less optimal habitat. Third, *A. opacum* may be more efficient at capturing and consuming prey with high nutritional value. Fourth, the habitat at Grafton Ponds may be suboptimal for *A. mabeei,* as a result of large-scale vegetative changes. Only the fourth hypothesis is addressed here because the data acquired during this study are insufficient to address the other three hypotheses at this time.

Habitat Effects

The difference in condition (the relative difference in mass corrected for snout-vent length during wet and dry years) between *Ambystoma mabeei* and *A. opacum* also may result from large-scale changes in habitat. Prior to the early 1900s parts of the Grafton Plain were dominated by pine savanna (American Lumberman 1907). This area now is dominated by second-growth deciduous forest. The change in the dominant vegetation may have affected the relationship between these salamanders in two ways. First, changes in the vegetative structure may have invoked a negative effect on the physiological condition of *A. mabeei* and/or a positive impact on the condition of *A. opacum*, which may have shifted the balance of their interactions in favor of *A. opacum.* Second, major changes in the vegetation of Grafton Ponds may have allowed *A. opacum* to disperse into habitat previously occupied solely by *A. mabeei.*

The habitat characteristics associated with pine savanna include peaty acidic soil, acidic water, and fire dependence. Fire-maintained plant communities may differ from those not maintained by fire in ways that differentially affect the physiology or behavior of the two species. Differences in the characteristics between fire- and nonfire-maintained habitats (such as structural heterogeneity, soil types, chemistry and moisture gradients) may also be reflected in the composition of prey species. For example, *Ambystoma mabeei* might be feeding on suboptimal prey because their preferred prey is no longer available.

Diet

Because larval *Ambystoma mabeei* from Virginia populations of were represented in the dietary analysis by a small sample size from only one year's collection, inferences drawn from these data are necessarily inconclusive. However, the dramatic differences that were found between the stomach contents of Virginia specimens and those from more southern populations warrant attention.

High loads of gastric parasites may have major implications both for larval survival and for the long-term persistence of the population. However, there have been few studies on the host-parasite relationships between amphibians and nematodes (Rankin, 1937; Duellman and Trueb, 1986). Parasites may affect the infected host in two ways. First, they occupy space within the stomach and reduce the volume available for food storage and processing. Second, they rob the salamander of nutrients. Larval salamanders may only be minimally affected by the presence of gastric parasites, because they may be able to consume sufficient food to compensate for the presence of the worms. However, once the larvae begin to undergo the physiologically taxing process of metamorphosis the loss of nutrients may lead to starvation and death of otherwise healthy larvae.

The type of prey consumed may explain the high rate of parasitism in *Ambystoma mabeei* from Virginia. In addition to the higher number of parasitic nematodes in the stomachs of Virginia specimens, the relative proportion of prey types was different in Virginia salamanders than in those from the Carolinas. The most frequently encountered food items in specimens from the Carolinas were copepods and cladocerans, followed by a variety of other prey items that occurred in different frequencies. Conversely, isopods and amphipods were the most frequently encountered prey in the stomachs of *A. mabeei* from Virginia. Significantly, isopods and amphipods are known to be common vectors for nematodes that parasitize the gastrointestinal tract of vertebrates (Rupert and Barnes, 1994; MacNeil et al., 1999).

The differences in prey identified from the stomachs of northern and southern *Ambystoma mabeei* may reflect differences in prey availability. In Virginia, many of the breeding ponds of *A. mabeei* are shaded, so the proliferation of planktonic algae and herbivorous plankters may be reduced (Cole, 1994). However, the reduced light penetration, cooler water, and increased accumulation of leaf litter would favor detritovores and scrapers, such as isopods and amphipods (Cole, 1994).

Alternatively, interactions with larval *Ambystoma opacum* may prevent larval *A. mabeei* from acquiring desired prey in two ways. First, larval *A. mabeei* at Grafton Ponds may be out-competed for their preferred prey by *A. opacum*. Second, larval *A. mabeei* may be unable to obtain preferred prey as a result of behavioral modifications induced by larval *A. opacum*. For example, if larval *A. mabeei* spend a greater amount of time within the leaf litter substrate to avoid predation, they presumably would encounter interstitial crustaceans and insects more frequently than planktonic species. However, further research will be required to determine whether the contents of the stomachs examined during this study are representative of other years and other populations

Future Research

Because this study was conducted on a species about which little is known, it has generated many more questions than answers. Before we can begin to understand the status and fate of *Ambystoma mabeei* in Virginia, there are several major areas in which further research is needed. These include studies of community ecology, landscape ecology and investigations into parasitology and physiological ecology of both the larvae and adults.

Adult *Ambystoma mabeei* are known to have the highest thermal tolerance of any species of salamander (Hutchinson, 1961). However, there have been no studies concerning their sensitivity to osmotic gradients, pH, or other potential stressors to which they may be exposed in nature. Studies of these issues may elucidate some of the characteristics of the terrestrial habits of this species. The ecophysiology of the larvae of *A. mabeei* also requires further investigation. Such studies should include the responses of larvae to various biotic and abiotic features such as pH, substrate (leaf litter type), and temperature.

Studies on the ecological interactions between adult *Ambystoma mabeei* and *A. opacum* would also provide valuable insights into this system. *In situ* caging experiments involving adult *A. mabeei* and *A. opacum* could be used to explore the terrestrial ecology of both species. Interspecific interactions such as aggression or territoriality may also be elucidated in laboratory or mesocosm studies.

The interactions between the larvae of these two species should also be investigated. Because larval *Ambystoma opacum* occupy the pond as much as two months prior to the arrival of *A. mabeei,* they may inflict significant mortality on hatchling *A. mabeei* through direct predation and/or competition. Alternatively, there may be habitat partitioning by the two species. Prey preferences of larval *A. mabeei* should be investigated to determine whether they are restricted to feeding on less desirable prey or whether the preferred prey is unavailable. Studies comparing the diets of larval *A. mabeei* and *A. opacum* in a more inclusive sample may also help answer these questions. Studies of the incidence of gastric and other parasites and their effects on larval survivorship and adult fitness of both *A. mabeei* and *A. opacum* also are needed.

From the perspective of conservation and management, the most important area for further research concerning the ambystomatid salamanders in Grafton Ponds pertains to the effects of changes in the vegetative community at the landscape scale. Such changes, especially those involving complete shifts in forest type, must certainly have major effects on all aspects of the community. Studying how changes in the vegetative structure have affected *A. mabeei* and *A. opacum* will help to answer questions concerning their adaptation to particular habitats and will provide insights into effective ways of recovering populations that have been impacted by inappropriate forestry practices.

Potential studies concerning *Ambystoma mabeei* at the landscape level might include: (1) further investigation into the vegetative history of the Grafton Pond complex;

(2) studies of the effects of canopy closure and shade on invertebrate and vertebrate assemblages in the ephemeral ponds and surrounding upland communities; (3) identifying changes in soil and water chemistry after a major vegetative shift; (4) modeling studies employing geographic information systems or other tools to determine whether the habitat associations of *A. mabeei* are indicative of fire-dependent communities; (5) investigations designed to identify plant communities that are not fire-dependent, but that may be used to restore the key physical characteristics lost when the original vegetative community was destroyed; and (6) study of the practicality and efficacy of instituting prescribed burns into the Grafton Pond management plan.

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