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Using Life History and Ecology as Tools to Manage a Threatened Salamander Species¹

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Selected aspects of the life history and ecology of the small-mouthed salamander (*Ambystoma texanum* Matthes) relevant to the management of this threatened species in Iowa are presented. The population studied utilizes flooded woodland habitat during courtship, breeding and egg laying, and during the entire larval period. Larval foraging strategies in this habitat included ontogenetic but no diel shifts in prey selection. Synchronous, nocturnal breeding migration allowed effective use of drift fences for capture of adults used in captive breeding, courtship behavior studies, and the estimation of breeding population size. Large numbers of spermatophores, apparently indiscriminate mate choice, and the relatively large number of eggs produced by females makes captive breeding programs potentially very successful. Because larvae are particularly vulnerable to predation by fish and larval tiger salamanders, ephemeral ponds are required for breeding and larval habitat. The primary management objective should be to preserve ephemeral woodland ponds and adjacent terrestrial habitat favorable for larval and adult survival.

INDEX DESCRIPTORS: Small-mouthed salamander, *Ambystoma texanum*, ecology, life history, Iowa, endangered species management

Amphibians are often perceived to be of only marginal value in ecosystem dynamics. Burton and Likens (1975a), as part of the Hubbard Brook ecosystem research program, have shown these perceptions to be overstated. They found salamanders to be more efficient than either birds or mammals in converting assimilated energy into new growth and more or equally productive in terms of annual tissue production. Furthermore, salamander biomass at Hubbard Brook in the summer was about double that of birds and about equal to the small mammal biomass (Burton and Likens 1975b). The role of amphibians in freshwater systems can be even more pronounced. In the absence of fish, amphibians are often the top predators and consequently can and do affect the systems' community structure (Dodson 1970; Morin 1981; Wilbur et al. 1983).

This study focuses on one of Iowa's threatened amphibian species, the small-mouthed salamander (*Ambystoma texanum*) (Roosa 1977; Christiansen 1981). In Iowa, *A. texanum*'s distributional range is limited to the southern tiers of counties, with Iowa populations representing the northwest limit of the species range (Conant 1975). In southern Illinois, Indiana, Ohio, and northern Kentucky, *A. texanum* is more common (Petranka 1982a). The higher relative abundance of this species in Kentucky is mainly due to its ability to adapt to the absence of natural ephemeral pond habitats and utilize first order stream habitat or other small, fishless tributaries, something which other species of *Ambystoma* have been unable to do (Petranka 1982a).

A. texanum is conspicuously understudied. This lack of background information on basic ecology and habitat requirements of Iowa populations greatly hampers the ability of managers and scientists to protect this species. Petranka (1982a,b, 1983, 1984a,b) and Petranka and Sih's (1986) recent work on the systematics and ecology of populations in Kentucky has focused on the stream-form of *A. texanum* (Petranka 1982a), as compared to the pond-form ecological type common in Iowa.

Christiansen and Burken (1978), and Christiansen (1981) document general habitat requirements and the potential distribution of *A. texanum* in Iowa, but have focused more on systematics and general population trends. Whitaker et al. (1980), studying populations in Illinois, provide the only other published description of pond-form *A. texanum* food habits prior to our account of the foraging ecology of larvae in Iowa (McWilliams 1986). One other major area of *A. texanum* research which has relevance to management of Iowa populations involves recent work documenting hybridization between *A.*

texanum and *A. laterale* (Downs 1978; Kraus 1985) and *A. platineum* (Morris and Brandon 1984).

The study presented here has added importance because Flaming Prairie Preserve, the location of the population used in this study (see Fig. 1), would be affected by the recent Army Corp of Engineers proposal for widening the Mississippi River levee. Thus, this population was studied to help assess the potential impact the disturbance of that marsh and flooded woodland habitat would have on the Flaming Prairie *A. texanum* population.

Elsewhere we have presented results concerning larval *A. texanum* foraging strategies and feeding ecology (McWilliams 1986). We include a summary of those results in this paper and utilize the findings to delineate larval salamander habitat requirements. In addition, migration patterns, breeding season, breeding population size, and sex ratio of adult *A. texanum* are described for the study population in 1985 and 1986. We will focus here on how these results can be applied to the management of *A. texanum* populations in Iowa.

Finally, because there is considerable controversy over the breeding habits common to *A. texanum* (Petranka 1982a, 1982c), a laboratory experiment was performed to elucidate the courtship behavior exhibited by individuals from an Iowa population. In addition, the experiment was designed to test for male and female responses to varying numbers of conspecifics during courtship. These aspects of the life history of *A. texanum* are important because the various breeding types differ in their pattern of spermatophore deposition and often the number and size of eggs laid (Arnold 1976). Such factors affect the reproductive capacity and ultimate fitness of *A. texanum* and may be important in revealing why this species is threatened in Iowa.

MATERIALS AND METHODS

Study Area

Salamanders were collected from and field work carried out at Flaming Prairie Preserve (Sec. 29 Port Louisa Twp., T-75N, R-2W) in Louisa County, Iowa. The Preserve is directly adjacent to the Mississippi River levee (Fig. 1) and is operated by the Louisa County Conservation Commission headquartered in Wapello, Iowa. Flaming Prairie has three "ponds" on its 30 ha, the most northerly being essentially a continuously vegetated marsh with little open water (Fig. 1). Adult and larval *A. texanum* were found along all three wooded sides of the marsh; however, the most densely populated and most accessible area for research was along the northern edge of the marsh. All results presented here are based on collections from the

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flooded woodland at the northern edge of this marsh (see enlarged area in Fig. 1).

The flooded woodland is covered with a canopy of deciduous trees (predominantly red maples (*Acer rubrum*) resulting in a substrate of leaf litter and fallen branches throughout the study area. Aquatic macrophytes were sparsely distributed and only *Myriophyllum sp.* and *Ranunculus sp.* were usually present. The woodland was flooded ephemerally, containing standing water from ice-out until mid-August, 1984, and until mid-June, 1985.

Foraging Ecology

A detailed description of the invertebrate and larval sampling

procedures can be found in McWilliams (1986). Invertebrate relative abundance was measured using a Stovepipe sampler (Welch 1948) and an Ekman dredge. Triplicate samples using both samplers were taken at three different times-of-day (TOD), repeated three times during the approximately nine-week larval period, and duplicated over two years, totaling 18 sampling periods. Use of invertebrates by larval *A. texanum* was quantified by sampling up to 10 larvae during each of these same 18 sampling periods. Volumetric and numeric methods were used to enumerate the stomach and intestine contents of all larvae collected. Usage and availability values were compared using the ranking procedure of Johnson (1980) to help interpret the

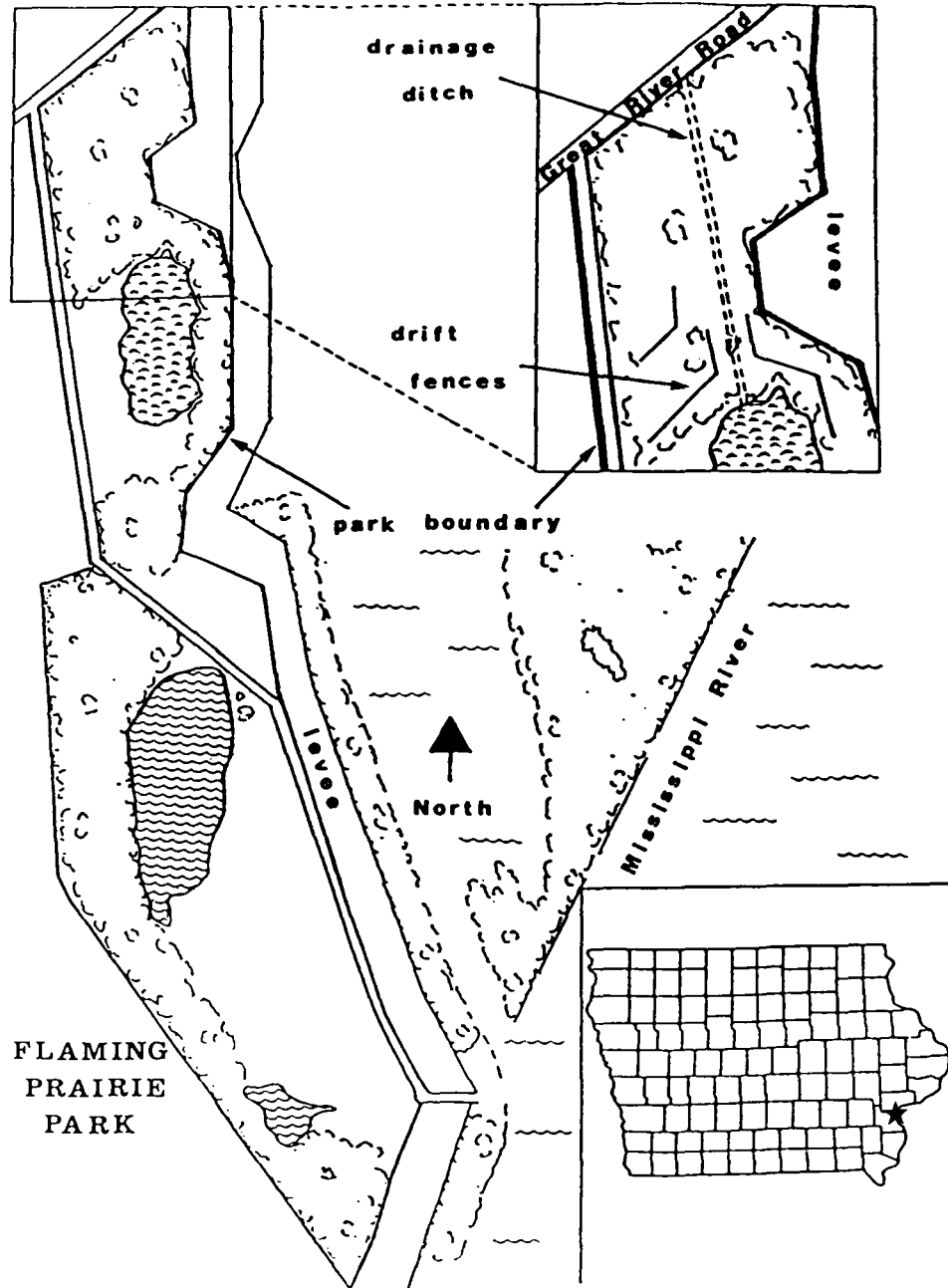


Figure 1: Diagram of Flaming Prairie Preserve and its location in Iowa. Enlarged area encloses the study site and details the location of the drift fences used in capturing adults migrating to the flooded woodland to breed. Only the shoreline of the marsh is shown since the shoreline of the flooded woodland was more variable with time of year and extent of flooding.

Table 1: Food habits of larval small-mouthed salamanders (*Ambystoma texanum*). Values for larval size classes are the average percent by volume or number for 93 larvae (22 other larvae collected were outside the ranges used for the three size classes of larvae). General diet is calculated by averaging across all larvae sampled.*

| Prey Type | Larval Size (snout-vent length) | | | | | | | |
|--------------|---------------------------------|-------|----------|-------|----------|-------|--------------|-------|
| | 10-15 mm | | 18-22 mm | | 24-29 mm | | General Diet | |
| | N = 21 | | N = 35 | | N = 37 | | N = 115 | |
| | % Vol. | % No. | % Vol. | % No. | % Vol. | % No. | % Vol. | % No. |
| Isopoda | 2.7 | 4.9 | 65.6 | 48.6 | 67.5 | 49.1 | 54.1 | 40.8 |
| Ostracoda | 48.8 | 55.3 | 22.2 | 39.0 | 5.4 | 25.5 | 19.6 | 37.0 |
| Cladocera | 42.0 | 24.5 | 4.7 | 4.3 | 5.3 | 5.2 | 12.4 | 8.4 |
| Chironomidae | 1.0 | 0.7 | 4.3 | 1.3 | 13.9 | 5.2 | 7.6 | 2.9 |
| Amphipoda | 0.7 | 1.7 | 4.0 | 5.3 | 7.0 | 8.8 | 4.6 | 5.9 |
| Copepoda | 4.5 | 12.2 | 0.9 | 1.6 | 1.6 | 3.5 | 1.8 | 4.9 |

*from data presented in McWilliams (1986)

results in terms of selectivity.

Migration and Reproductive Biology

Drift fences (Gibbons and Semlitsch 1982) were used to document migration patterns and breeding population size of *A. texanum* in the spring of 1985 and 1986. In November 1984, drift fences made from 50-cm high aluminum flashing were placed about 15 m and 30 m from the shoreline of the flooded woodland (Fig. 1). Three drift fences, 30 m, 37 m and 46 m in length, were placed parallel to the shoreline, with #10 tin cans buried at approximately 3-m intervals on both sides of the fence. Plastic covers were placed over the tin cans and remained in place until 15 February 1985 and 1 March 1986. Drift fences were buried at least 10 cm into the ground to inhibit adults from burrowing under the fence. This left about 40 cm of flashing above the ground surface, enough height to deter salamanders from climbing over the fence.

Once the pitfall trap covers were removed, drift fences were monitored at least once each day until the first salamander was caught. Subsequently, the monitoring was conducted each morning (700-1000 hrs) and evening (1700-2000 hrs). During the last two weeks in March 1985, when fewer salamanders were caught, traps were occasionally checked only once each day. The data from these two weeks in March are pooled for sex ratio calculations (see Table 1) and excluded from the TOD analysis. Each salamander captured was weighed, sexed, and measured for snout-vent length (SVL) and snout-tail length (STL), then placed on the opposite side of the fence.

In 1985, 15 females and 35 males captured using the drift fences were brought back to Iowa State University and placed in an environmental chamber set at 16°C. Each female was allowed to breed with either one, two, or three males and courtship behavior, egg deposition patterns, and clutch size were recorded.

RESULTS

Foraging Ecology

A total of nine invertebrate groups was found in the larval gut compared to 14 groups found in the environment. Five groups including dragonfly nymphs (Odonata, Anisoptera), hydra (Hydrozoa), adult beetles (Coleoptera), springtails (Collembola), and mosquito larvae (Diptera, Culicidae) were regularly found in the invertebrate samples, but were never found in the stomachs of larvae. Of the nine invertebrate groups consumed by *A. texanum* larvae, three groups (Gastropoda, Odonata (suborder Zygoptera), and Coleoptera larvae) occurred fewer than five times and are assumed to have been eaten incidentally. The remaining six groups are listed in Table 1.

Isopoda and Ostracoda comprised ca. 75% of the diet on average

(Table 1) and were found in over 90% of the 115 larvae examined. Cladocera was the next most important prey type in the diet, accounting for ca. 10% of the diet contents. Chironomids (Diptera, Chironomidae), Amphipoda, and copepods (Eucopepoda) occurred in the larval diet with similar frequencies (ca. 5%).

In terms of availability, chironomids were the most abundant prey in mid-May, whereas isopods became the predominant prey type by early June and continued to account for over 60% of the available prey population for the remainder of the larval period (McWilliams 1986). Each of the other four invertebrate groups consistently accounted for approximately 5% of the prey relative abundance.

When the results were analyzed seasonally (see McWilliams 1986 for details), ontogenetic shifts in foraging strategy become apparent. Young larvae (i.e., <15 mm SVL) foraged primarily on cladocerans, ostracods, and copepods (Table 1) which are active mostly in the water column. Older larvae (18-22 mm SVL) shifted to a diet consisting primarily of benthic prey, specifically isopods (Table 1). This shift in diet composition was associated with a shift in preference from zooplankton feeding when young to feeding on benthic prey when older (McWilliams 1986).

No significant TOD differences were found in terms of diet composition or prey preference (McWilliams 1986). Larvae fed throughout the diel period and failed to show a shift from diurnal benthic feeding to nocturnal zooplankton feeding.

Migration, Population Size, and Sex Ratio

Adult *A. texanum* are fossorial and are conspicuous to most human observers only during early spring when they migrate on the soil surface towards ponds where they breed and lay their eggs. The Flaming Prairie population migrated relatively synchronously in both 1985 and 1986 (Table 2). Of all adults captured in either year, approximately 50% of the breeding population was caught migrating on a single night, with 76% of all adults captured within one week of this peak migration night in 1985. A total of 79 adults was captured in 1985, whereas 47 adults were captured during the shortened monitoring period in 1986.

In 1985, emigrating adults were first captured on 8 March, with 43% of the population having left the breeding ponds by 31 March (Table 2). Emigration was relatively synchronous in 1985, with 65% of adults captured migrating on the night of 30 March. The discrepancy between the total number of adults immigrating and emigrating is probably the result of either individuals moving down the drainage ditch (see Fig. 1) a short distance before exiting the pond and thus eluding capture, or some adults remaining in the breeding ponds until after drift fence monitoring ended.

Since the drift fences did not enclose the marsh and because not all

adults may migrate to breeding ponds each year (Husting 1965; Semlitsch 1983; Stenhouse 1985), the population estimates derived from this study are minima. Since no adults were ever seen migrating across the two roads enclosing the woodland adjacent to the breeding ponds (Fig. 1), this woodland area probably represents the wintering habitat used by adults. Considering this woodland area (4.05 ha) as the adult terrestrial habitat and the minimum population size as 79 adults, the population density of *A. Texanum* is estimated to be 19.5 adults/ha.

In 1985 and 1986, 75% and 95%, respectively, of the adults were captured in the morning monitoring of the drift fences. Thus, most migration occurred during the night period. The sex ratio of migrating adults was generally skewed towards males (Table 2). The sex ratio was most skewed early in the season, indicating males tended to migrate earlier than females.

Reproductive Biology

Males laid up to 128 spermatophores in a single courtship (\bar{x} = 70.6, SD = 32.2, N = 25). Females picked up an average of 25.9 spermatophores (SD = 14.6, N = 12) in a given courtship sequence; however, when left together in a tank for over 24 hrs, some males and females initiated courtship again. A single courtship bout, defined as the time between the first sexual contact and the last spermatophore laid followed by at least two hours with no sexual activity, lasted on average 82.4 min. (SD = 26.5 min.). The upper limit on the number of courtships a female may participate in seems mostly a product of the time since the female initiated picking up spermatophores; i.e., females began laying eggs approximately 40 hrs after picking up their first spermatophore, with their receptivity to males declining dramatically as laying time approached.

Females laid a large number of eggs (\bar{x} = 275.1, SD = 106.6, range = 117-448). Eggs were consistently laid in bunches of 10-50 along twigs placed in the aquarium with the female. Females generally took about 8-10 hrs to complete egg laying.

DISCUSSION

A. texanum larvae inhabiting a flooded woodland foraged on a restricted number of prey items compared to available prey population abundance. Unlike some *Ambystoma* (e.g., *A. tigrinum* and *A. opacum*

(Hassinger et al. 1970)), *A. texanum* larvae did not exhibit diel changes in foraging strategy. This lack of diel shift in foraging may be due to unique characteristics of flooded woodland invertebrate activity and/or the lack of predation pressure (McWilliams 1986), combined with a life history strategy involving a short, accelerated larval stage which forces larvae to feed throughout the day (Petranka and Petranka 1980; Petranka 1984a). Ontogenetic shifts in foraging strategy were evident; young larvae fed predominantly on zooplankton, while older larvae fed predominantly on benthic prey.

These aspects of foraging ecology have important implications for management of *A. texanum* populations in Iowa. Larvae fed on a variety of food types which are common in wetlands and in this respect can probably inhabit areas much beyond their present range. The larval stage is potentially limited by a combination of intraspecific competition for food (Petranka and Sih 1986), interspecific competition for limited resources (Burton 1976; Orr and Maple 1978; Brophy 1980), predation (Morin 1983; Stenhouse et al. 1983), and often loss of habitat through the drying of ponds used by larvae (Petranka 1984a; Semlitsch 1987). Of these factors, regulation of predation and the length of time the wetland contains water offer the most promise for management purposes.

A. texanum larvae are highly vulnerable to predation and in the presence of fish are quickly exterminated (Petranka 1983). Thus, it is necessary to exclude other vertebrate predators from larval habitat. Invertebrate predators will prey on salamander larvae (Holomuzki 1986), however, they occur infrequently at our study site and are more difficult to exclude. Exclusion of fish predators can best be accomplished by keeping water regimes ephemeral so fish can not survive, and water levels shallow so warm temperatures can allow high invertebrate production and faster growth rates for the salamander larvae. Larval metamorphosis begins in early June in southeast Iowa with most of the larval population gone by mid-July. Thus, management of water levels from ice-out until the end of July would create an ideal habitat for larval survival.

Interspecific competition between *A. tigrinum* and *A. texanum* is potentially very great. In fact, this study was originally conceived to focus on sympatric populations and their competitive interactions; however, preliminary surveys found no suitable sympatric populations. *A. tigrinum* larvae are carnivorous and cannibalistic (Lannoo and

Table 2: Spring breeding migration of adult small-mouthed salamanders in Louisa County, Iowa. Plastic covers over the pitfall traps were removed on 15 February 1985 and 1 March 1986 and replaced on 15 April 1985 and 19 March 1986. Sex ratio is calculated as the cumulative number of males/females in the pond, both corrected for emigration.

| Year | March | Immigration | | Emigration | | Sex ratio |
|------|-------|-------------|-------------|------------|-------------|-----------|
| | | No. males | No. females | No. males | No. females | |
| 1985 | 3 | 5 | 2 | 0 | 0 | 2.50 |
| | 4 | 26 | 12 | 0 | 0 | 2.21 |
| | 5-6 | 0 | 0 | 0 | 0 | 2.21 |
| | 7 | 4 | 0 | 0 | 0 | 2.50 |
| | 8 | 0 | 1 | 1 | 0 | 2.27 |
| | 9 | 1 | 1 | 0 | 0 | 2.19 |
| | 10 | 1 | 0 | 0 | 0 | 2.25 |
| | 11 | 5 | 9 | 0 | 2 | 1.78 |
| | 12 | 1 | 3 | 0 | 0 | 1.62 |
| | 13-31 | 3 | 5 | 16 | 15 | 1.81 |
| | | Total: | 46 | 33 | 17 | 17 |
| 1986 | 12 | 5 | 2 | 0 | 0 | 2.50 |
| | 13 | 17 | 9 | 0 | 0 | 2.00 |
| | 14 | 7 | 2 | 0 | 0 | 2.23 |
| | 15 | 2 | 0 | 0 | 0 | 2.38 |
| | 16-19 | 0 | 0 | 0 | 0 | 2.38 |
| | | Total: | 31 | 13 | 0 | 0 |

Bachmann 1984), much larger than *A. texanum* at any given ontogenetic period, and can quickly exterminate *A. texanum* from laboratory aquaria (pers. obs.). However, there are enough differences in life history between these two species to manage for one or the other. *A. texanum* is adapted to more ephemeral habitats than *A. tigrinum*, with accelerated growth, and hatching and metamorphosis occurring at much smaller sizes. Thus, by strategically draining wetlands at the critical time between *A. texanum* and *A. tigrinum* metamorphosis (i.e. typically early August for our study population), exclusion of permanent populations of *A. tigrinum* is possible.

The widening of the Mississippi levee at Flaming Prairie Preserve has the potential to directly affect both adult and larval *A. texanum* habitat. Hydrological considerations must be taken into account to ensure the water regime described above would be maintained. Furthermore, the destruction of the woodland adjacent to the wetland would reduce overwintering habitat and perhaps even directly kill adults during construction. If destruction of part of this woodland is necessary, a large portion of the breeding population could be captured using drift fences and then released after construction was completed or adults could simply be moved to other suitable habitat.

Under natural conditions, adult *A. texanum* migrate to the breeding ponds synchronously and primarily during the night, i.e., 76% of adults captured during the breeding migration in 1984 were captured in a one-week period, with all adults migrating during March. Because individual salamanders were not marked, we can only provide an estimate of the breeding season duration and can not determine how long specific individuals remained in the flooded woodland. Given that the time from first immigration to first emigration was 5 days for males and 8 days for females (Table 2), the minimum time an individual spends in the breeding ponds would be ca. one week. The biggest pulse of emigration in 1985 occurred on 30 March. Assuming some of these individuals were from the first immigration pulse on 4 March, the breeding season duration could last as long as ca. 3-4 weeks.

Mass migration enables road deaths to be reduced by simply closing particular roads for the short period of time during which most adults migrate. Synchronous migration also facilitates estimating population size and capturing animals for captive breeding.

Mass migration, coupled with the use of ephemeral waters for breeding and larval habitat, may place a strong selective pressure on early breeding and speed in courtship (vs. efficiency). *A. texanum* males lay relatively large numbers of spermatophores in a short period of time compared to other *Ambystoma* species (Arnold 1976), with little syncopation in behavior with females to help ensure a given spermatophore is picked up by a female. Captive breeding is facilitated by *A. texanum*'s apparently indiscriminate mate choice and an emphasis on speed in courtship. Individual males can breed with successive females enabling relatively few captive animals to provide a successful breeding program. In addition, compared to other congeners (Salthe 1969), *A. texanum* females lay relatively large numbers of eggs (150-450) and will readily breed with at least three males providing a greater chance for egg fertilization.

The courtship behavior and mating strategy of *A. texanum* do not provide a sufficient behavioral isolating mechanism preventing hybridization with certain other congeners. However, hybridization is not as much a problem in Iowa since *A. tigrinum*, the only common *Ambystoma* species in Iowa, is not known to regularly hybridize with *A. texanum* (but see Bogart et al. 1987). There is some concern, however, if Iowa populations of *A. laterale* expand and become sympatric with *A. texanum* because these two species can hybridize (Downs 1978; Kraus 1985).

If managers and biologists decide further protection efforts are necessary, the life history aspects of *A. texanum* and the foraging ecology results outlined here should help in developing a successful conservation program. The primary objective of a management plan

should include preserving ephemeral woodland pond habitat. This can best be accomplished by either protecting existing natural areas with this type of habitat or managing water levels in marshes with wooded shorelines to favor *A. texanum* larval survival.

Habitat requirements of overwintering adults is an important area for future research. We suspect it is primarily the inability of adults to overwinter successfully further north which restricts the northward expansion of *A. texanum*'s range. Thus, it is critical to understand these overwintering requirements to enhance our ability to preserve this threatened species in Iowa. Unfortunately, the types of habitats ideal for salamanders are rarely of economic or political worth in their pristine state. This creates a conflict which until now has caused *A. texanum* habitat to be regularly destroyed.

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Errata: Catalogue of Botany Department Greenhouses

In the recent article on the Iowa State University Botany Department greenhouse collections (Pohl and Lewis 1988) some of the pages are not in the proper sequence. The proper sequence of pages should be 8, 11, 10, 9, 12, 13.

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