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Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influences

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Summary

1. We address the question of whether individual variation in arrival date of breeding salamanders at a temporary pond is repeatable among years.
2. We present data on variation in the date of arrival of individually marked males and females, and date of pond-filling over 12 years at a breeding site. These data allow us to partition variances within and among individuals, but remove the effects of annual environmental differences by standardizing annual return dates.
3. Date of arrival differed significantly among individual males and females. Repeatability for date of return of individual males was ($r = 0{\cdot}0665$), but significantly higher for females ($r = 0{\cdot}1662$).
4. Snout–vent length had no effect on the date of return for females, but small males returned earlier than large males.
5. We suggest that variation in arrival time for both sexes is determined primarily by environmental variation, but variation among females has a greater potential genetic component. Differing selective pressures between the sexes may contribute to the maintainance of differential amounts of genetic variation.

Key-words: amphibian, arrival time, breeding migration, repeatability.

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Introduction

Reproductive synchrony is widespread among both plant and animals. Stabilizing selection may maintain high synchrony in a population, centred around the optimal timing of an event, through differential reproductive success, but presumably would eliminate genetic variation and any potential for further changes (Lack 1954; Perrins 1970; van Noordwijk, van Balen & Scharloo 1981; Findlay & Cooke 1982). However, variation in the timing of reproduction could be maintained by a mixed evolutionary stable strategy (ESS) based on differential arrival times of individuals (Parker & Courtney 1983; Parker 1985). Theoretically, it also has been shown that the evolutionary equilibrium between fitness and a heritable trait such as breeding date can also be maintained by an association between the heritable trait and a non-heritable trait, such as maternal nutritional state (Price, Kirkpatrick & Arnold 1988). The effect of nutritional state can shift the average breeding date away from the optimum. Thus, the relationship between genetic and phenotypic variation in reproductive traits, and environmental predictability is important to understanding the processes underlying life-history strategies.

In a review, Ims (1990) noted three types of environmental factors that may affect the timing of reproductive events and contribute to differential success of plants and animals: (i) climatic conditions such as rainfall, temperature and photoperiod; (ii) internal cues from endogenous rhythms; and (iii) biological interactions or 'social' cues. In amphibians, variation in the arrival time of breeding adults appears to be influenced strongly by annual variation in environmental conditions (Savage 1935; Packer 1960; Frazer 1966; Hurlbert 1969; Gittins 1983; Semlitsch 1985). Many amphibians are dependent on transient, unpredictable aquatic habitats for reproduction and larval development. Reproductive events of amphibians are often synchronized to the annual hydrological cycle of ponds. Because larval amphibians are adapted for rapid growth and development in transient, but resource-rich temporary ponds (Wilbur 1980), the optimal time

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of arrival for breeding adults theoretically coincides with environmental conditions that maximize offspring success and minimize adult mortality. We have assumed that most environmental variation is related to climatic conditions and that social factors do not affect salamander breeding migrations.

We have addressed the problem of phenotypic variation in the time of arrival for breeding salamanders, *Ambystoma talpoideum* (Holbrook), at a temporary pond. We asked whether individual differences in arrival dates of breeding adults are repeatable among years; i.e. whether an individual tends to arrive early or late consistently, relative to the population mean. We reason that the optimal time of arrival for this species would coincide with winter filling of the breeding pond. Because courtship and oviposition of this species occurs in the water, arrival before pond-filling cannot contribute to mating success and may increase mortality of adults from physical exposure or predation (Douglas 1979; Heyer 1979; Harris 1980; personal observation). Arrival later in the season may reduce mating opportunities and increase the probability of larval competition, predation and pond-drying prior to metamorphosis, and thereby reduce larval development, growth and survival (Alford & Wilbur 1985; Wilbur & Alford 1985; Wilbur 1987; Morin, Lawler & Johnson 1990). Variation among individuals within a year may reflect variation in the distance that must be travelled from summer home ranges to the pond. Home range habitat selection presumably involves many environmental factors besides distance from the pond, and may have a genetic component. We also consider the possibility that phenotypic variation reflects genetic variation in the population in timing of the response to environmental cues associated with breeding migrations (e.g. rainfall, temperature) and is maintained by temporal fluctuations in the environmental optimum for arrival and subsequent reproductive success. We hypothesize that stabilizing selection could maintain relative synchrony in arrival time of pond-breeding salamanders, but that the stable equilibrium point varies temporally with environmental conditions, and therefore maintains genetic and phenotypic variation in the population.

In this paper we present data on: (i) annual variation in the distribution of dates of arrival over 12 years for breeding males and females; (ii) annual variation in pond-filling over the same time; and (iii) individual variation in date of arrival within and among years, relative to the population means. We calculate repeatability to estimate the upper limit of genetic variation in date of arrival within individuals and independent of annual variation in environmental conditions (Falconer 1981; Lessells & Boag 1987). Last, we test the effects of body size on variation in return date as it might relate to physiological state.

Methods

STUDY POND

During the last 12 years (1978–90), studies of amphibians have been conducted at Rainbow Bay in Barnwell County, South Carolina, USA on the US Department of Energy's Savannah River Site. Rainbow Bay is a temporary pond of natural, but unresolved, geologic origin called a 'Carolina bay' (Sharitz & Gibbons 1982). These freshwater ponds are abundant on the Atlantic Coastal Plain of the south-eastern US and serve as major breeding sites for numerous species of amphibians. During our studies at Rainbow Bay we have collected and identified 27 species of amphibians. Rainbow Bay is 1·0 ha in area and has a maximum water depth of 1·04 m. It usually fills with water in early winter and dries by mid-summer; however, considerable annual variation occurs in dates of filling and drying. Rainbow Bay is surrounded by second-growth forests and pine plantations with deep, well-drained sandy soils. Vegetation, rainfall, temperature and other characteristics of the site have been reported in other studies (Semlitsch 1981, 1985, 1987; Pechmann *et al.* 1989, 1991).

MONITORING DATE OF ARRIVAL

Ambystoma talpoideum migrate to breeding ponds on rainy nights during the winter months, primarily from November to February in South Carolina (Semlitsch 1985). Courtship and oviposition occur shortly after pond filling, and post-breeding adults emigrate primarily in March. Adults return to the surrounding terrestrial habitats where they remain fossorial until the next breeding season (Semlitsch 1981). Individuals are usually philopatric to the pond from which they metamorphosed, with some individuals living 6–8 years.

Rainbow Bay is completely encircled by a 440-m drift fence of aluminium flashing (50 cm high, buried 10–15 cm in the ground) with paired pitfall traps (40-l buckets) inside and outside the fence at 10-m intervals (Gibbons & Semlitsch 1981). Pitfall traps have been checked for *A. talpoideum* migrating into or out of Rainbow Bay each day from 21 September 1978 to 1 September 1990 during this study. Complete censuses of breeding adults and metamorphosing juveniles have been achieved each year as *A. talpoideum* cannot cross the fence. All individuals were marked by clipping toes, but marking varied among years. During the 1979 season most juvenile *A. talpoideum* were marked individually, as were approximately 100 juveniles in 1984 and 1000 juveniles in 1987. The remaining juveniles in 1979, 1984 and 1987, and all juveniles produced in other years were given annual cohort marks. Most cohort-marked juveniles breeding for the first time during the 1980–84 breeding seasons were given individual marks upon recapture. All other adults were given individual marks during the first 6 years of the study. Individuals were recognizable even with some toe regeneration. Immigrating breeding adults were recognized by prominent secondary sex characteristics (i.e. females gravid with ova and males with swollen cloacal glands). Date of arrival of individually marked adults was recorded each year on the day of first capture in a pitfall trap on the outside of the fence. Snout–vent length (SVL, mm) was measured and toes were reclipped if necessary. All salamanders were processed in the field and released immediately on the opposite side of the fence, the presumed direction of migration (Semlitsch 1981; 1985; Semlitsch, Scott & Pechmann 1988).

DATA AND STATISTICAL ANALYSES

We defined the breeding year according to the earliest (1 September, Day 1) and latest (30 April, Day 242; 243 in leap years) arrival dates. Date of arrival was converted to day of arrival within each breeding year. We then standardized day of arrival to remove environmental differences among years (e.g. rainfall, temperature and pond-filling) for each season and sex (using all 8242 captures of females and 10 057 captures of males over 12 years, marked and unmarked) by calculating a standardized return day with a mean of 0 and a variance of 1·0 (PROC STANDARD; SAS Institute Inc. 1985), resulting in a *Z*-score for each individual. A comparison of the standardized day of arrival of the same individual in two or more subsequent years was used to assess individual consistency. Among all individually marked, returning adults with unambiguous records, 496 males and 367 females had two or more returns in different breeding seasons. Their *Z*-scores were used in an analysis of variance to test for an individual effect on standardized day of return. We also used these standardize *Z*-scores to test the effect of size (SVL) on standardized day of first returns. Data for males and females were analysed separately.

To estimate the limit to which return date is genetically determined we calculated the index of repeatability. Repeatability (r) of a character (the within-individual correlation coefficient) can be used to set upper limits to the degree of genetic determination or heritability (Falconer 1981). Repeatability was calculated by dividing the among-individual variance (S_A^2) in day of arrival by the total-individual variance in day of arrival (i.e. within-individual variance (S^2) plus among-individual variance):

$$r = S_A{}^2/(S^2 + S_A{}^2).$$

Variance components were calculated from mean squares among (MS_A) and within (MS_W) individuals in the analysis of variance, and a coefficient (n_0) related to sample size per individual (i.e. number of years each individual returned to breed), according to Lessells & Boag (1987):

$$S_A{}^2 = (MS_A - MS_W)/n_0$$

and

$$n_0 = [1/(a-1)]\cdot\left[\sum_{i=1}^{a} n_i - \left(\sum_{i=1}^{a} n_i^2 \Big/ \sum_{i=1}^{a} n_i\right)\right]$$

where a is the number of individuals and n_i is the number of returns for the ith individual. We also calculated standard error (SE) for repeatability according to Leafloor & Batt (1990), and then tested for differences between mean repeatability of males and females by a t-test (Zar 1974; pp. 105–107).

Results

Date of pond-filling varied from 6 September to 24 April, but filling took place in December, January or February in 9 of the 12 years of records (Table 1). Most of the breeding adults typically arrived shortly before pond-filling. Mean date of arrival varied from 19 November in 1980 to 26 January in 1979 for males ($\bar{X}$ = day 116), and from 9 December in 1980 to 20 February in 1989 for females ($\bar{X}$ = day 134; Fig. 1). The correlation between mean day of arrival and day of pond-filling was strongly positive for males (intercept = 73·60, slope = 0·3189, $r^2 = 0{\cdot}703$) and females (intercept = 94·52, slope = 0·2966, $r^2 = 0{\cdot}676$; Fig. 2). Day of arrival for males and females was also highly correlated ($r = 0{\cdot}942$, $P < 0{\cdot}0001$), but day of arrival for males average 18 days earlier than for females ($t = 7{\cdot}87$, $P < 0{\cdot}0001$; Figs 1 & 2). Smaller males tended to arrive earlier than large males ($F = 4{\cdot}20$, df = 1, 166, $P = 0{\cdot}042$), but large and small females arrived at the same time ($F = 0{\cdot}01$, df = 1, 117, $P = 0{\cdot}957$).

Among the 496 males, 345 returned to the breeding site twice, 109 returned three times, 32 returned four times, 8 returned five times, and 2 returned six times (not necessarily in consecutive years). The

Table 1. Dates of filling and first drying of Rainbow Bay 1979–90. The breeding year is defined from 1 September to 31 August (see Methods)

Breeding year	Date filled	Day filled	Date dried
1979	8 Feb	161	9 Aug
1980	6 Sep (1979)	6	16 Jun
1981	11 Feb	164	4 May
1982	1 Jan	123	6 Jul
1983	12 Dec (1982)	103	11 Jul
1984	20 Dec (1983)	111	27 Sep
1985	6 Feb	159	4 Apr
1986	1 Dec (1985)	92	24 Apr
1987	12 Dec (1986)	103	2 Jun
1988	24 Apr	237	26 Apr
1989	9 Apr	221	28 Apr
1990	8 Dec (1989)	99	4 Apr

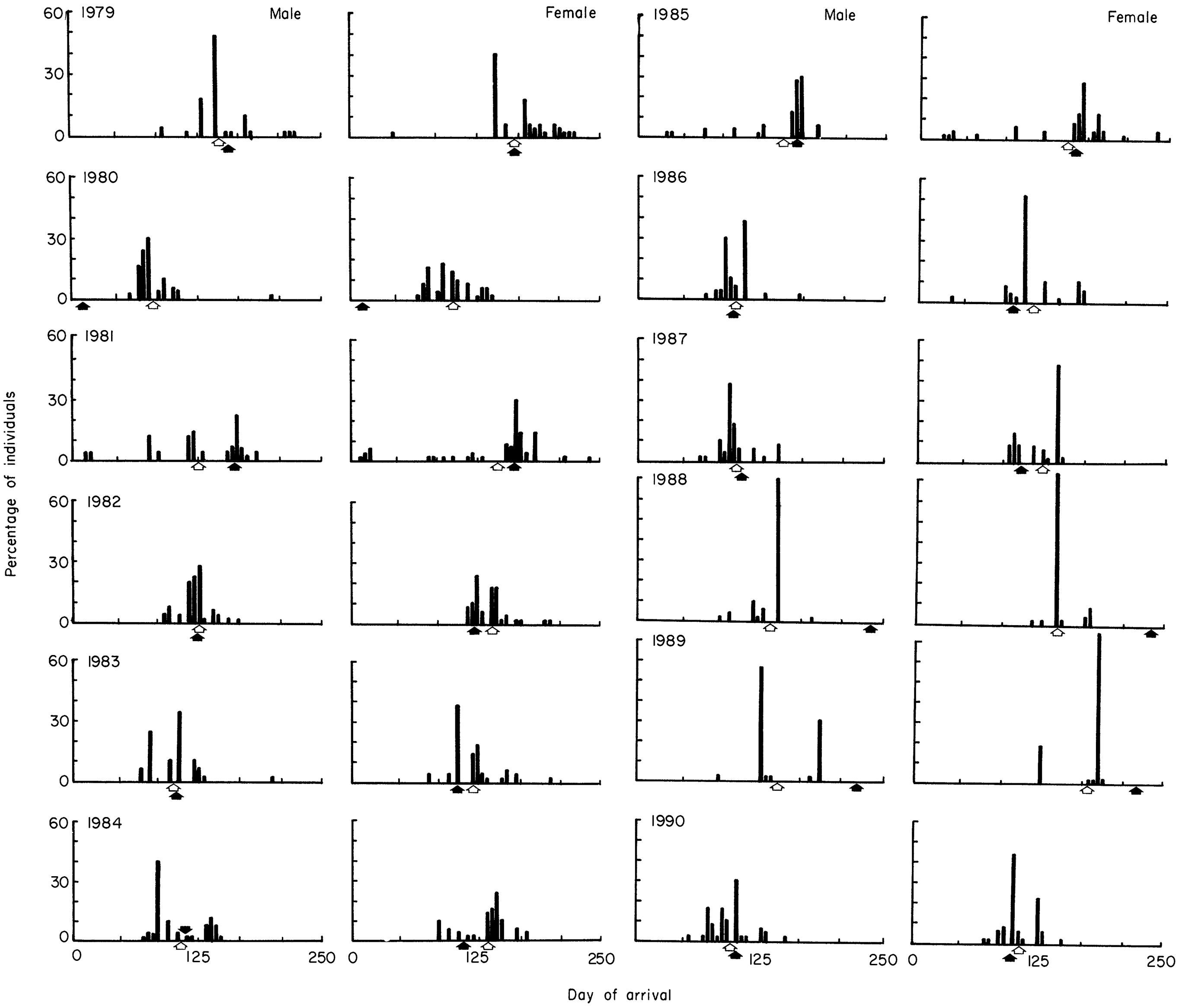

Fig. 1. Frequency histograms for day of arrival of all males and females breeding at Rainbow Bay during the period 1979–1990. Mean arrival day for each year is indicated by an open arrow, day of pond-filling by a closed arrow.

standardized day of arrival for males differed significantly among individuals (Table 2). Repeatability of individual males was low ($r = 0{\cdot}0665$, standard error (SE) $= 0{\cdot}035$, sample size coefficient $(n_0) = 2{\cdot}4129$) despite this significant difference (Fig. 3). Among the 367 females, 269 returned to the breeding pond twice, 76 returned three times, 17 returned four times, 4 returned five times, and 1 returned six times. The standardized day of arrival for females also differed significantly among individuals (Table 2). Repeatability for individual females was also low ($r = 0{\cdot}1662$, $\mathrm{SE} = 0{\cdot}043$, $n_0 = 2{\cdot}3428$; Fig. 3), but was significantly higher than for males ($t = 12{\cdot}46$, $\mathrm{df} = 861$, $P < 0{\cdot}001$).

Table 2. Summary of the analysis of variance for the effect of individual on standardized day of arrival of males and females

Source of variation	df	MS	*F*	*P*
Male (model $R^2 = 0{\cdot}453$)				
Individual	495	0·8446	1·17	0·0272
Error	712	0·7194		
Female (model $R^2 = 0{\cdot}521$)				
Individual	366	0·9828	1·47	0·0001
Error	493	0·6699		

Discussion

The time of arrival of adult salamanders at Rainbow Bay shows considerable annual variation, as does the time of filling of this temporary pond that serves as the breeding and oviposition site for these salamanders. The results of our study support the hypothesis that variation in arrival time of males and females at the breeding site is determined primarily by environmental conditions. Although the majority

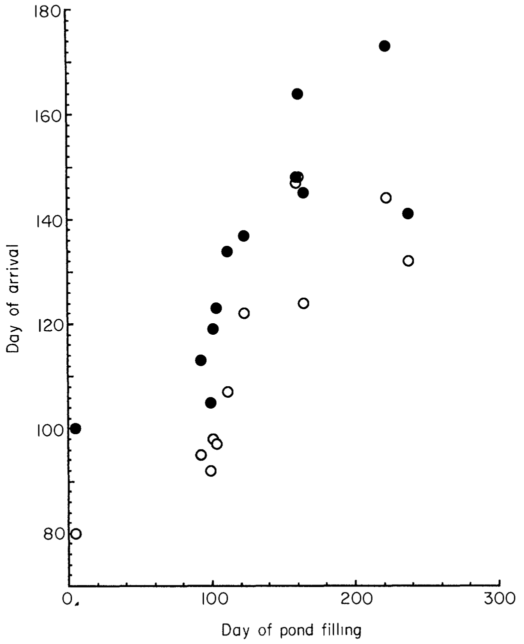

Fig. 2. Relationship between mean day of arrival of males (○) and females (●) and the day of pond filling for 12 years.

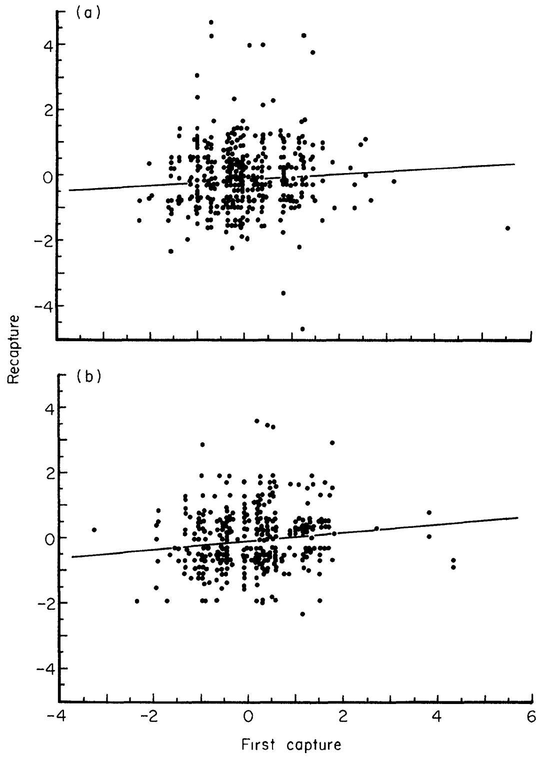

Fig. 3. Scatterplot of standardized dates of first capture and recapture for (a) males ($n = 496$) and (b) females ($n = 367$) captured two or more times at Rainbow Bay.

of variation in arrival time is due to environmental effects, significant differences between the sexes in repeatability suggests that males and females may be under different selective pressures, and that females may have maintained higher levels of genetic variation.

ENVIRONMENTAL DETERMINANTS OF ARRIVAL TIME

Weather conditions of migration to ponds are probably the largest proximate determinant of time of arrival of salamanders within the breeding season. *Ambystoma talpoideum* migrations are constrained to warm, rainy nights because of physiological tolerances and ecological requirements (Semlitsch 1981, 1985; Semlitsch & Pechmann 1985). The time period of migrations, within years, usually is contracted during 'wet' years and protracted in 'dry' year (Semlitsch 1985). Total breeding population size is also correlated with the cumulative rainfall during the breeding season (Semlitsch 1987; Pechmann *et al.* 1991). The correlations between mean day of arrival and day of pond filling are related to the correlation between migratory activity and rainfall, as the timing of pond-filling is determined by rainfall (Sharitz & Gibbons 1982; Lide 1991). Breeding shortly after pond-filling is advantageous because it maximizes the time larvae have to develop before the pond dries and minimizes initial competition and predation. Pond-drying is a frequent cause of catastrophic larval mortality (Semlitsch 1987; Pechmann *et al.* 1989, 1991).

Distance of emigration from the pond after the breeding season may also influence time of arrival in the following year. Individuals with summer home ranges near the pond (e.g. <20 m) would probably arrive earlier in the breeding season than individuals with summer home ranges a long distance from the pond (e.g. 200–300 m; Semlitsch 1981), if opportunities to migrate are limited by weather (Semlitsch & Pechmann 1985; Pechmann & Semlitsch 1986). It is not known if individuals return to the same summer home range each year so that a correlation in time of arrival each year could be due to distance of migration and, if so, whether there is a genetic component to an individual's selection of home range distance. Selection of summer home range also could involve many criteria besides convenience for rapid return to the breeding pond. Any connection between individual repeatability of arrival date and genetic determination of arrival date *per se* is speculative because of these possibilities, but should be the same for both sexes.

Physiological body condition is also known to affect the timing of reproduction in many vertebrates (Price, Kirkpatrick & Arnold 1988; Ims 1990). It is well known that body size is directly related to egg number and egg size in amphibians, but the effects of nutrition, food level, reproductive history on current reproductive condition may also be important (Fraser 1980). Thus, food intake and foraging success may be related to reproductive condition. Microhabitat conditions (moisture) for foraging during the non-breeding season could influence gonadal development and fat storage, and therefore be important in determining an individual's reproductive 'readiness' and time of arrival. We did find an effect of snout–vent length on the time of arrival for males, but small males arrived earlier. These small males were probably the last to metamorphose from the previous season, were closer to the pond, and smaller in size because they had less time to grow before the breeding season (Semlitsch, Scott & Pechmann 1988). There was no effect of body size on the arrival time of females. This probably results from small females not breeding in their first year after metamorphosis, allowing more growth and an increase in body size before they eventually breed. Thus, size was probably more indicative of whether indivdiuals would breed or not, especially in their first year (Semlitsch, Scott & Pechmann 1988), than their time of arrival.

MAINTENANCE OF GENETIC VARIATION AND DIFFERENCES BETWEEN THE SEXES

Within many species of salamanders early arrival of males at the breeding pond is well known (Hurlbert 1969; Douglas 1979; Semlitsch 1985). Males probably can increase reproductive success by arriving just before females in order to encounter and mate with as many females as possible. Annual variation among males may be related simply to the timing of environmental cues used to 'predict' female availability and pond-filling. Douglas (1979) suggested that selection should act on behavioural traits related to the early arrival of males that increase the number of successful encounters with females. He also suggested that males may be more sensitive than females to temperature and rainfall cues. In addition, it is known that males remain at the pond longer than females (Douglas 1979; Semlitsch 1981), again enhancing mating success by increasing the probability of encountering females.

Our data indicate that additive genetic variance in arrival time of males is probably minimal. Heritability of a trait can be equal to repeatability, but it can never be greater (Falconer 1981). We suggest that selection has eliminated most or all additive genetic variance for male arrival time because fitness is always enhanced by arriving just before the pond fills, and courtship and breeding commences. Conversely, the relationship between reproductive success of females and arrival time may be more variable. Even though females arrive after males and presumably enhance their fitness by having a broader choice of males (Douglas 1979), reproductive success is also related to larval survival. Larval survival in all pond-breeding amphibians is highly variable among years and usually quite low (<5%; Wilbur 1980; Semlitsch 1987). Early breeding maximizes the amount of time available for larval development before pond-drying and probably minimizes predation risk, but pond-freeze early in the season can cause high mortality in eggs or larvae (Harris 1980; Jackson, Scott & Estes 1989). Late breeding leaves less time for larval development, but pond water temperature which accelerates development is higher later in the season and larval food resources may be more abundant later in some years (Taylor *et al.* 1988). Variable selection in time and space is thought to be important for the maintenance of genetic and phenotypic variation in the timing of life-history events (reviewed in Kalisz 1986). Because *A. talpoideum* are usually philopatric to their breeding pond it is unlikely that variable selection in space is as important as variable selection among years, within a population. Although arrival time of females probably has been under selection to coincide with pond-filling and mate availability in a similar fashion as males, we suggest that higher additive genetic variance in arrival time of females is maintained by variable temporal selection on reproductive success among years. Because males can fertilize more than one clutch of eggs during the breeding season they can distribute their success (failure) among females. Females, however, produce only a single clutch of eggs within a breeding season, and can only enhance their fitness through the successful production of offspring in one reproductive event.

The timing of life-history events in variable environments such as temporary ponds can have strong effects on both survival and reproductive fitness. Our results indicate that the phenotypic variation in arrival time of breeding salamanders is primarily determined by annual variation in climatic conditions. The correlation of reproductive fitness with physical cues related to climatic variation may have eliminated most genetic variance, particularly in males. Our results are different from those for the timing of reproductive events in bird populations, typically showing high repeatability within individuals (van Noordwijk, van Balen & Scharloo 1981; Findlay & Cooke 1982; Newton & Marquiss 1984; Leafloor & Batt 1990). We suggest, however, that our findings are general for organisms such as terrestrial amphibians that are strongly dependent on physical factors (i.e. moisture and temperature).

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