

Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*

HOWARD H. WHITEMAN¹

Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, U.S.A.
and
Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, CO 81224, U.S.A.

SCOTT A. WISSINGER

Biology Department, Allegheny College, Meadville, PA 16335, U.S.A.
and
Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, CO 81224, U.S.A.

AND

ANDREW J. BOHONAK

Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, U.S.A.
and
Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, CO 81224, U.S.A.

Received December 16, 1993

Accepted July 27, 1994

WHITEMAN, H.H., WISSINGER, S.A., and BOHONAK, A.J. 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Can. J. Zool.* **72**: 1780–1787.

Seasonal movements of a subalpine population of metamorphic tiger salamanders, *Ambystoma tigrinum nebulosum*, were explored from 1990 to 1992. Metamorphic adults bred in permanent and semipermanent habitats during June of each year. After breeding, some individuals returned to the terrestrial environment, but many remained and congregated in nonpermanent ponds. Metamorphic adults in nonpermanent ponds included those that moved from permanent ponds, those that bred and remained in semipermanent ponds, and those that did not breed but migrated from the terrestrial environment after the breeding season. Dietary analyses indicated that metamorphic adults in nonpermanent ponds have significantly greater numbers, biomass, and calories of prey in their gut than the few metamorphic adults remaining in permanent ponds. This difference was due to the presence of fairy shrimp (*Branchinecta coloradensis*), which composed 91% of metamorphic adult diets in nonpermanent ponds and accounted for three times the average caloric value of all prey in gut samples from metamorphic adults in permanent ponds. Intraspecific competition also may have contributed to movement into nonpermanent ponds: post-breeding densities of metamorphic adults in permanent ponds were inversely related to the densities of other morphs (paedomorphic adults and large larvae). We conclude that metamorphic *A. t. nebulosum* in this population utilize nonpermanent ponds after the breeding season because of the abundance of high-quality aquatic prey and reduced competition from conspecific morphs.

WHITEMAN, H.H., WISSINGER, S.A., et BOHONAK, A.J. 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Can. J. Zool.* **72** : 1780–1787.

Les déplacements saisonniers ont été étudiés chez une population subalpine de la Salamandre tigrée, *Ambystoma tigrinum nebulosum*, de 1990 à 1992. Les adultes à métamorphose se reproduisent dans les habitats permanents ou semi-permanents en juin de chaque année. Après la reproduction, certains individus regagnent le milieu terrestre, mais plusieurs demeurent et se rassemblent dans les étangs temporaires. Les adultes à métamorphose des étangs temporaires comptent ceux qui sont arrivés des étangs permanents, ceux qui se sont reproduits et sont restés dans les étangs non permanents et ceux qui ne se sont pas reproduits mais qui ont quitté le milieu terrestre après la saison de reproduction. L'analyse des contenus stomacaux a démontré que les proies consommées par les adultes à métamorphose des étangs non permanents sont présentes en plus grand nombre, constituent une biomasse plus importante et contiennent une plus grande quantité de calories que les proies consommées par les quelques adultes à métamorphose restés dans les étangs permanents. La différence est attribuable à la présence de *Branchinecta coloradensis* qui composait 91% du régime alimentaire des adultes à métamorphose dans les étangs temporaires et qui équivalait à plus de trois fois la valeur calorifique moyenne reliée à toutes les proies consommées par les adultes à métamorphose dans les étangs permanents. La compétition intraspécifique peut également avoir contribué à la migration vers les étangs temporaires : dans les étangs permanents, la densité des adultes à métamorphose après la reproduction était en relation inverse avec la densité des autres formes (adultes pédomorphes et larves avancées). Il faut conclure que les adultes à métamorphose d'*Ambystoma* de cette population utilisent les étangs temporaires après la saison de reproduction à cause de l'abondance des proies aquatiques de haute qualité qui s'y trouvent et à cause de la compétition peu importante des autres formes de cette espèce.

[Traduit par la Rédaction]

Introduction

Clarifying the ecological constraints and the evolutionary mechanisms by which animals select habitats is a fundamental

¹Present address: Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, U.S.A.

question in behavioral ecology (e.g., Alcock 1989). Animal movements and distributions are related to changes in climatic conditions (Dingle 1978; Cox 1985), resource abundance (Brown 1975; Gross 1987), strength of competition (Hairston 1980; Waser 1985), predation pressure (Schaller 1972; Hairston 1986), parasite density and prevalence (Sutherst et al. 1986;

Moore et al. 1988), breeding opportunities (Norris 1967; Bradbury et al. 1989), and social interactions (Rabenold 1987; Wiedenmann and Rabenold 1987). Movement patterns are perhaps most distinct in species that obligately travel from one environment to another to complete their life cycle. Obligate environmental shifts include migrations by insects (Dingle 1978; Rankin 1985), salmon (Gross 1987), sea turtles (Carr 1967), birds (Cox 1985), and mammals (Norris 1967), which may move across large geographic areas between wintering and breeding areas. On a smaller scale, similar shifts in habitat use occur in elevationally migrating birds (Rabenold and Rabenold 1985) and mammals (Baker 1978) and seasonally breeding amphibians (Husting 1965; Douglas 1979; Semlitsch and Pechmann 1985; Semlitsch et al. 1993).

Movement patterns of amphibians are poorly documented compared with those of other vertebrates because of low recapture rates (e.g., Merchant 1972), inefficient marking techniques (Seale and Boraas 1974; Nishikawa and Service 1988), and the secretive nature of many species. However, clarifying amphibian movements is important for understanding adaptations to severe environments, such as estivation (Reno et al. 1972; McClanahan et al. 1976), water-loss tolerance (McClanahan 1967; Ruibal et al. 1969), and alternative life histories (Pfennig 1990; Whiteman 1994). Amphibians exploit a variety of harsh habitats, including desert pools (Webb and Roueche 1971; Pfennig 1990), alpine ponds (Sexton and Bizer 1978; Wissinger and Whiteman 1992), and acidic marshes (Beebee and Griffin 1977; Clark 1986). However, surprisingly little information is available regarding how habitat quality influences amphibian distributions and movements and what mechanisms are used to maintain homeostasis when breeding migrations or other movements occur.

The movement patterns of ambystomatid salamanders (Caudata: Ambystomatidae) are particularly unclear, since they typically spend most of their life cycle in subterranean burrows and congregate only briefly at aquatic breeding sites (Duellman and Trueb 1986). Although seasonal patterns of migration from terrestrial environments to breeding areas are well established (e.g., Husting 1965; Semlitsch 1985), movements after the breeding season are poorly understood (Baker 1978; Hairston 1987; but see Semlitsch 1981). In this paper we document seasonal migration patterns over a 3-year period in a high-elevation population of tiger salamanders. We found that many metamorphic adults in this population remain in the aquatic habitat long after breeding and congregate in those ponds with low conspecific density and high prey abundance. We use these data to predict the fitness consequences associated with postbreeding movements in this population.

Materials and methods

Study organism and study site

The Arizona tiger salamander, *Ambystoma tigrinum nebulosum*, is common in a variety of habitats and elevations from western Colorado and Utah to south-central New Mexico and central Arizona (Behler and King 1979). The population studied here is located within the Mexican Cut Nature Preserve in the Elk Mountains of western Colorado. The Mexican Cut watershed contains 24 subalpine (3400 m) ponds that vary in hydroperiod and other abiotic and biotic variables (Wissinger and Whiteman 1992). Permanent ponds at Mexican Cut have remained aquatic for at least 50 years (R. Willey, personal communication), semipermanent ponds may or may not dry during autumn in a given year, and vernal ponds predictably dry each year in July or August. Because of a short growing season and low pond

temperatures, larval salamanders at Mexican Cut require at least two growth seasons to complete development (Wissinger and Whiteman 1992). Thus, populations in permanent ponds are stage-structured (sensu Wilbur 1984), with several year classes of larvae as well as paedomorphic and metamorphic adults (Sexton and Bizer 1978; Wissinger and Whiteman 1992). The Mexican Cut watershed is isolated and all ponds are easily censused, providing an ideal site to follow salamander movements.

Salamander censuses

Adult and larval salamanders at Mexican Cut were monitored during the summers of 1990–1992; movement patterns described here are exclusively those of metamorphic adults, since paedomorphic adults and larvae were rarely observed to move between ponds (through transient aquatic connections). Salamanders were captured in the ponds by hand or using dip nets, and identified visually to age-class, morph (through size and presence or absence of larval characters such as gills and tail fin), and sex (through the presence of large dark papillae posterior to the cloaca of males). Individuals were measured for snout–vent length (SVL) and mass, scored for general body condition, and individually marked with unique toe clips.

Mark and recapture censuses (usually weekly, sometimes biweekly) provided data on movements of individuals between ponds. Densities of metamorphic and paedomorphic adults are based on complete or nearly complete censuses of all individuals within a pond. Larval densities are based on Lincoln–Peterson mark–recapture estimates. Estimated densities are presented only for those salamanders that overlap in diet with metamorphic adults (other metamorphic adults, paedomorphic adults, and larvae >70 mm SVL; S.A. Wissinger, W.S. Brown, and H.H. Whiteman, unpublished data). Densities of conspecifics were not normally distributed and variances were heteroscedastic between permanent and semipermanent ponds, therefore a Mann–Whitney *U* statistic was used to test for differences in density between pond types.

Salamander diets and prey abundance

Dietary data were obtained in July and August 1990 by flushing salamander foreguts using a modified gastric-lavage technique (Legler and Sullivan 1979; Zerba 1989). Stomach contents were stored in 90% ethanol and later identified to genus based on specimens in quantitative benthos and plankton samples. The size of each prey item was measured on a Wild M8 dissecting microscope using taxon-specific measurements that had been used previously to correlate size and biomass (S.A. Wissinger, unpublished data). Biomass–size regressions or stage-specific size to biomass conversions for each prey taxon were based on field-collected individuals that were measured, dried for 24 h at 60°C, then weighed to the nearest 0.01 mg on a Cahn C-31 electrobalance. The biomass values obtained from these regressions were converted to caloric contents using data summarized in Cummins and Wuycheck (1971).

The distributions of total number of prey items, total biomass, and total number of calories between metamorphic adults in both nonpermanent and permanent ponds were non-normal, and variances were heteroscedastic between pond types. Thus, we used Mann–Whitney *U* tests to compare the diets of metamorphic adults between permanent and nonpermanent ponds.

Collection of rainfall and water-temperature data

Rainfall was measured continuously during 1991–1992 using a Tru-Chek rain gauge. Maximum, minimum, and midday water temperatures were taken in nine of the major ponds (five permanent, four semipermanent) on an almost daily basis using maximum–minimum thermometers during the ice-free season of 1991–1992. Midday temperature data were analyzed with a repeated-measures two-way ANOVA on pond type and date (Sokal and Rohlf 1981). Both variables exhibited slightly heteroscedastic variances that were not controlled through transformation. ANOVA is robust for heteroscedasticity, and moderate departures from this assumption have little impact on the ability of the analysis to detect differences among treatment means (Scheffé 1959; Morin 1983).

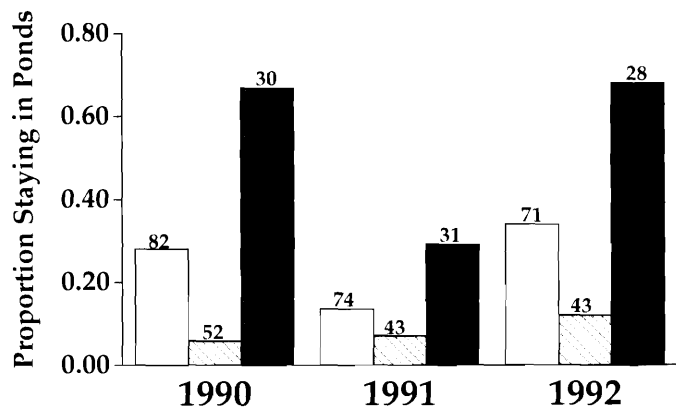


FIG. 1. Proportion of metamorphic adults remaining within all ponds (open bars), permanent ponds (hatched bars), and semipermanent ponds (solid bars). χ^2 tests were performed between permanent and semipermanent ponds; 1990: $\chi^2 = 35.0$, $p < 0.001$; 1991: $\chi^2 = 11.0$, $p < 0.001$; 1992: $\chi^2 = 24.0$, $p < 0.001$; all $df = 1$. No differences were evident between the sexes. Numbers above the bars represent sample sizes.

Results

Seasonal movement patterns of metamorphic adults

Metamorphic adult movement patterns varied as a function of season and pond permanence. Individuals migrated to both semipermanent and permanent ponds from terrestrial overwintering sites during the early June breeding season. Metamorphic adults were significantly more likely to enter permanent than semipermanent ponds at this time of year (138/227 (60.8%); $\chi^2 = 221.1$, $df = 1$, $p < 0.001$; data were pooled across sexes and years because no significant differences were evident within each variable). Metamorphic adults were never observed in vernal ponds in June.

In July, many individuals within the pond system remained in the aquatic habitat, rather than leaving to enter the terrestrial environment, and the proportion of individuals staying was significantly affected by pond hydroperiod (Fig. 1). In all years, a higher proportion of individuals remained in semipermanent ponds than in permanent ponds (Fig. 1). In contrast, hydroperiod did not affect the decision to leave the pond system or switch ponds. In each year, individuals leaving both permanent and semipermanent habitats were more likely to enter the terrestrial environment than another pond (comparison between pond types: 1990: $\chi^2 = 1.8$, $p = 0.18$; 1991: $\chi^2 = 0.25$, $p = 0.62$; 1992: $\chi^2 = 0.16$, $p = 0.69$; all $df = 1$). Of those individuals that did switch ponds, most entered a semipermanent habitat, irrespective of the hydroperiod of the source pond (pooled across years; from permanent ponds: 21/25 (84.0%); from semipermanent ponds: 7/9 (77.8%); $\chi^2 = 0.18$, $p = 0.67$, $df = 1$). During this period of movement in July and early August, many new individuals that were not present during the breeding season entered the pond system and congregated primarily in semipermanent ponds (117/142 (82.4%); $\chi^2 = 136.1$, $df = 1$, $p < 0.001$). The combined effect of these movements resulted in a significantly different distribution pattern between the two pond types in July and August compared with June ($\chi^2 = 66.1$, $df = 1$, $p < 0.001$).

These movement patterns produced a significant pond type by month interaction in metamorphic adult distribution (Fig. 2), which did not differ significantly across the 3 years of this

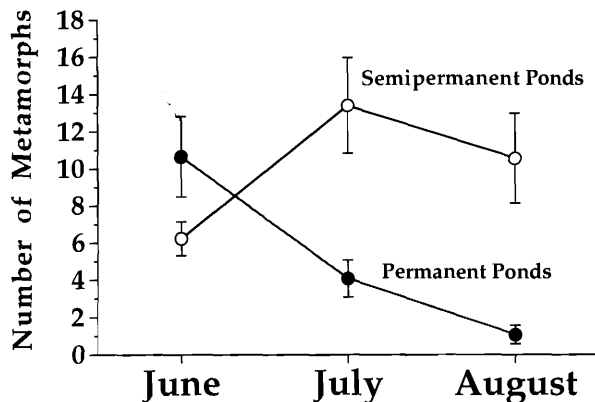


FIG. 2. Distribution of metamorphic adults in permanent (●) and semipermanent (○) ponds during the 3 months of salamander activity at Mexican Cut ($F_{[4,66]} = 5.78$, $p < 0.001$). Values are given as means ± 1 SE of four ponds over 3 years of data collection ($n = 12$ pond-years for each).

study ($p > 0.05$). One-way ANOVA revealed that semipermanent ponds did not differ significantly in the mean number of metamorphic adults between months ($F_{[2,33]} = 1.81$, $p > 0.17$). The number of metamorphic adults in permanent ponds, however, differed significantly among months, with decreasing numbers over time ($F_{[2,33]} = 19.2$, $p < 0.001$; Scheffé's post hoc test, all $p < 0.02$).

Annual differences in the timing of the metamorphic adult breeding migration to the pond system depended on the phenology of snowmelt and pond icemelt (see Wissinger and Whiteman 1992). In contrast, midseason movements were associated with rainfall after the breeding season. Emigration after breeding, immigration of nonbreeders, and interpond movements of metamorphic adults from permanent to nonpermanent ponds occurred in pulses during rainstorms in July. These movements were predictable, and on several occasions we observed metamorphic adults moving across land during July rainstorms.

Environmental correlates of movement patterns

Temperature

Temperature differences between pond types could underlie correlations between pond hydroperiod and salamander movement patterns. Based on a repeated-measures ANOVA, we found that midday water temperatures were significantly higher in permanent than in semipermanent ponds in both 1991 and 1992, regardless of date (1991: $F_{[1,209]} = 19.9$, $p < 0.0001$; 1992: $F_{[1,214]} = 71.8$, $p < 0.0001$). In both years, water temperature in permanent ponds averaged about 1°C higher than in semipermanent ones ($\bar{x} \pm SE$: 1991: 13.2 ± 0.3 vs. 12.3 ± 0.2 °C; 1992: 14.2 ± 0.2 vs. 12.9 ± 0.2 °C).

Pond permanence and conspecific density

Conspecific densities were pooled across years because no year effect was present ($p > 0.67$). Densities of potentially competing conspecifics (metamorphic adults, paedomorphic adults, or larvae > 70 mm) were significantly higher in permanent ponds than in semipermanent ponds ($\bar{x} \pm SE$: permanent ponds: $0.24 \pm 0.05/\text{m}^2$; semipermanent: $0.05 \pm 0.01/\text{m}^2$; $U = 39$, $Z = -2.49$, $p < 0.014$). Larvae contributed heavily to this difference, composing $68 \pm 10\%$ ($\bar{x} \pm SE$) of the density in permanent ponds compared with only $3 \pm 7\%$ in semipermanent ponds (pooled across years; $U = 16$, $Z = -3.61$,

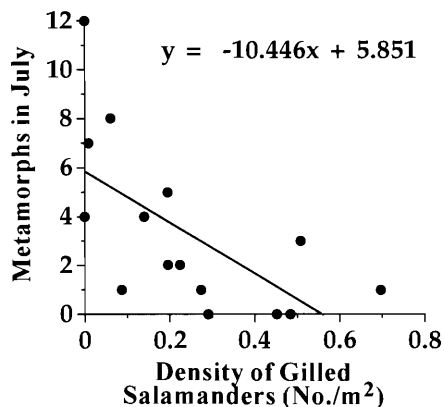


FIG. 3. Number of metamorphic adults present in permanent ponds as a function of the density of gilled salamanders (paedomorphic adults and large larvae) during July ($F_{[1,13]} = 8.46$, $p < 0.013$, $R^2 = 0.39$). Data are pooled across years.

$p < 0.001$). In addition, within permanent ponds the number of metamorphic adults in July was inversely related to the density of paedomorphic adults and larvae (Fig. 3).

Pond permanence and diet

Metamorphic adult diets in permanent ponds differed dramatically from those in nonpermanent (semipermanent and vernal) ponds. Metamorphic adults in permanent ponds fed mainly on benthic aquatic insects (caddisflies, hemipterans, beetles, chironomid midges, etc.) and terrestrial insects that fell on the surface, which together composed 85% of the calories in their diet (Fig. 4). In contrast, benthic and terrestrial insects composed only 8% of metamorphic adult calories in nonpermanent ponds and fairy shrimp (*Branchinecta coloradensis*) accounted for 91%. Smaller crustacean zooplankton (diaptomid copepods, daphnid and chydorid cladocerans) composed less than 5% of the calories in the diets of metamorphic adults in both pond types (Fig. 4).

In addition to interpond differences in the type of prey in metamorphic adult guts, there were significantly greater numbers, biomass, and calories of total prey per metamorphic adult in nonpermanent than in permanent ponds (Fig. 5). The stomach contents of metamorphic adults in nonpermanent ponds contained more than twice the calories (545 ± 76 ; $\bar{x} \pm SE$) of those in permanent ponds (175 ± 64 ; Fig. 5). In fact, the average caloric value (496 ± 78) of fairy shrimp in metamorphic adults from nonpermanent ponds was greater than that of all prey items in metamorphic adults in permanent ponds (175 ± 64 ; $U = 134.0$, $p = 0.014$). These results are due in part to the significantly greater mean size of metamorphic adults in nonpermanent (93.2 ± 1.9 mm; $\bar{x} \pm SE$) than permanent ponds (82.6 ± 3.2 mm; $\bar{x} \pm SE$; $t = 3.75$, $p = 0.008$, $df = 58$). However, when we accounted for this difference by calculating total numbers, biomass, and calories per millimetre SVL, we found that for a given body size, metamorphic adult guts in nonpermanent ponds still contained significantly greater numbers of prey, higher total biomass, and more calories than those in permanent ponds (numbers of prey: $U = 188.5$, $p = 0.017$; total biomass: $U = 181.0$, $p = 0.026$; calories: $U = 170.0$, $p = 0.015$).

Salamander movements and distributions of fairy shrimp

Given the importance of fairy shrimp as metamorphic adult prey in nonpermanent ponds, we compared the spatial and

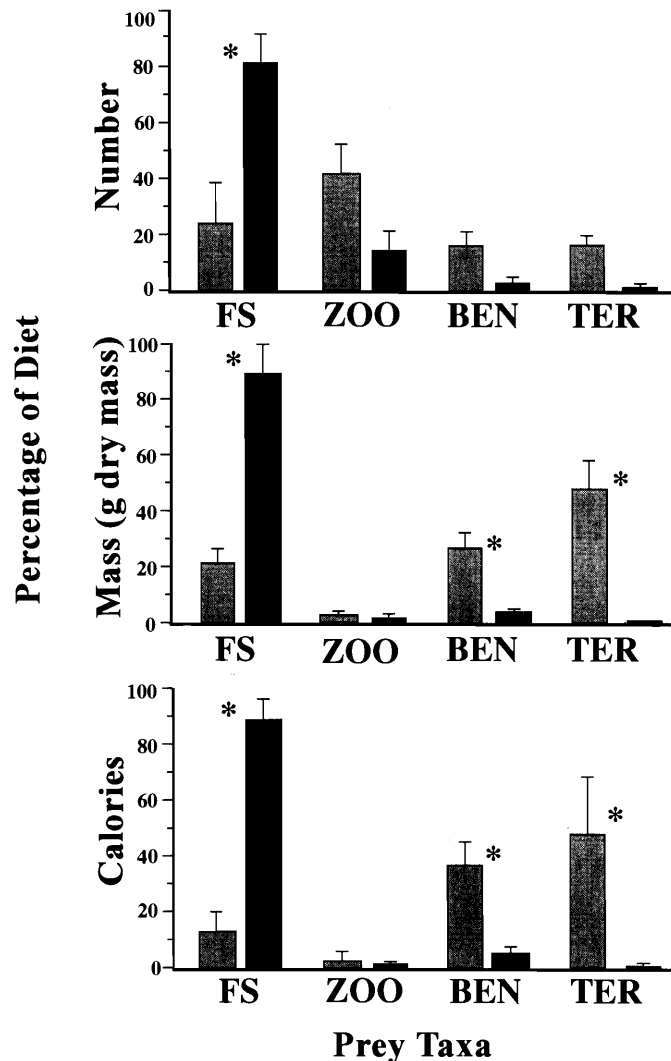


FIG. 4. Percent composition of metamorphic adult diets in permanent and nonpermanent ponds in terms of number, mass, and calories ($\bar{x} \pm 1$ SE). FS, fairy shrimp; ZOO, other zooplankton; BEN, benthic invertebrates; TER, terrestrial insects. Shaded bars signify permanent ponds and solid bars nonpermanent ponds. Comparisons across pond types for each taxonomic grouping were made with Mann-Whitney U tests. *, $p < 0.05$.

temporal occurrences of fairy shrimp to metamorphic adult movements. After the breeding season, metamorphic adults were more likely to migrate to ponds with fairy shrimp than to those without ($\chi^2 = 18.06$, $p = 0.0001$, $df = 1$), and all 18 ponds with fairy shrimp were visited by metamorphic adults during July. The timing of midseason movements to fairy shrimp ponds was related to rainfall (see above), but was always after fairy shrimp hatching. Semipermanent ponds always remained through the end of August (sometimes drying in September–October), yet the metamorphic adults that congregated in these ponds emigrated during the first 2 weeks of August. Thus, salamander emigration to terrestrial habitat was not forced by pond drying, but coincided with the decline and disappearance of fairy shrimp.

Discussion

Seasonal movements of metamorphic ambystomatids are usually associated with breeding opportunities in which sala-

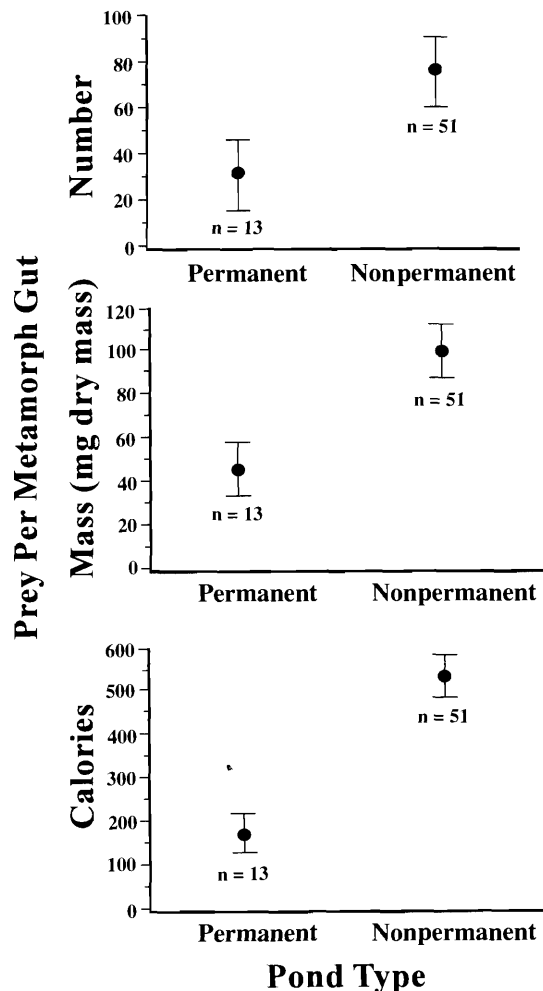


FIG. 5. Mean prey per metamorphic adult gut (± 1 SE) in permanent versus nonpermanent ponds, in terms of number, mass, and calories. Number: $U = 174.5$, $p = 0.009$; biomass: $U = 179.0$, $p = 0.02$; calories: $U = 165.0$, $p = 0.012$.

manders typically return to the terrestrial environment after reproducing (Husting 1965; Douglas 1979; Semlitsch and Pechmann 1985). This behavioral sequence is not surprising, since metamorphic adults are adapted for terrestrial predation and are poor aquatic foragers (Lauder and Shaffer 1986). In our study population, many metamorphic adults *remain* in the aquatic environment for weeks after breeding is completed (Fig. 1). One hypothesis to account for this behavior is that harsh abiotic terrestrial conditions make it advantageous to remain in the pond system. In addition to the overall aridity of the alpine climate at Mexican Cut, soils are thin to non-existent in this bedrock-dominated habitat (Wissinger and Whiteman 1992). This hypothesis is supported by observations of metamorphic adult philopatry at these and nearby ponds (Heath 1975; H.H. Whiteman and S.A. Wissinger, unpublished data), as well as observations of metamorphic tiger salamanders in other montane (J.P. Collins, personal communication) and desert (Webb and Roueche 1971) habitats. A second, non-mutually exclusive hypothesis for pond fidelity is the presence of a rich aquatic food resource, which may be more energetically valuable than terrestrial prey, even after accounting for decreased foraging success. The Mexican Cut ponds support a diverse assemblage of zooplankton and

invertebrates (S.A. Wissinger, W.S. Brown, and A.J. Bohonak, unpublished data) that may be more productive than the surrounding subalpine forest in terms of suitable prey. Both hypotheses suggest that remaining within the aquatic habitat can be viewed as an adaptation to avoid harsh terrestrial environments.

Metamorphic salamanders at Mexican Cut not only remain in the aquatic environment later than other ambystomatids, but selectively aggregate in nonpermanent ponds as the summer progresses (e.g., Fig. 2). Individuals in permanent ponds are more likely to enter the terrestrial environment after breeding, whereas individuals in semipermanent ponds are more likely to remain in their respective ponds. Some individuals leaving permanent ponds move to nonpermanent ones; in addition, a group of nonbreeding metamorphic adults appear after summer rains in July, and tend to congregate in nonpermanent ponds.

This relationship between metamorphic adult distribution and pond hydroperiod is correlated with the presence of fairy shrimp. Fairy shrimp constitute 91% of the calories that metamorphic adults consume in nonpermanent ponds, and alone exceed the entire caloric value of metamorphic adult stomach contents in permanent ponds (Figs. 4, 5). All ponds with fairy shrimp, irrespective of hydroperiod, were visited by metamorphic adults in July. Metamorphic adult movements also appear to be temporally related to fairy shrimp phenologies, i.e., they tend to move into ponds with fairy shrimp when shrimp abundance is high, and leave as shrimp decline prior to pond drying. Finally, metamorphic adults are more successful at capturing fairy shrimp than other common aquatic prey (caddisfly and mosquito larvae, midge pupae, and copepods; H.H. Whiteman, S.A. Wissinger, and W.S. Brown, submitted for publication). These results support the hypothesis that metamorphic adults remain in the aquatic environment and congregate in nonpermanent ponds at Mexican Cut to obtain easy to catch, energetically valuable prey.

Fairy shrimp distribution is not the only covariate of pond permanence that might explain salamander movement patterns. For example, temperature varies with hydroperiod and is positively correlated with growth rate in amphibians (e.g., Wilbur and Collins 1973; Smith-Gill and Berven 1979). Thus, metamorphic adults would be predicted to remain in the warmest ponds. We found that semipermanent ponds were significantly colder than permanent ones (albeit by only 1°C), exactly the opposite of the prediction. In addition, the preferred temperature range of metamorphic salamanders (approximately 18–24°C; Heath 1975) is higher than maximum July temperatures in the semipermanent ponds at our study site (15–16°C). Thus, the migration of metamorphic adults into semipermanent ponds cannot be explained by interpond temperature differences.

High densities of conspecifics could decrease the growth of metamorphic adults through resource limitation (Wilbur and Collins 1973) and influence where individuals congregate to feed. Metamorphic adults are predicted to prefer ponds with the lowest densities of conspecifics (other metamorphic adults, paedomorphic adults, and larvae) of similar size. Movements of metamorphic adults correspond to this prediction: semipermanent ponds have significantly lower densities of potential competitors, and metamorphic adults that are found in permanent ponds are more abundant in ponds with low densities of larvae and paedomorphic adults (Fig. 3). High densities of these other life stages may exclude metamorphic adults from foraging opportunities and lead to decreased growth rela-

tive to that of metamorphic adults in ponds with fewer competitors. This is especially true in view of the fact that gilled salamanders are more successful at foraging in aquatic habitats than metamorphic individuals (Lauder and Shaffer 1986) and thus should be stronger exploitative competitors. Density-dependent effects are common in larval amphibians (e.g., Wilbur and Collins 1973; Wilbur 1976; Semlitsch 1987; Van Buskirk and Smith 1991) and should be present when metamorphic adults compete with larvae and paedomorphic adults for shared resources.

The presence of fairy shrimp and the absence of potential conspecific competitors are confounded in this system, and their relative importance to the pond-specific nature of foraging by metamorphic adults cannot be separated. In fact, previous studies have suggested that the abundance of fairy shrimp in nonpermanent habitats at Mexican Cut is related to the absence of salamander larvae and paedomorphic adults, which exclude them from permanent ponds (Dodson 1970; Sprules 1972). Our data support this hypothesis, because salamander densities are significantly lower in semipermanent ponds. Metamorphic adults have decreased foraging success on fairy shrimp relative to paedomorphic adults (H.H. Whiteman, S.A. Wissinger, and W.S. Brown, submitted for publication), suggesting that nonpermanent ponds also provide a refuge in terms of predator efficiency. However, this refuge from salamander predation is incomplete, since fairy shrimp make up a large proportion of the diet of metamorphic adults (Fig. 4). This observation leaves open the possibility that fairy shrimp distributions may also be related to some other direct or indirect effect of pond permanence (Pfennig 1990; A.J. Bohonak, S.A. Wissinger, and W.S. Brown, unpublished data).

Given the obvious benefits of entering nonpermanent ponds, or even permanent ponds with few competitors, why do many metamorphic adults leave the pond system altogether? This question is complicated by the observation that individuals breeding in permanent ponds are more likely to leave the pond system and enter the terrestrial environment than those breeding in semipermanent ponds. This suggests that the terrestrial environment may be better suited for metamorphic adult growth than some permanent ponds, or that some metamorphic adults are better at terrestrial feeding than others.

Metamorphic adults that remain within the pond system congregate in ponds that maximize foraging productivity, and increase their calorie consumption relative to individuals that congregate in less productive ponds. An increase in calories should lead to higher growth rates and a larger body size. Because body size is positively correlated with fecundity and survival in amphibians (Kaplan and Salthe 1979; Wilbur 1980), metamorphic adults that feed in nonpermanent ponds should be increasing their fitness relative to individuals that remain under suboptimal conditions of high densities and low prey availability. If individuals show clear patterns of pond usage over several years (i.e., some individuals typically inhabit nonpermanent ponds, some typically inhabit permanent ponds, and some usually enter the terrestrial environment), metamorphic adults utilizing nonpermanent ponds may have increased fitness relative to the other alternatives. Because metamorphic adults in this population do not return to the pond system every year, our current data analysis from three field seasons is not sufficient to test this hypothesis.

Although the payoff to individuals that remain in the aquatic versus the terrestrial environments remains to be understood, these results and others (e.g., Partridge 1976; Werner et al.

1983; Holomuzki 1986) support the hypothesis that animals utilize different habitats according to potential fitness gains. Clarifying the role of habitat choice is clearly important for understanding animal adaptations to a variety of ecological circumstances, including harsh environments. Our results suggest that metamorphic tiger salamanders can respond adaptively to such harsh environments by delaying dispersal to the terrestrial environment to which they are adapted for feeding, and instead foraging in the resource-rich aquatic environment.

Acknowledgements

We thank W. Brown, C. Cowan, G. Blake, K. Buhn, S. Horn, J. Jannot, G. McCrabb, J. McGrady, R. Moorman, H. Mun, G. Rouse, G. Sparks, T. Ticknor, D. Weigel, and R. Willey for field and (or) laboratory assistance. We are grateful to the Rocky Mountain Biological Laboratory and The Nature Conservancy for access to the Mexican Cut Nature Preserve and especially to S. Lohr, b. barr, A. Carpenter, and L. Swift for facilitating this work. An earlier version of this manuscript benefited from the comments of R. Howard, J. Collins, R. Semlitsch, P. Carter, J. Lucas, P. Waser, N. Buschhaus, W. Brown, J. Young, and two anonymous reviewers. H.H.W. was supported by grants from the Theodore Roosevelt Fund (American Museum of Natural History), the Helen Gaige Fund (American Society of Ichthyologists and Herpetologists), the Lee R.G. Snyder Fund (Rocky Mountain Biological Laboratory), a Sigma Xi grant-in-aid, the Colorado Division of Wildlife, a National Science Foundation Dissertation Improvement Grant (DEB-91-22981), two David Ross Summer Fellowships (Purdue University), and a Purdue Research Foundation Fellowship. S.A.W. was supported by The Nature Conservancy (Colorado Field Office), Howard Hughes and Faculty Department Grants from Allegheny College, and a Presidential Young Investigator Award from the National Science Foundation (BSR-89-58253). A.J.B. was supported by grants from Sigma Xi (Cornell and National chapters), the Theodore Roosevelt Fund (American Museum of Natural History), the Lee R.G. Snyder Fund, The Nature Conservancy (Colorado Field Office), an Edna Bailey Sussman Environmental Internship, and a U.S. Department of Agriculture Hatch Grant to N.G. Hairston, Jr. Manuscript preparation was supported in part by contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

- Alcock, J. 1989. Animal behavior: an evolutionary approach. Sinauer Associates, Inc., Sunderland, Mass.
- Baker, R.R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London.
- Beebe, T.J.C., and Griffin, J.R. 1977. A preliminary investigation into natterjack toad (*Bufo clamita*) breeding site characteristics in Great Britain. *J. Zool.* (1965–1984), **181**: 341–350.
- Behler, J.L., and King, F.W. 1979. The Audubon Society field guide to North American reptiles and amphibians. Alfred A. Knopf, New York.
- Bradbury, J.W., Gibson, R.M., McCarthy, C.E., and Vehrencamp, S.L. 1989. Dispersion of displaying male sage grouse. II. The role of female dispersion. *Behav. Ecol. Sociobiol.* **24**: 15–24.
- Brown, J.L. 1975. The evolution of behavior. Norton Publishers, New York.
- Carr, A. 1967. Adaptive aspects of the scheduled travel of *Chelonia*. In *Animal orientation and navigation*. Edited by R.M. Storm. Oregon State University Press, Corvallis. pp. 35–55.
- Clark, K.L. 1986. Distributions of anuran populations in central

- Ontario relative to habitat acidity. *Water Air Soil Pollut.* **30**: 727–734.
- Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *Am. Nat.* **126**: 451–474.
- Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Verh. Int. Ver. Limnol.* **18**: 1–158.
- Dingle, H. 1978. Evolution of insect migration and diapause. Springer-Verlag, New York.
- Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.* **15**: 131–137.
- Douglas, M.E. 1979. Migration and sexual selection in *Ambystoma jeffersonianum*. *Can. J. Zool.* **57**: 2303–2310.
- Duellman, W.E., and Trueb, L. 1986. *Biology of amphibians*. McGraw-Hill, New York.
- Gross, M.R. 1987. Evolution of diadromy in fishes. *Am. Fish. Soc. Symp.* No. 1. pp. 14–25.
- Hairston, N.G. 1980. Evolution under interspecific competition: field experiments on terrestrial salamanders. *Evolution*, **34**: 409–420.
- Hairston, N.G., Sr. 1986. Species packing in *Desmognathus* salamanders: experimental demonstration of predation and competition. *Am. Nat.* **127**: 266–291.
- Hairston, N.G., Sr. 1987. Community ecology and salamander guilds. Cambridge University Press, Cambridge.
- Heath, A.G. 1975. Behavioral thermoregulation in high altitude tiger salamanders, *Ambystoma tigrinum*. *Herpetologica*, **31**: 84–93.
- Holomuzki, J.R. 1986. Effect of microhabitat on fitness components of larval tiger salamanders, *Ambystoma tigrinum nebulosum*. *Oecologia*, **71**: 142–148.
- Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. *Copeia*, 1965: 352–362.
- Kaplan, R.H., and Salthe, S.N. 1979. The allometry of reproduction: an empirical view in salamanders. *Am. Nat.* **113**: 671–689.
- Lauder, G.V., and Shaffer, H.B. 1986. Functional design of the feeding mechanism in lower vertebrates: unidirectional and bidirectional flow systems in the tiger salamander. *Zool. J. Linn. Soc.* **88**: 277–290.
- Legler, J.M., and Sullivan, L.J. 1979. The application of stomach flushing to lizards and anurans. *Herpetologica*, **35**: 107–110.
- McClanahan, L.L. 1967. Adaptations of the spadefoot toad, *Scaphiopus couchii*, to desert environments. *Comp. Biochem. Physiol.* **20**: 73–99.
- McClanahan, L.L., Shoemaker, V.H., and Ruibal, R. 1976. Structure and function of the cocoon of a ceratophryd frog. *Copeia*, 1976: 179–185.
- Merchant, H. 1972. Estimated population size and home range of the salamanders *Plethodon jordani* and *Plethodon glutinosus*. *J. Wash. Acad. Sci.* **62**: 248–257.
- Moore, J., Simberloff, D., and Freehling, M. 1988. Relationships between bobwhite quail social-group size and intestinal helminth parasitism. *Am. Nat.* **131**: 22–32.
- Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecol. Monogr.* **53**: 119–138.
- Nishikawa, K.C., and Service, P.M. 1988. A fluorescent marking technique for individual recognition of salamanders. *J. Herpetol.* **22**: 351–353.
- Norris, K.S. 1967. Some observations on the migration and orientation of marine mammals. In *Animal orientation and navigation*. Edited by R.M. Storm. Oregon State University Press, Corvallis. pp. 101–125.
- Partridge, L. 1976. Field and laboratory observations on the foraging and feeding techniques of blue tits (*Parus caeruleus*) and coal tits (*Parus ater*) in relation to their habitats. *Anim. Behav.* **24**: 534–544.
- Pfennig, D.W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia*, **85**: 101–107.
- Rabenold, K.N., and Rabenold, P.P. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of dark-eyed juncos in the southern Appalachians. *Auk*, **102**: 805–819.
- Rabenold, P.P. 1987. Recruitment to food in black cultures: evidence for following from communal roosts. *Anim. Behav.* **35**: 1775–1785.
- Rankin, M.A. 1985. Migration: mechanisms and adaptive significance. *Univ. Tex. Contrib. Mar. Sci. Suppl.* No. 27.
- Reno, H.W., Gehlbach, F.R., and Turner, R.A. 1972. Skin and aestivational cocoon of the aquatic amphibian, *Siren intermedia* Le Conte. *Copeia*, 1972: 625–631.
- Ruibal, R., Tevis, L., Jr., and Roig, V. 1969. The terrestrial ecology of the spadefoot toad *Scaphiopus hammondi*. *Copeia*, 1969: 571–584.
- Schaller, G.B. 1972. *The Serengeti lion*. University of Chicago Press, Chicago.
- Scheffé, H. 1959. *The analysis of variance*. Wiley Press, New York.
- Seale, D., and Boraas, M. 1974. A permanent mark for amphibian larvae. *Herpetologica*, **30**: 160–162.
- Semlitsch, R.D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). *Can. J. Zool.* **59**: 315–322.
- Semlitsch, R.D. 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. *Copeia*, 1985: 477–489.
- Semlitsch, R.D. 1987. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. *Ecology*, **68**: 1003–1008.
- Semlitsch, R.D., and Pechmann, J.H.K. 1985. Diel pattern of migratory activity for several species of pond-breeding salamanders. *Copeia*, 1985: 86–91.
- Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1993. Phenotypic variation in the arrival time of salamanders: individual repeatability and environmental influences. *J. Anim. Ecol.* **62**: 334–340.
- Sexton, O.J., and Bizer, J.R. 1978. Life history patterns of *Ambystoma tigrinum* in montane Colorado. *Am. Midl. Nat.* **99**: 101–118.
- Smith-Gill, S.J., and Berven, K.A. 1979. Predicting amphibian metamorphosis. *Am. Nat.* **113**: 563–585.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry*. W.H. Freeman & Co., San Francisco.
- Sprules, W.G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology*, **53**: 375–386.
- Sutherst, R.W., Floyd, R.B., Bourne, A.S., and Dallwitz, M.J. 1986. Cattle grazing behavior regulates tick populations. *Experientia (Basel)*, **42**: 194–196.
- Van Buskirk, J., and Smith, D.C. 1991. Density-dependent population regulation in a salamander. *Ecology*, **72**: 1747–1756.
- Waser, P.M. 1985. Does competition drive dispersal? *Ecology*, **66**: 1170–1175.
- Webb, R.G., and Roueche, W.L. 1971. Life history aspects of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan desert. *Great Basin Nat.* **31**: 193–212.
- Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**: 1540–1548.
- Whiteman, H.H. 1994. Evolution of facultative paedomorphosis in salamanders. *Q. Rev. Biol.* **69**: 205–221.
- Wiedenmann, R.N., and Rabenold, K.N. 1987. The effects of social dominance between two subspecies of dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.* **35**: 856–864.
- Wilbur, H.M. 1976. Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. *Ecology*, **57**: 1289–1296.
- Wilbur, H.M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.* **11**: 67–93.
- Wilbur, H.M. 1984. Complex life cycles and community organiza-

- tion in amphibians. *In* A new ecology: novel approaches to interactive systems. *Edited by* P.W. Price, C.N. Slobodchikoff, and W.S. Gaud. John Wiley and Sons, New York. pp. 195–224.
- Wilbur, H.M., and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. *Science* (Washington, D.C.), **182**: 1305–1314.
- Wissinger, S.A., and Whiteman, H.H. 1992. Fluctuation in a Rocky Mountain population of salamanders: anthropogenic acidification or natural variation? *J. Herpetol.* **26**: 377–391.
- Zerba, K.E. 1989. Individual variation in diet of larval tiger salamanders (*Ambystoma tigrinum nebulosum*) in Arizona. Ph.D. dissertation, Arizona State University, Tempe.