



University of Richmond
UR Scholarship Repository

Biology Faculty Publications

Biology

2-2009


Sex- and Context-Dependent Migration in a Pond-Breeding Amphibian

Kristine L. Grayson

University of Richmond, kgrayson@richmond.edu

Henry M. Wilbur

Follow this and additional works at: <http://scholarship.richmond.edu/biology-faculty-publications>

 Part of the [Population Biology Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

Recommended Citation

Grayson, Kristine L., and Henry M. Wilbur. "Sex- and Context-Dependent Migration in a Pond-Breeding Amphibian." *Ecology* 90, no. 2 (February 2009): 306-12. doi:10.1890/08-0935.1.

This Article is brought to you for free and open access by the Biology at UR Scholarship Repository. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of UR Scholarship Repository. For more information, please contact scholarshiprepository@richmond.edu.

Sex- and context-dependent migration in a pond-breeding amphibian

KRISTINE L. GRAYSON¹ AND HENRY M. WILBUR

Department of Biology, University of Virginia, Charlottesville, Virginia 22904 USA

Abstract. Partial migration, variation in the percentage of a population that completes a migration, can be influenced by the local environment and condition of an individual. We examined the direct and interacting effects of habitat quality and gender on migration decision by manipulating population density and sex ratio in a factorial field experiment using aquatic enclosures. In partially migrating red-spotted newts (*Notophthalmus viridescens*), we measured the percentage of newts migrating to the terrestrial habitat vs. overwintering as pond residents. Density significantly influenced migration, with 63% of newts migrating from high-density enclosures compared to 39% from low-density enclosures. Newts also migrated earlier from high-density enclosures, but no significant effects of the sex ratio treatment were found. Females migrated earlier than males, and 64% more females developed the migrant phenotype, suggesting important sex-based trade-offs of migration. No differences were found between migrants and residents in initial body size, counter to our prediction that larger individuals would be more likely to remain pond residents. This study demonstrates experimentally that migration can be a plastic response influenced by both local density and gender.

Key words: density dependence; migration phenology; *Notophthalmus viridescens*; partial migration; phenotypic plasticity; population sex ratio; red-spotted newt; reversible phenotypic polymorphism.

Reports

INTRODUCTION

Many migratory species have intrapopulation variation in migration distance or timing (differential migration), while others vary in the portion of the population that migrates (partial migration; reviewed by Lundberg 1988). Studies testing the mechanisms that affect partial migration are important for understanding the evolution of migration and adaptations to environmental uncertainty. This study tests the influence of the environment and the role of individual state on partial migration in a species of pond-breeding amphibian, the red-spotted newt (*Notophthalmus viridescens*).

Seasonal migrations of sexually mature, pond-breeding amphibians from terrestrial habitats to aquatic breeding sites typically occur in the spring (reviewed by Russell et al. 2005). While all individuals of most species, such as *Ambystoma* spp. (Church et al. 2007), exit the aquatic habitat after the breeding season and return to the terrestrial habitat (complete migration), individual *N. viridescens* can either migrate or remain resident in the pond for the winter (Sever 2006). Although partial migration is common in fish, birds, mammals, and insects (Dingle 1980, Swingland 1983), few examples in amphibians have been documented. Dispersal occurs during the juvenile stage in this species (the red eft stage) and the vast majority of migratory adults return to the same breeding ponds (Gill 1978). Although migratory behavior in some species is herita-

ble (Berthold and Pulido 1994), genotypes in other species express phenotypic plasticity (Harris et al. 1990, Olsson et al. 2006). Laboratory studies showing that the migrating phenotype and corresponding physiological adaptations to a terrestrial environment can be induced in *N. viridescens* (e.g., Walters and Greenwald 1977), and mark-recapture field data showing that individuals can change migration tactic from year to year (K. Grayson, unpublished data), indicate a high degree of plasticity in this species.

In species with migratory plasticity, the decision to remain a resident or to migrate is often influenced by environmental factors. The general prediction for partially migrating populations is that under unfavorable conditions an increased portion of the population will migrate (Cohen 1967). Environmental conditions may be poor for a variety of reasons, due to abiotic factors, such as pond-drying or anoxia, or due to biotic factors, such as reduced food availability or competition, that typically vary with population density. Recent transplant studies in salmonid fish have shown that individuals in high-density populations favor migration, whereas those in low-density populations favor residency (Olsson et al. 2006). Facultative paedomorphic salamanders, such as *Ambystoma talpoideum*, are another example of a migration polyphenism that is highly influenced by population density or drying of the pond (e.g., Semlitsch et al. 1990).

In addition to density, social environment may contribute to the quality of the resident habitat. An asymmetry between the sexes in competitive ability for resources has been proposed as a mechanism for increasing migration tendency in the less dominant sex

Manuscript received 20 May 2008; revised 6 October 2008; accepted 14 October 2008. Corresponding Editor: D. K. Skelly.

¹ E-mail: kgrayson@email.virginia.edu



PLATE 1. (Left) The aquatic phenotype and (right) the terrestrial phenotype of adult red-spotted newts (*Notophthalmus viridescens*). Photo credits: Pierson Hill (left) and K. L. Grayson (right).

(Ketterson and Nolan 1976). Sex-based differences in migration are also predicted by the arrival time hypothesis, in which the sex competing more intensely for mates benefits from being resident at the breeding site (Ketterson and Nolan 1976, Alerstam and Hedenstrom 1998). These hypotheses predict for this study that female newts should be more likely than males to migrate. A less tested hypothesis is whether sex ratio influences migration. For species with competitive mating systems, mating harassment by males can be costly for both sexes (Rowe et al. 1994). In *N. viridescens*, males engage females in prolonged bouts of amplexus aimed at increasing female receptiveness (Massey 1988). Multiple males often attempt to engage a single female in courtship and wrestle amplexed pairs, trying to dislodge the first courting male; this competition has been shown to be more intense in higher male-biased sex ratios (Verrell 1983). In the smooth newt, *Triturus vulgaris*, female newts have been shown to be averse to competitive sexual encounters involving multiple males (Verrell 1984). Consequently, a male-biased environment could increase the tendency of females to migrate in order to avoid costs of male harassment (Baguette et al. 1998). Additionally, male newts have been shown to spend more time in courtship under increasing male competition, which may incur energetic costs (Verrell 1983, 1985). Male newts could also be expected to increase migration from a male-biased environment due to the lack of females and increased competition (Nummelin 1988).

This study experimentally tests both the independent and interactive effects of habitat quality, social environment, and gender on partial migration in the red-spotted newt. Unlike many migrating vertebrates, *N. viridescens* is amenable to field experiments. Under high density and a male-biased sex ratio, we expected a greater portion of newts in each enclosure to migrate as opposed to remaining resident in the pond. Additionally, we tested for state-based differences in body size and sex between

migrants and residents, expecting that more females and smaller-sized individuals are likely to migrate.

MATERIALS AND METHODS

Study species

At the end of the breeding season at the study site, in late summer and early fall, adult red-spotted newts can either migrate back to the terrestrial habitat or remain resident in the breeding pond for the winter. *Notophthalmus viridescens* is well known for its variation in life cycle and migration pattern (ranging from completely migratory to partially migratory to permanently aquatic) across its wide range (reviewed by Sever 2006). In many partially migrating species, migrants utilize an alternate phenotype involving morphological and physiological changes to increase survival during the journey or in the alternate habitat (Olsson et al. 2006). *N. viridescens* individuals that overwinter in the pond retain the aquatic phenotype that all individuals have during the breeding season: a large dorsal tail fin and smooth, mucous-covered skin. Migrants develop a distinct alternate terrestrial phenotype with a reduced tail fin and darker granular skin more resistant to desiccation (Walters and Greenwald 1977, Davis and Grayson 2007; see Plate 1). The discrete aquatic and terrestrial phenotypes are reversible, as migrants transform back to the aquatic phenotype when returning to the same breeding pond in the spring.

Study site

The experiment was conducted in Station Pond at Mountain Lake Biological Station, Giles County, Virginia, USA (elevation 1160 m). Station Pond is a 0.65-ha, stream-fed, fishless permanent pond. It was constructed in 1965 and supports a large population of *N. viridescens* (estimated population 7600–12 700, sampled using a robust mark–recapture design; K. Grayson, unpublished data). Thirty-six pond enclosures consisting

of a wooden frame with polyethylene netting (0.32-cm mesh, XV-1348, Industrial Netting, Minneapolis, Minnesota, USA) were placed around Station Pond on 14 April 2007 (length = 3.66 m, width = 1.22 m, height of end in pond = 1.22 m, and height of end on bank = 0.61 m; Appendix A). The surface area of water within each enclosure was $3.83 \pm 0.04 \text{ m}^2$, mean \pm SE (volume = $2.23 \pm 0.02 \text{ m}^3$, mean \pm SE) with $52.0 \pm 3.00 \text{ cm}$ of terrestrial area exposed on the shallow end; the variation in area was due to small differences in slope around the pond. Enclosures were divided into three spatial blocks to account for this variation as well as other potential environmental differences around the pond. On 16 April, 120 g of dry leaf litter from the surrounding forest was randomly added to each enclosure as a substrate. Silt and detritus also drifted through the mesh to cover the plastic bottom within a week.

Experimental design

We used a 2×3 factorial design in which we manipulated the population density (low = 12, medium = 24, high = 36 total newts) and sex ratio (2:1 or 1:2 males: females) within each enclosure. The low-density treatment most closely represented the density estimated for the whole pond (1.5–2.6 newts/m²; K. Grayson, unpublished data). Station pond, however, is over 5 m deep; much higher newt densities, similar to our medium-density treatment, are found in shallower habitat, where our enclosures were located (6.0–8.8 newts/m²; Kraus 2006; personal observations). The estimated sex ratio of Station Pond, 2.4–2.8 males: 1 female (K. Grayson, unpublished data), is similar to the male-biased sex ratio treatment used in this experiment and is consistent with other estimates in natural populations (Gill 1978, Massey 1988).

The treatments were assigned to enclosures using a randomized complete-block design with unequal replication of the density treatments (replicates per sex ratio treatment: high density = 3, medium density = 6, and low density = 9, for a total of 36 enclosures with 720 newts). We increased the number of replicates for low-density treatments so that the total number of adult newts in each density treatment was similar. This was done to increase the precision of estimates (survival and percentage migrating) for enclosures that were calculated from a lower number of individuals.

All newts used in the enclosures were collected from Station Pond and were individually photographed, weighed, and randomly assigned to enclosures on 23 April (males) and 25 April (females). Enclosures were checked daily from 23 April to 15 September between 07:00 and 09:00 hours EDT (Eastern Daylight Time) and after rain showers. Newts found out of the water attempting to leave an enclosure were confirmed as migratory due to behavior (out of the water, pacing at the terrestrial end of the enclosure) and transition to the terrestrial phenotype (distinct dry, granular skin and reduced tail fin; Walters and Greenwald 1977). Migrat-

ing individuals were photographed, weighed, and released in the surrounding forest. From 9 to 14 September, funnel traps were used to capture newts remaining in the water. On 15 September, the enclosures were removed from the pond and emptied. The termination date was based on data from prototype enclosures in the previous year where the last migrant was found on 30 August, and a lack of migrants found after rains in September (92% of migrants found in this study were collected before 15 August). All newts remaining in enclosures were collected, photographed, and released back into Station Pond. One enclosure was damaged during removal and the remaining newts escaped (treatment = medium density, male-biased). Seven of eight females were captured from this enclosure prior to removal and therefore the data for females were still used in all analyses. Data from captured male newts were still used for analyses based on individual data (migration date), but not for analyses based on enclosure-level data (survival and percentage migrating).

Data analysis

Photographs of the dorsal pattern of red spots were used to identify individuals within an enclosure. These unique spot patterns are stable over the adult life span and have been used in several studies as a marking system in this species (e.g., Gill 1978); see Appendix B. All individuals captured were successfully matched to their initial photographs, with the exception of one enclosure in which a hole resulted in stocked newts escaping and newts from the outside pond entering (treatment = medium density, female-biased). This enclosure was excluded from all analyses.

Newt survival was evaluated by comparing the number of newts recovered to the initial number of newts of each sex placed in each enclosure. Migration decision was evaluated by comparing the number of newts migrating to the total number of newts recovered for each sex in each enclosure. We calculated the percentage migrating and percentage remaining resident from the final number found alive, because newts that did not survive could not be assigned to either outcome. However, calculating migration outcome from initial density had no impact on the analysis due to the high proportion of newts surviving (see *Results*; average difference in percentage migrating when calculated from initial density, as opposed to the final number found alive was $2.44\% \pm 0.37\%$, mean \pm SE, maximum difference = 4.04%). The portion of newts surviving and the portion migrating were analyzed using a generalized linear mixed-model with a binomial distribution of errors (Proc GLIMMIX, SAS, version 9.1, SAS Institute, Cary, North Carolina, USA). The three-way model included density treatment, sex ratio treatment, and newt gender as fixed effects and block as a random effect.

We also tested the effect of the treatments and the difference between the sexes in migration timing.

TABLE 1. Results from three-way generalized linear mixed-model analyses testing the effect of density (high, medium, or low), sex ratio (male- or female-biased), and gender on survival, migration outcome, and migration date of red-spotted newts (*Notophthalmus viridescens*).

Source	Survival			Migration outcome			Date of migration		
	df	F	P	df	F	P	df	F	P
Density	2, 53	0.19	0.83	2, 53	10.75	<0.001	2, 49	6.10	0.004
Sex ratio	1, 53	2.78	0.10	1, 53	0.31	0.58	1, 49	3.12	0.08
Gender	1, 53	0.14	0.71	1, 53	26.13	<0.001	1, 49	9.57	0.003
Density × sex ratio	2, 53	0.35	0.71	2, 53	0.57	0.57	2, 49	0.03	0.97
Density × gender	2, 53	0.46	0.63	2, 53	1.75	0.18	2, 49	1.05	0.36
Sex ratio × gender	1, 53	0.08	0.78	1, 53	1.54	0.22	1, 49	1.30	0.26
Density × sex ratio × gender	2, 53	0.48	0.62	2, 53	1.08	0.35	2, 49	0.67	0.51

Notes: Spatial block was a random factor for all analyses. The variance among enclosures was also included as a random factor for the analysis of migration date. N = female data from 34 enclosures and male data from 33 enclosures for survival and migration outcome (see *Materials and Methods* and *Results* for enclosures excluded from the original 36). N = female data from 33 enclosures and male data from 30 enclosures for date of migration (in five cases an enclosure had no migrants of one sex). All analyses were conducted using the GLIMMIX procedure in SAS, version 9.1.

Migration date was calculated as the number of days since the start of the experiment when an individual was found attempting to migrate. The number of days was log transformed to achieve normality. We used a generalized linear mixed model with a normal distribution of errors with the same fixed and random effects as before. In addition, to account for the common environment of individuals in the same enclosure, the variance among enclosures was used as the error term; this is tantamount to analyzing enclosure means.

Lastly, we tested if body size or mass influenced the tendency to migrate. Body size was measured as snout-vent length from newt photographs, as in Davis and Grayson (2007), and mass was measured to the nearest 0.01 g. Initial body condition of individuals before being assigned to enclosures was calculated as the residuals from a regression of body mass and body size (snout-vent length; Schulte-Hostedde et al. 2005). Using logistic regression, these residuals were compared between newts that migrated and those that remained in the pond. Initial condition was used because final body mass of migrants and residents could not be compared: the transition to the migrating phenotype involves unknown changes in water balance (Walters and Greenwald 1977).

RESULTS

After 4.5 months in the enclosures, 93.1% of newts were recovered alive. Survival within enclosures was $94.9\% \pm 0.98\%$ (mean \pm SE), with the exception of one enclosure where recovery was 41.7% (treatment = medium density, male-biased). It is unknown whether recovery in this enclosure was low due to mortality or escape, and this clear outlier was excluded from all analyses. Survival was not significantly different between treatments or genders (Table 1).

The percentage of migrants per enclosure was significantly affected by density ($P < 0.001$, Table 1), with 62.4% more migration occurring from high-density than low-density enclosures. Significant differences between the sexes were found as well ($P < 0.001$), with an average of $60.3\% \pm 3.6\%$ (mean \pm SE) of females

migrating from an enclosure compared to $36.7\% \pm 3.9\%$ of males (Fig. 1A). Similarly, migration timing was significantly affected by density ($P = 0.004$) and sex ($P = 0.003$). Although migration date ranged from 37 to 134 days since the start of the experiment (1 June–6

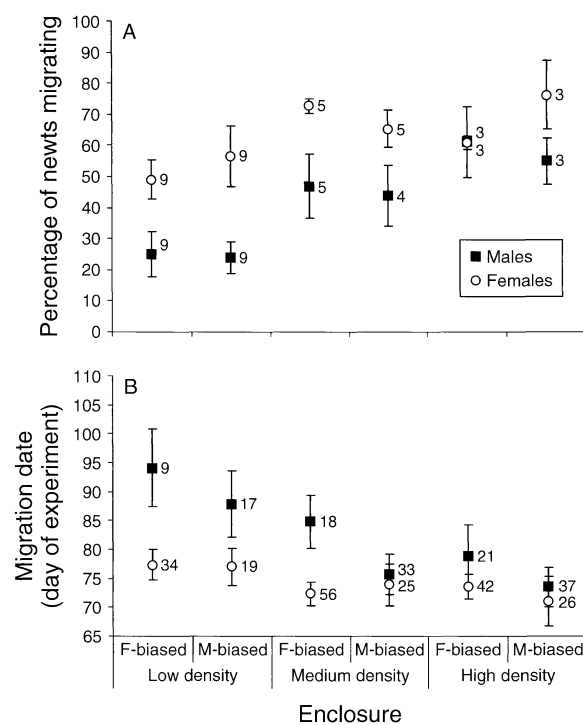


FIG. 1. (A) Percentage (mean \pm SE) of male and female red-spotted newts (*Notophthalmus viridescens*) migrating from enclosures of different density and sex ratio bias (F, female-biased; M, male-biased). (B) Migration date (mean \pm SE) of individual *N. viridescens* males and females (the number of days since the start of the experiment, i.e., 85 days = 19 July). The number of enclosures is indicated for each point in panel (A); total migrants = 202 females and 135 males. Males and females were in the same enclosures (i.e., there were nine female-biased low-density enclosures total, with data on males and females collected for each enclosure). The number of migrating individuals is indicated for each point in panel (B).

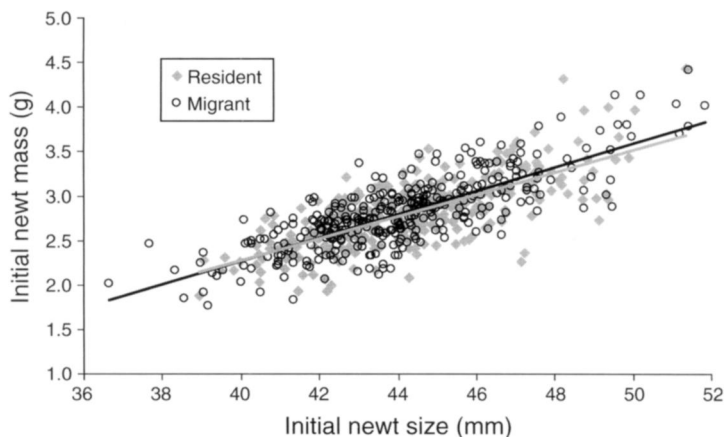


FIG. 2. Linear regression of initial body size (snout-vent length, mm) and initial body mass for newts that ultimately migrated or remained resident. Support for the body size hypothesis would be indicated by residents being larger (aggregated to the right) or heavier (aggregated above the regression line); neither scenario was found.

Reports

September), on average, migrating individuals attempted to leave high-density enclosures 8 days earlier than low-density enclosures and females migrated 6 days earlier than males (Fig. 1B). Sex ratio treatment did not significantly affect migration outcome or timing, nor were any of the interactions significant (Table 1). However, an interesting trend within density treatment was that males, on average, migrated earlier from male-biased enclosures than from female-biased enclosures ($P = 0.08$; Fig. 1B).

A significant positive relationship was found between initial body size and initial body mass for males ($R^2 = 0.59$, $P < 0.0001$) and females ($R^2 = 0.51$, $P < 0.0001$). The residuals from this relationship, which is an index of initial body condition (Schulte-Hostedde et al. 2005), did not significantly predict the migration decision of male ($\chi_1^2 = 1.12$, $P = 0.29$) or female newts ($\chi_1^2 = 0.50$, $P = 0.48$; Fig. 2).

DISCUSSION

This experiment demonstrates that habitat quality and gender can interact to influence migratory tactics in species with plasticity. The ability of red-spotted newts to increase their propensity to migrate in response to density indicates that partial migration can be a plastic response to unfavorable environmental conditions. The difference between the sexes in several aspects of migration suggests that the costs and benefits of migration for males and females are different. As opposed to our prediction, no asymmetries in initial condition were found between migrants and residents.

As predicted, newts were able to assess their habitat and adjust migration tactic and timing in response to the unfavorable environment created by the density treatment. Theoretical work (Lundberg 1987, Kaitala et al. 1993, Taylor and Norris 2007) and recent field research (Olsson et al. 2006) have highlighted the important effects of density on partial migration. Few partial migration studies on vertebrates, however, have shown density effects using replicated field experiments, probably because of the difficulties of enclosing wide-ranging animals. However, density effects are well known in the

ecological literature, documented in topics ranging from dispersal to metamorphosis, disease, and phenotypic plasticity (e.g., Wilbur 1972, Matthysen 2005). Most commonly, environments under increasing density induce change in individuals, ranging from changes in habitat to spatial location, diet, behavior, or phenotype. In this study the unfavorable environment of higher densities increased the propensity to migrate in *N. viridescens*.

In addition to altering migration decision based on population density, significant sex-based asymmetries were found. A greater percentage of females migrated from enclosures compared to males, consistent with migrations patterns seen in an adjacent natural population (K. Grayson, unpublished data). However, we found no support for our hypothesis that more females would remain as residents when released from a male-biased sex ratio. Differential migration between the sexes has been observed for numerous species, often with males remaining resident or wintering closer to the breeding grounds than do females (Ketterson and Nolan 1976, reviewed by Alerstam and Hedenstrom 1998). This study is the first, however, to experimentally demonstrate this response and its interacting effects with the environment. For newts, the arrival time hypothesis may explain why fewer males migrate. For male pond-breeding amphibians, order of arrival and sperm precedence are very important to reproductive success (Jones et al. 2002, Tennessen and Zamudio 2003). Fall breeding opportunities, because females are able to store sperm, may also be important for male *N. viridescens* (Sever 2006). The results from this study on timing of migration may indicate that male newts are able to detect these opportunities; males tended to depart later from female-biased enclosures.

One question that remains is why some female newts would adopt the resident phenotype at all. A possibility is that frequency dependence plays a role, with the resident tactic becoming more favorable as a greater percentage of the population migrates (Lundberg 1987). Due to the abundance of available males during the spring breeding season, fall and winter mating oppor-

tunities are unlikely to increase the fitness of female newts and make remaining in the breeding pond overwinter advantageous. However, the ability to feed during the winter may increase fat reserves and, consequently, egg production in the spring (Adams and Rae 1929). Migrating newts spend the winter in torpor in the terrestrial habitat, whereas newts in the aquatic habitat are able to stay active even under ice cover (Petranka 1998). A winter diet study of *N. viridescens* found that feeding occurs during all months (Morgan and Grierson 1932). These benefits may be weighed against the risk of anoxia in the pond, resulting in winter kill, or of pond-drying. Research is underway in a natural population to differentiate among these hypotheses about the dynamics and trade-offs of partial migration.

Contrary to our expectations, neither initially larger nor heavier newts were more likely to remain resident. Asymmetries are expected when partial migration is condition dependent and individuals that are in better condition or more dominant are expected to seek the better habitat (Alerstam and Hedenstrom 1998, Brodersen et al. 2008, Gillis et al. 2008). We expected larger newts to remain resident to take advantage of spring reproductive opportunities and a reproductive advantage over migrants. Migrants take anywhere from days to weeks to return to the aquatic phenotype (*personal observations*) and residents that already have larger tail fins should be competitively superior (Able 1999). However, larger individuals may be more susceptible to mortality due to pond-freezing and the resulting low oxygen concentration (Harris 1980). However, to fully evaluate the role of conditional asymmetries, one needs to know the body mass of newts prior to migrating but before transitioning to the terrestrial phenotype. Newts were not repeatedly sampled in enclosures to obtain these data because repeated disturbance could have affected migration decision. A future study could incorporate a repeated measure of body condition or further investigate the physiology of the transition to the migrant phenotype.

In conclusion, studies of migration plasticity contribute to a larger body of work focused on how organisms adapt to handle environmental change. This study shows how partial migration in an amphibian can be an adaptation for avoiding unfavorable environments. Habitat quality, manipulated through population density, highly influences the decision to migrate while mating dynamics in this species may explain sex-based asymmetries in migration. By determining the factors influencing migratory decisions within a population, we can further understand the ecology and evolution of partial migration and plasticity.

ACKNOWLEDGMENTS

We thank Mountain Lake Biological Station for funding and research support. Industrial Netting of Minneapolis, Minnesota, USA, supported this research by donating the netting for the enclosures. We thank S. Thompson, J. Jackson, and J. Heemyer

for field assistance. T. McNamara and P. Grayson provided design and construction assistance. Thank you to UVA (University of Virginia) and Virginia Tech students who assisted with enclosure construction. The VA Tech Wildlife Society and the Davidson College Dendrology course assisted with the launch and removal of the enclosures. J. Kraus and L. Green provided valuable advice on data analysis. We also thank A. Davis for obtaining newt measurements from photographs. This manuscript was improved by comments from the Vonesh lab group at VCU (Virginia Commonwealth University), R. Harris, and K. Burke. This work was supported by an NSF Graduate Research Fellowship to K. L. Grayson and NSF Grant DEB 0414118 to H. M. Wilbur.

LITERATURE CITED

- Able, D. J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioral Ecology and Sociobiology* 46:423–428.
- Adams, A. E., and E. E. Rae. 1929. An experimental study of the fat-bodies in *Triturus (Diemyctylus) viridescens*. *Anatomical Record* 41:181–203.
- Alerstam, T., and A. Hedenstrom. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Baguette, M., C. Vansteenwegen, I. Convi, and G. Neve. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclissiana eunomia*. *Acta Oecologica* 19: 17–24.
- Berthold, P., and F. Pulido. 1994. Heritability of migratory activity in a natural bird population. *Proceedings of the Royal Society of London B* 257:311–315.
- Brodersen, J., P. A. Nilsson, L. Hansson, C. Skov, and C. Bronmark. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* 89: 1195–1200.
- Church, D. R., L. L. Bailey, H. M. Wilbur, W. L. Kendall, and J. E. Hines. 2007. Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* 88:891–903.
- Cohen, D. 1967. Optimization of seasonal migratory behavior. *American Naturalist* 101:5–17.
- Davis, A. K., and K. L. Grayson. 2007. Improving natural history research with image analysis: the relationship between skin color, sex, size, and stage in adult red-spotted newts (*Notophthalmus viridescens viridescens*). *Herpetological Conservation and Biology* 2:65–70.
- Dingle, H. 1980. Ecology and evolution of migration. Pages 1–101 in S. A. Gauthreaux, Jr., editor. *Animal migration, orientation, and navigation*. Academic Press, New York, New York, USA.
- Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48:145–166.
- Gillis, E. A., D. J. Green, H. A. Middleton, and C. A. Morrissey. 2008. Life history correlates of alternative migratory strategies in American Dippers. *Ecology* 89: 1687–1695.
- Harris, R. N. 1980. The consequences of within-year timing of breeding in *Ambystoma maculatum*. *Copeia* 1980:719–722.
- Harris, R. N., R. D. Semlitsch, H. M. Wilbur, and J. E. Fauth. 1990. Local variation in the genetic basis of paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution* 44: 1588–1603.
- Jones, A. G., E. M. Adams, and S. J. Arnold. 2002. Topping off: a mechanism of first-male sperm precedence in a vertebrate. *Proceedings of the National Academy of Sciences (USA)* 99:2078–2081.
- Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. *American Naturalist* 142:59–81.
- Ketterson, E. D., and V. Nolan, Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57: 679–693.

- Kraus, J. M. 2006. Resource subsidies and predator distribution at an aquatic-terrestrial boundary. Dissertation. University of Virginia, Charlottesville, Virginia, USA.
- Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. *Journal of Theoretical Biology* 125:351–340.
- Lundberg, P. 1988. The evolution of partial migration in birds. *Trends in Ecology and Evolution* 3:172–175.
- Massey, A. 1988. Sexual interactions in red-spotted newt populations. *Animal Behaviour* 36:205–210.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403–416.
- Morgan, A. H., and M. C. Grierson. 1932. Winter habits and yearly food consumption of adult spotted newts, *Triturus viridescens*. *Ecology* 13:54–62.
- Nummelin, M. 1988. The territorial behavior of four Ugandan water strider species (Heteroptera, Gerridae): a comparative study. *Annales Entomologica Fennici* 54:121–134.
- Olsson, I. C., L. A. Greenberg, E. Bergman, and K. Wysujack. 2006. Environmentally induced migration: the importance of food. *Ecology Letters* 9:645–651.
- Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.
- Rowe, L., G. Arnqvist, A. Sih, and J. J. Krupa. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends in Ecology and Evolution* 9:289–293.
- Russell, A. P., A. M. Bauer, and M. K. Johnson. 2005. Migration in amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies. Pages 151–203 in M. T. E. Ashraf, editor. *Migration of organisms*. Springer-Verlag, New York, New York, USA.
- Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* 86:155–163.
- Semlitsch, R. D., R. N. Harris, and H. M. Wilbur. 1990. Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. *Evolution* 44:1604–1613.
- Sever, D. M. 2006. The “false breeding season” of the eastern newt, *Notophthalmus viridescens*. *Bulletin of the Chicago Herpetological Society* 41:149–153.
- Swingland, I. R. 1983. Intraspecific differences in movement. Pages 102–115 in I. R. Swingland and P. J. Greenwood, editors. *The ecology of animal movement*. Clarendon Press, Oxford, UK.
- Taylor, C. M., and D. R. Norris. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters* 3:280–283.
- Tennessen, J. A., and K. R. Zamudio. 2003. Early male reproductive advantage, multiple paternity and sperm storage in an amphibian aggregate breeder. *Molecular Ecology* 12:1567–1576.
- Verrell, P. A. 1983. The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Behavioral Ecology and Sociobiology* 13:307–313.
- Verrell, P. A. 1984. Responses to different densities of males in the smooth newt, *Triturus vulgaris*: “One at a time, please.” *Journal of Herpetology* 18:482–484.
- Verrell, P. A. 1985. Is there an energetic cost to sex? Activity, courtship mode and breathing in the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Monitore Zoologico Italiano* 19:121–127.
- Walters, P. J., and L. Greenwald. 1977. Physiological adaptations of aquatic newts (*Notophthalmus viridescens*) to a terrestrial environment. *Physiological Zoology* 50:88–98.
- Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* 53:3–21.

APPENDIX A

Field enclosures in Station Pond at Mountain Lake Biological Station (*Ecological Archives* E090-021-A1).

APPENDIX B

Two examples of using spot patterns to individually identify newts (*Ecological Archives* E090-021-A2).