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Life history benefits of residency in a partially migrating pond-breeding amphibian

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Abstract. Species with partial migration, where a portion of a population migrates and the other remains residential, provide the opportunity to evaluate conditions for migration and test mechanisms influencing migratory decisions. We conducted a five-year study of two populations of red-spotted newts (*Notophthalmus viridescens*), composed of individuals that either remain as residents in the breeding pond over the winter or migrate to the terrestrial habitat. We used multistate mark–recapture methods to (1) test for differences in survival probability between migrants and residents, (2) determine if migrants breed every year or skip opportunities for reproduction, and (3) estimate the frequency of individuals switching migratory tactic. We used estimates of life history parameters from the natural populations in combination with previous experimental work to evaluate processes maintaining partial migration at the population level and to assess mechanisms influencing the decision to migrate. Based on capture–recapture information on over 3000 individuals, we found that newts can switch migratory tactics over their lifetime. We conclude that migrants and residents coexist through conditional asymmetries, with residents having higher fitness and inferior individuals adopting the migrant tactic. We found that newts are more likely to switch from residency to migrating than the reverse and males were more likely to remain as residents. Migration differences between the sexes are likely driven by reproduction benefits of residency for males and high energetic costs of breeding resulting in lower breeding frequencies for females. Environmental conditions also influence partial migration within a population; we found support for density-dependent processes in the pond strongly influencing the probability of migrating. Our work illustrates how migration can be influenced by a complex range of individual and environmental factors and enhances our understanding of the conditions necessary for the evolution and maintenance of partial migration within populations.

Key words: breeding probability; capture–recapture; life history trade-offs; migration phenology; multistate mark–recapture; Notophthalmus viridescens; *partial migration; red-spotted newts; skipping reproduction; survival.*

INTRODUCTION

Migration is an adaptation to seasonally variable environments that functions to aggregate animals for breeding, allows for the exploitation of alternate resources, or enables avoidance of physiological limits on survival (Dingle 1996). Because most environments are temporally variable, the evolution of migration could be expected to be ubiquitous among mobile animal populations (Fretwell 1980). Residency can be maintained, however, when the fitness benefits of migrating to the alternate habitat do not outweigh the current habitat and the costs of making the journey (Alerstam and Hedenstrom 1998). Thus, depending on the environmental context, a population can range from completely migratory to completely residential based on the fitness of each tactic (Taylor and Norris 2007). In order to evaluate hypotheses concerning the evolution and maintenance of migration within populations, it is critical to understand the fitness consequences of migration compared to residency.

Whereas a large body of theory considers the conditions that select for the evolution of migration, these hypotheses are difficult to test under natural conditions. Populations containing both migratory and resident individuals (partial migration; Lundberg 1988) present a unique opportunity to measure the fitness of individuals adopting either tactic in the same population. Partial migration has been predicted to be maintained in a population through life history trade-offs or conditional asymmetries. Migrants and residents can have equal fitness through trade-offs in life history traits or temporal fluctuations in the optimal tactic (Lundberg 1987). Condition-dependent hypotheses predict that migration is influenced by attributes of individuals, where one tactic can have higher fitness and inferior individuals assume the other tactic to make the best of a bad situation (Alerstam and Hedenstrom 1998). When migration is condition-dependent, several

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mechanistic hypotheses have been proposed to account for differences between resident and migrant subpopulations (reviewed in Ketterson and Nolan 1983, Boyle 2008). These hypotheses were developed to account for differential migration in birds and have been widely applied to partially migratory species. The body size hypothesis predicts that smaller individuals have lower body condition and therefore migrate because they are less likely to survive in the breeding habitat over winter and more likely to survive in the nonbreeding habitat. Larger individuals in better condition can remain as residents (Ketterson and Nolan 1976). In the dominance hypothesis, resource competition results in dominant individuals outcompeting subordinates for residency (Gauthreaux 1982). The arrival-time hypothesis proposes that the sex that competes more intensely for breeding resources will obtain reproductive benefits from residency and be more likely to stay in the breeding habitat (Myers 1981). Finally, environmental conditions can also impact the portion of a population that becomes migrants, with models suggesting an important role for density dependence (Kaitala et al. 1993, Taylor and Norris 2007) and field studies showing higher rates of migration from lower quality shared habitats (Nilsson et al. 2006, Olsson et al. 2006, Grayson and Wilbur 2009).

Testing these hypotheses and measuring the costs and benefits of each tactic requires detailed multiyear data that follows individuals from natural partially migratory populations. These studies are extremely rare and have been limited to birds (Gillis et al. 2008, Jahn et al. 2010). Determining the life history parameters of each tactic can be complicated by detection issues, such as migrants returning to alternate breeding sites or irregular breeding schedules of migrants. In this study we used multistate mark–recapture methods to measure life history trade-offs between terrestrial migrants and aquatic residents in a partially migratory amphibian, the red-spotted newt (*Notophthalmus viridescens*). Our use of multistate models allowed us to account for detection and generate robust estimates of life history parameters of migrants and residents, reproductive frequency of migrants, and the probability of transitioning between these states. Partial migration studies have also been limited by the difficulties of following large populations of wide-ranging individuals. Due to the fidelity of adult *N. viridescens* to breeding ponds (Gill 1978) and the tractability of amphibian migration, we were able to follow over 3000 newts and estimate life history parameters in two populations.

We generated specific hypotheses about the costs and benefits of migrating compared to residency in *N. viridescens*, expecting partial migration to be maintained by trade-offs between survival and reproduction. We predicted migrant newts would have survival benefits over resident newts. Specifically, we expected that pond residents would undergo greater temporal fluctuations in winter survival probabilities compared to migrants. In years with mild winters, the breeding pond may have higher survival because resident newts have access to aquatic food sources, while migrants in the terrestrial habitat are in torpor (Morgan and Grierson 1932). However, residents may experience high mortality during severe winters when snow cover can lead to anoxia (Bradford 1983). Winterkills are common in ponds and lakes, but their frequency and severity can be difficult to predict and depends on the hydrological properties of the pond, the length of snow and ice cover, the amount of oxygen stored at freezing, and the rate of organic matter decomposition (Meding and Jackson 2001).

We predicted that the survival benefits from migrating would trade off with the reproductive advantages of residency to equate the fitness of each tactic over time. Pond residents, males in particular, have a reproductive advantage over migrants due to being competitively superior at securing mating opportunities (Grayson and McLeod 2009, Bloch and Grayson 2010). In addition, migrant salamanders from the families Ambystomatidae and Salamandridae are known to skip breeding opportunities and spend multiple years in the terrestrial habitat between breeding events (e.g., Gill 1985, Church et al. 2007, Gamble et al. 2009). We expected that migrant newts would skip one or more years of breeding before returning to the breeding pond. We predicted this probability would be higher for female migrants compared to male migrants based on the higher energetic investment associated with egg-laying (Trivers 1972). With sex-based asymmetries in the reproductive benefits of residency, we expected the probability of residency to support the arrival time hypothesis, with more males remaining as pond residents over winter.

Lastly, we expected that individual newts would be likely to switch migratory tactics over their lifespan, and these transition probabilities would be influenced by individual attributes and the condition of the shared pond habitat (Lundberg 1987, Gillis et al. 2008). Under both the body size hypothesis and the dominance hypothesis, inferior individuals (lower condition or socially subordinate) are predicted to migrate; we expected larger newts would be more likely to remain as residents. To investigate the role of the pond habitat on the probability of migrating, we tested if newt density within natural ponds explained changes in the migration probability. We predicted high-density conditions would increase the probability of migrating.

MATERIALS AND METHODS

Study species

In northern and central portions of the range of *N. viridescens*, aquatic larvae typically metamorphose into a terrestrial juvenile or red eft stage, which lasts between three and seven years before reaching sexual maturity and selecting a breeding site (Forester and Lykens 1991). Newts are found in a wide variety aquatic habitats ranging from large permanent lakes to small temporary ponds. Populations of adult *N. viridescens* can vary from completely residential to partially migratory to completely migratory, with permanent aquatic habitats that do not freeze completely in winter favoring residency (Sever 2006). In permanent ponds at our study site, adult newts either reside in the breeding pond for the winter or migrate to the forest in late summer and early fall (see Plate 1). After emerging from winter refuges, newts migrate to breeding ponds in March and April. Adult newts have also been shown to skip breeding opportunities and spend multiple years in the terrestrial habitat between breeding events (Gill 1985, Nichols et al. 1987). We also observed a fall migration of maturing efts into the ponds; these individuals overwintered in the pond before their first breeding season (as in Hurlbert 1969).

Study site

We studied the *N. viridescens* populations associated with two small ponds, Sylvatica Pond (SY; area = 354 m^2, depth = 0.7 m) and Horton Pond (HR; area = 223 m^2, depth = 1.1 m; Appendix A), at Mountain Lake Biological Station (MLBS, Giles County, Virginia, USA; 37°22′32″ N, 80°31′20″ W, elevation 1160 m). These ponds are separated by ~100 m and were depressions in an abandoned roadbed that occasionally held water before they were enlarged in the late 1960s. They are rain fed, permanent, and fishless.

Data collection

Drift fences were constructed in May 2005 of aluminum flashing to completely encircle both ponds. Pairs of pitfall traps (19-L plastic buckets) were installed on each side of the drift fence every 6–8 m to capture animals during migrations. Pitfall traps were opened and checked daily from 15 June to 10 October 2005, 15 March to 29 September 2006, 1 March to 2 October 2007, 4 March to 1 October 2008, and 8 March to 7 May 2009. After capture, amphibians were released on the opposite side of the fence. During the late fall and winter (October–February), newt movements were believed to be minimal (Gill 1978; D. Church, *unpublished data*). During this period, lids were placed on the pitfall traps and a sliding door, installed between each pitfall trap pair, was opened.

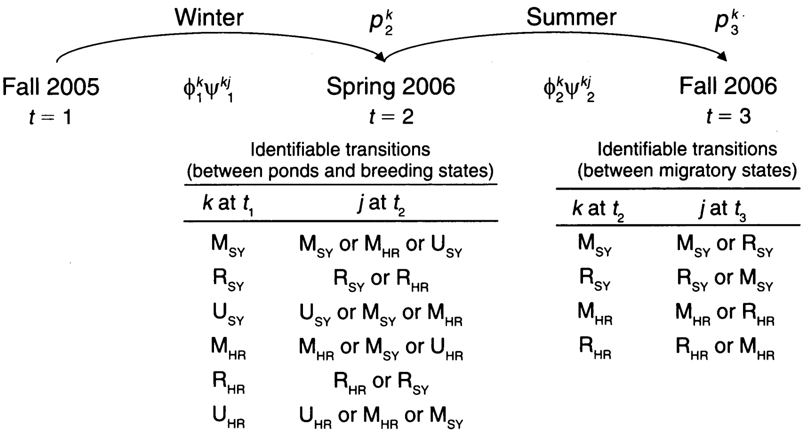
Resident individuals in both ponds were sampled each spring and fall. Fall sampling was conducted in September by dragging a 10-m bag seine 3–6 times through the pond. This method is highly effective, but is disruptive to the pond environment. In the spring, we were concerned about disturbing mating and egg laying of all amphibian species breeding in the ponds, and therefore sampled residents using plastic minnow traps. Spring trapping occurred over 8–14 nights between March and May and was dictated by weather and activity at the drift fence. Traps baited with glow sticks were submerged at dusk (Grayson and Roe 2007). Individuals were collected the following morning, processed, and returned the same day.

Each captured newt was photographed so we could use the pattern of dorsal red spots to identify individuals (see Appendix B of Grayson and Wilbur 2009). Additionally, all captured newts were given a single injection of visible implant elastomer each year to confirm photographic matching of individuals and to visually identify newts as recaptures (VIE, Northwest Marine Technology, Shaw Island, Washington, USA; Bailey 2004). Digital photographs of captured newts from fall 2005 were sorted based on sex and the number of dorsal red spots. Photographic matching for all subsequent captures (2006–2009) by visual comparison allowed construction of a capture history for each individual.

Multistate mark–recapture analysis

General model.—We used multistate mark–recapture models (MSMR; Arnason 1973, Lebreton et al. 2009) to estimate transition probabilities between migratory tactics (resident or migrant), ponds (SY or HR), and breeding states (breeders and unobservable nonbreeders), as well as state-specific survival probabilities, while accounting for unequal capture probabilities. MSMR models include three types of parameters (Fig. 1): (1) apparent survival probability, ϕ_t^k, is the probability that a marked animal in state k survives and remains within the study population from time t to $t + 1$, where t represents a sampling period, (2) transition probability, ψ_t^{kj}, is the probability that an animal in state k at time t is in state j at time $t + 1$, given that it survives, and (3) capture probability, p_t^k, is the probability that an animal known to be alive in state k at time t is captured ($t = 2 \ldots T$, where T is the total number of sampling periods).

State definitions.—We assigned a pond and migratory state for each capture based on the study site and knowledge of *N. viridescens* natural history. The resident state (R) was assigned to individuals captured in the fall seine or in the spring trapping (signifying newts that remain in the breeding pond over winter). The migrant state (M) was assigned to individuals captured exiting the breeding pond in the fall to overwinter in the forest and recaptured individuals entering the pond to breed in the spring. Migrant individuals that skip breeding opportunities (and stay in the terrestrial habitat) transition into an unobservable, nonbreeder state (U; $p_t^{\mathrm{U}} = 0$). An unavoidable assumption necessary in MSMR models with unobservable states is that survival probability for the unobservable state must be assumed equal to an observable state (Kendall 2004, Bailey et al. 2009). We assumed survival probabilities for nonbreeders were equal to migrant individuals during the same period (i.e., $\phi_t^{\mathrm{M}} = \phi_t^{\mathrm{U}}$). We felt that nonbreeder survival probabilities were more closely associated with migrants than residents, and that survival varied more among seasons (winter or summer) than among habitats (pond or forest). Accordingly, we assumed that nonbreeder survival probabilities during both summer and winter



Identifiable transitions (between ponds and breeding states)	
k at t_1	j at t_2
M_{SY}	M_{SY} or M_{HR} or U_{SY}
R_{SY}	R_{SY} or R_{HR}
U_{SY}	U_{SY} or M_{SY} or M_{HR}
M_{HR}	M_{HR} or M_{SY} or U_{HR}
R_{HR}	R_{HR} or R_{SY}
U_{HR}	U_{HR} or M_{HR} or M_{SY}

Identifiable transitions (between migratory states)	
k at t_2	j at t_3
M_{SY}	M_{SY} or R_{SY}
R_{SY}	R_{SY} or M_{SY}
M_{HR}	M_{HR} or R_{HR}
R_{HR}	R_{HR} or M_{HR}

FIG. 1. Diagram of parameters estimated via multistate mark–recapture models (MSMR) for $t = 3$ sampling periods (of $T = 8$ total periods from fall 2005 to spring 2009). The parameters ϕ_t^k, ψ_t^{kj}, and p_t^k are defined in the *Materials and methods: General model* section. States were defined as migrant (M), resident (R), or nonbreeder (U) red-spotted newts (*Notophthalmus viridescens*) specific to either Sylvatica (SY) or Horton (HR) Pond. Transitions between states for $t = 1$, ψ_1^{kj}, are the same for $t = 3, 5, 7$, and the transitions for ψ_2^{kj} are the same for $t = 4, 6$. For transitions between migratory states, individuals can either change migratory tactic (i.e., $\psi_{t=2.4.6}^{MR}$ or $\psi_{t=2.4.6}^{RM}$) or remain in the same migratory state (i.e., $\psi_{t=2.4.6}^{MM}$ or $\psi_{t=2.4.6}^{RR}$). For transitions between ponds and breeding states, migrants can return to breed again at the same pond (e.g., $\psi_{t=1.3.5.7}^{M_{SY}M_{SY}}$), breed at the other pond (e.g., $\psi_{t=1.3.5.7}^{M_{SY}M_{HR}}$), or skip a year of reproduction and remain unobservable in the forest (e.g., $\psi_{t=1.3.5.7}^{M_{SY}U_{SY}}$). Nonbreeders can remain in the forest and skip another year of reproduction (e.g., $\psi_{t=1.3.5.7}^{U_{SY}U_{SY}}$), return in the spring to breed at the same pond as their previous breeding attempt (e.g., $\psi_{t=1.3.5.7}^{U_{SY}M_{SY}}$), or breed at the other pond (e.g., $\psi_{t=1.3.5.7}^{U_{SY}M_{HR}}$). Residents can transition between ponds over winter through the connecting drainage (e.g., $\psi_{t=1.3.5.7}^{R_{SY}R_{HR}}$). All other transitions between states were set to zero in all models because they were not observed or were biologically unreasonable.

periods were approximately equal to survival probabilities of migrants during the same time periods. We included two additional states for individuals first captured entering a pond in either the spring or the fall (denoted as "tactic," see description in *Model sets* and Appendix B).

Model constraints.—A fully time-specific MSMR model that includes estimates of all possible transitions between states is both biologically unreasonable and statistically unidentifiable (Gimenez et al. 2004, Bailey et al. 2010). Based on the phenology of *N. viridescens* at the study site, and consistent with MSMR assumptions, transitions between ponds and breeding states (indicating breeding probability) only occurred just prior to the spring sampling period (i.e., for $t = 1, 3, 5, 7$) and transitions between migrant and resident states only occurred just prior to the fall sampling period (i.e., for $t = 2, 4, 6$; Fig. 1). All other transitions between states were either not observed or biologically unreasonable, and thus were set to zero in all models. We applied additional constraints based on our sampling methods and to avoid parameter redundancy (where a model is not identifiable because it contains parameters that cannot be uniquely estimated; see Appendix B; Gimenez et al. 2004, Bailey et al. 2010).

Model sets.—Our global model, ϕ(time × sex × pond × tactic) ψ(time × sex × pond × tactic) p(time × sex × pond × tactic) allowed parameters to differ (1) across years for specific seasons (time), (2) between sexes (sex), (3) between ponds (pond), and (4) between migratory states (tactic). The global model and all reduced models included season-specificity (i.e., $t = 1, 3, 5, 7$ different from $t = 2, 4, 6, 8$). We followed a sequential modeling process where we first used the global model structure for ϕ and ψ and tested capture probability models (Lebreton et al. 1992). We tested eight capture probability structures with all biologically relevant combinations of time, sex, and pond effects (Appendix B and C). We explored yearly variation among spring samples ($p_{t=2.4.6=8}^k$) or with spring 2006 being an outlier ($p_{t=2.4=6=8}^k$), because the weather was particularly mild and drift fences were opened later that year (i.e., we expected $p_{t=2}^k < p_{t=4=6=8}^k$).

Next, using the top-ranked capture probability structure, we developed 18 candidate models for ϕ and ψ (Appendix C). To test our a priori hypotheses about differences between migrating and residency, we began by modeling ϕ and ψ under three migratory scenarios: (1) survival and transition probabilities vary among migrants, residents, and newly captured individuals (denoted as tactic; Appendix B), (2) migrants and newly captured individuals in the spring have the same survival and transition probabilities and residents and newly captured efts in the fall have the same survival and transition probabilities (denoted as tactic$_{\text{new=recap}}$), or (3) no differences between migratory states. We explored these three migratory scenarios using survival and transition parameters that were modeled as: (1) sex- and pond-specific, (2) sex-specific but pond-constant, (3)

TABLE 1. Model selection results for the top six candidate models based on quasi-likelihood Akaike Information Criteria ($QAIC_c$) for partially migratory adult red-spotted newts *Notophthalmus viridescens*.

Model structure						
ϕ	ψ	$QAIC_c$	$\Delta QAIC_c$	K	w	$-2\log(L)$
$t_{1,3,5,7}$ × sex × pond × $\text{tactic}_{\text{new=recap}}$	**density** + sex × $\text{tactic}_{\text{new=recap}}$	**7566.88**	**0**	**74**	**0.9998**	**25 653.45**
$t_{1,3,5,7}$ × sex × pond × $\text{tactic}_{\text{new=recap}}$	$t_{2,4,6}$ × sex × pond × $\text{tactic}_{\text{new=recap}}$	**7584.00**	**17.12**	**92**	**0.0002**	**25 585.42**
sex × tactic	sex × tactic	7599.55	32.67	38	0	26 019.14
sex × $\text{tactic}_{\text{new=recap}}$	sex × $\text{tactic}_{\text{new=recap}}$	7601.70	34.82	32	0	26 068.47
$t_{1,3,5,7}$ × sex × $\text{tactic}_{\text{new=recap}}$	$t_{2,4,6}$ × sex × $\text{tactic}_{\text{new=recap}}$	7607.97	41.09	52	0	25 950.26
$t_{1,3,5,7}$ × sex × pond × tactic	$t_{2,4,6}$ × sex × pond × tactic	7611.40	44.52	116	0	25 509.57

Notes: See Appendix C for the complete candidate model set. We adjusted for overdispersion based on median $\hat{c}$ results ($\hat{c}$=3.46). Relative $QAIC_c$ ($\Delta QAIC_c$), number of parameters (K), Akaike weight (w), and −2log likelihood ($-2\log(L)$) are also reported for each model. Model structures for apparent survival probability, ϕ, and transition probabilities, ψ, include variation among time, sexes, ponds, and migratory states (tactic). Transition probabilities between migratory states were also modeled as an additive function of density for relevant time periods, $t = 2, 4, 6$ (density). Yearly variation in ϕ and ψ was only included for seasons of interest to our a priori hypotheses: winter survival probability ($\phi^{k}_{t=1,3,5,7}$) and spring-to-fall transitions between migrating and residency ($\psi^{kj}_{t=2,4,6}$; Fig. 1). Summer survival probability and fall-to-spring transitions between ponds and breeding states were expected to be similar among years and were modeled accordingly (i.e., $\phi^{k}_{t=2=4=6}$ and $\psi^{kj}_{t=1=3=5=7}$). Differences among all four migratory states (migrants, residents, newly captured efts, and newly captured spring migrants) are denoted by "tactic," $\text{tactic}_{\text{new=recap}}$ denotes differences among migrants and residents only, with newly captured individuals set equal to the equivalent migratory state (Appendix B). Results from the top model, with and without the effect of density, respectively, are indicated in boldface.

pond-specific but constant among males and females, or (4) both sex and pond invariant.

Finally, we explored whether spatial and temporal differences in transition probabilities between migratory states could be explained by local densities, consistent with previous experimental work. We estimated newt densities for each pond (individuals per square meter) prior to the fall sampling period by adjusting the number of individuals captured by the appropriate sex- and state-specific capture probabilities. Using the top-ranked survival probability structure, we modeled transition probabilities among migratory states as a function of these density estimates.

We used Program MARK (White and Burnham 1999) to obtain maximum likelihood estimates of parameters and to rank our MSMR models. Akaike's Information Criterion corrected for overdispersion ($QAIC_c$) was used to select among competing models, and Akaike weights (w) were computed to identify the relative "weight" of evidence for each model conditional on the candidate model set (Burnham and Anderson 2002). A universal goodness-of-fit test for complex MSMR models with unobservable states currently does not exist; thus, we used our global model and the median $\hat{c}$ approach in Program MARK to estimate overdispersion and adjust model selection criteria (White and Burnham 1999). Finally, we verified the rankings of the candidate model set were the same under both top capture probability structures.

RESULTS

Capture methods

Our data included 8621 captures of 3428 unique individuals: 1625 females were captured 2743 times (mean = 1.7 captures per female) and 1803 males were captured 5878 times (mean = 3.3 captures per male; Appendix D). The timing of spring and fall migrations was consistent year-to-year and males arrived earlier and departed later than females (Appendix E).

Model selection

There was some evidence of overdispersion in our data based on median $\hat{c}$ results ($\hat{c} = 3.46$). We report $QAIC_c$ values for each candidate model and adjusted variance accordingly (Burnham and Anderson 2002). Simulation studies have shown that the median $\hat{c}$ procedure produces conservative estimates of $\hat{c}$ (slight positive bias), and $\hat{c} < 4$ suggests the model structure is adequate (White and Burnham 1999).

The top-ranked detection model, $p(t_{2,4=6=8}$ × sex × tactic) had 59% of the weight of evidence and suggested that capture probabilities differed among sexes, but not between ponds. As we suspected, capture probability was lower in spring 2006 compared to other spring samples. The next highest ranked detection model, $p(t_{2,4=6=8}$ × tactic), suggested that capture probabilities for males and females were similar (weight of evidence = 25%). All other capture probability structures had $\Delta QAIC_c > 3.0$, indicating a majority of support for the top two models (Burnham and Anderson 2002; Appendix C). The top capture probability structure was 2.36 times more likely than the second best structure and more general; thus, we used this structure to test our main biological hypotheses.

Among candidate models that did not include density effects, a single model, ϕ(time × sex × pond × $\text{tactic}_{\text{new=recap}}$) ψ(time × sex × pond × $\text{tactic}_{\text{new=recap}}$), represented the data better than any other model (Table 1). This model supports the hypothesis that migrants and residents have different apparent survival and transition probabilities, but newly captured individuals need not be modeled separately. We also found strong support for the model in which newt density within the

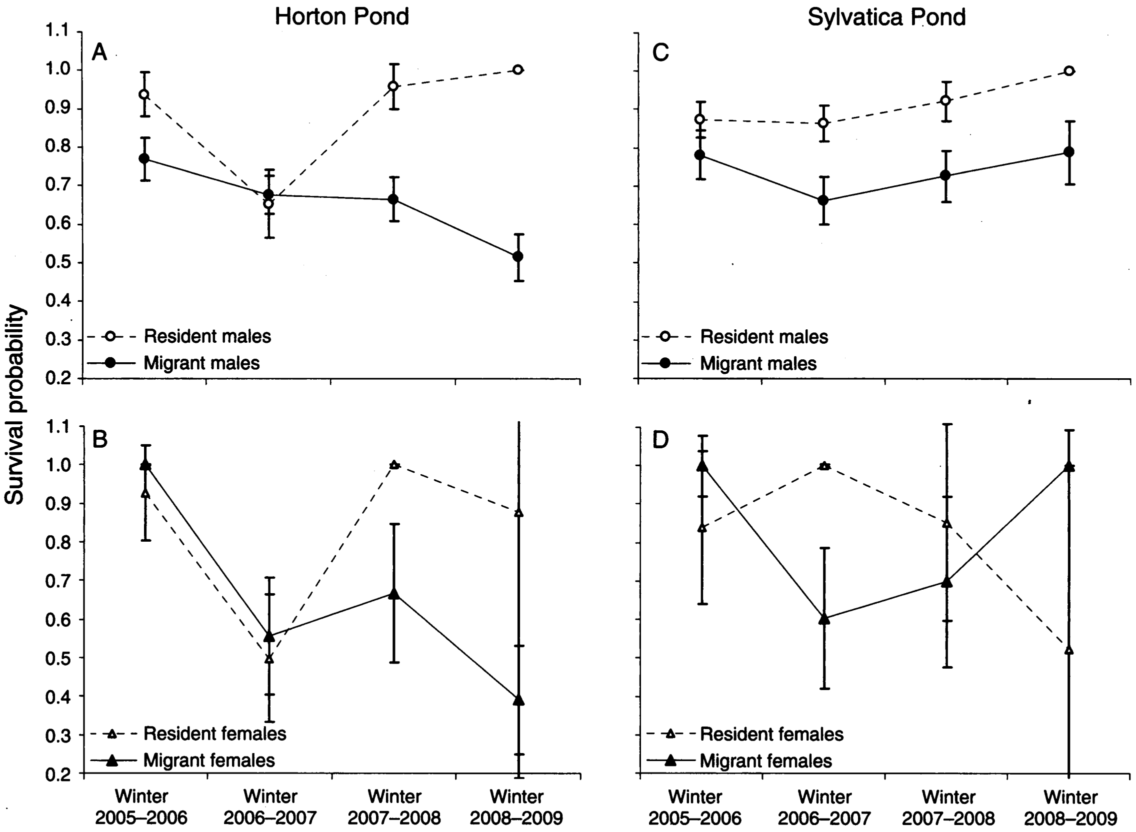


FIG. 2. Winter survival probabilities, $\hat{\phi}_{t=1,3,5,7}$ (estimate ± SE), for resident and migrant *N. viridescens* (A) males and (B) females at Horton Pond, and (C) males and (D) females at Sylvatica Pond, based on the top model (Table 1; Appendix C: Table C2). The study area was Mountain Lake Biological Station, Giles County, Virginia, USA.

ponds influenced transition probabilities between migratory states ($w = 1.00$; Table 1). As density increased, the probability of transitioning from a resident to a migrant increased (ψ^{RM}, $\hat{\beta} = 0.62 \pm 0.19$), and the probability of transitioning from a migrant to a resident decreased (ψ^{MR}, $\hat{\beta} = -0.43 \pm 0.21$; Appendix F).

Parameter estimates

Using estimates from our top model (Table 1), capture probabilities at the drift fence were high for both sexes in both seasons (estimate ± SE): males $\hat{p} = 0.94 \pm 0.02$ and females $\hat{p} = 0.92 \pm 0.05$ in the spring, and $\hat{p} = 0.90 \pm 0.02$ for both males and females in the fall. An exception was spring 2006, where a later opening date reduced capture probabilities for both sexes (males $\hat{p} = 0.75 \pm 0.05$ and females $\hat{p} = 0.44 \pm 0.10$). The fall sampling of residents using a seine was highly effective at detecting both males ($\hat{p} = 0.91 \pm 0.02$) and females ($\hat{p} = 0.84 \pm 0.08$). As expected, spring sampling of residents using minnow traps was less effective for males ($\hat{p} = 0.66 \pm 0.03$) and poor for females ($\hat{p} = 0.18 \pm 0.07$). The large difference between the sexes during spring trapping is likely due to male newts being more active in the water column, while female newts are more commonly found in edge and substrate habitat during the spring (K. L. Grayson, S. P. De Lisle, J. E. Jackson, S. J. Black, and E. J. Crespi, *unpublished manuscript*).

Apparent survival probability estimates during the breeding season (summer, $\hat{\phi}_{t=2=4=6=8}$) were generally high across sexes, ponds, and migratory states (range = 0.81–0.98) with the exception of migrant females in Sylvatica Pond ($\hat{\phi} = 0.49 \pm 0.05$; Appendix G). Contrary to our predictions, winter survival probabilities were generally higher for residents compared to migrants (Fig. 2). One notable exception was during winter 2006–2007 when survival estimates of migrants and residents were similar in Horton Pond (Fig. 2A, B). This dip in survival for residents is consistent with the only winterkill observed during the study. Apparent survival estimates for females were more variable and estimated with less precision compared to males, likely due to the fewer number of individuals due to lower capture and breeding probabilities (Appendix D).

Breeding probabilities were represented by transitions between migrant and nonbreeding states (and vice versa) prior to the spring sampling period. We found substantial differences between the sexes in breeding probability (Table 2). Over 90% of migrant males from both ponds returned to breed the next year (e.g.,

TABLE 2. Breeding and movement probabilities (i.e., transition probabilities) for adult *N. viridescens* that bred in the previous year (migrants, M) and individuals that skipped one or more breeding opportunities (nonbreeders, U) based on the top model (Table 1; Appendix C: Table C2).

	Breeders			Nonbreeders		
Sex and pond	ψ^{kj}	Estimate	SE	ψ^{kj}	Estimate	SE
Male						
SY	$\psi^{M_{SY}M_{SY}}$	0.81	0.04	$\psi^{U_{SY}M_{SY}}$	0.55	0.40
SY	$\psi^{M_{SY}M_{HR}}$	0.12	0.02	$\psi^{U_{SY}M_{HR}}$	0.07	0.12
SY	$\psi^{M_{SY}U_{SY}}$	0.07	0.04	$\psi^{U_{SY}U_{SY}}$	0.38	0.42
HR	$\psi^{M_{HR}M_{HR}}$	0.87	0.03	$\psi^{U_{HR}M_{HR}}$	1.00	0.00
HR	$\psi^{M_{HR}M_{SY}}$	0.09	0.02	$\psi^{U_{HR}M_{SY}}$	0.00	0.00
HR	$\psi^{M_{HR}U_{HR}}$	0.03	0.02	$\psi^{U_{HR}U_{HR}}$	0.00	0.00
Female						
SY	$\psi^{M_{SY}M_{SY}}$	0.28	0.06	$\psi^{U_{SY}M_{SY}}$	0.36	0.16
SY	$\psi^{M_{HR}M_{HR}}$	0.03	0.02	$\psi^{U_{SY}M_{HR}}$	0.04	0.04
SY	$\psi^{M_{SY}U_{SY}}$	0.69	0.06	$\psi^{U_{SY}U_{SY}}$	0.59	0.17
HR	$\psi^{M_{HR}M_{HR}}$	0.23	0.04	$\psi^{U_{HR}M_{HR}}$	0.24	0.11
HR	$\psi^{M_{HR}M_{SY}}$	0.04	0.02	$\psi^{U_{HR}M_{SY}}$	0.04	0.03
HR	$\psi^{M_{HR}U_{HR}}$	0.73	0.05	$\psi^{U_{HR}U_{HR}}$	0.72	0.12

Notes: All transitions occurred prior to the spring sampling period ($t = 1 = 3 = 5 = 7$). Movements between ponds (SY = Sylvatica and HR = Horton, both at the Mountain Lake Biological Station, Giles County, Virginia, USA) are indicated by individuals returning to breed at the other pond from their previous breeding attempt (i.e., $\psi^{M_{SY}M_{HR}}$ or $\psi^{U_{SY}M_{HR}}$). Transition probability (ψ_t^{kj}) denotes the probability that an animal in state k at time t is in state j at time $t + 1$, given that it survives.

$\hat{\psi}^{M_{SY}M_{SY}}_{\text{males}} + \hat{\psi}^{M_{SY}M_{HR}}_{\text{males}} = 0.93$) compared to only ~30% of migrant females. Additionally, males that skip a year of reproduction have higher probabilities of breeding the next year than females (Table 2). Stated differently, nonbreeding females are more likely to skip an additional, successive breeding opportunity than males ($\hat{\psi}^{UU}$).

Our model selection results also indicated differences in transition probability between migratory states across years and ponds. Local, season-specific density estimates provided a plausible explanation for spatial and temporal variation in these transition probabilities. At higher densities, resident newts were more likely to switch to migrating ($\hat{\psi}^{RM}$) and migrants were more likely to retain their tactic ($\hat{\psi}^{MM}$; Appendix F). Still, transition probabilities from migrant to resident tactics were low for both sexes (range = 0.03–0.16), suggesting that most newts in the migrant state are likely to remain as migrants. Conversely, newts were much more likely to transition from the resident state to the migrant state, especially females (ranges: $\hat{\psi}^{RM}_{\text{females}} = 0.36–0.67$ and $\hat{\psi}^{RM}_{\text{males}} = 0.17–0.43$). In other words, male newts were more likely than females to remain in the resident state, especially at low densities (Appendix F).

Transitions between ponds were indicated by migrants or nonbreeders returning to breed at the other pond from their previous breeding attempt. Estimates of these transitions were low for migrants of both sexes (range = 0.0–0.12; Table 2). Residents could move between ponds along the connecting drainage, but this was estimated to occur infrequently for males ($\hat{\psi}^{R_{SY}R_{HR}}_{\text{males}} = \hat{\psi}^{R_{HR}R_{SY}}_{\text{males}} = 0.03 \pm 0.009$) and was never observed for females.

Our estimates of model parameters assume fidelity of adult newts to the areas surrounding the Sylvatica and Horton Pond complex. Permanent emigration to a breeding pond outside the study area would be included in apparent survival estimates and would lower estimates of breeding probability (Church et al. 2007). However, we believe that permanent movements to outside the study area were rare based on (1) the low estimates of movement we observed between our connected ponds, (2) extensive sampling of the only other known *N. viridescens* breeding pond within a kilometer (Appendix A), and (3) the total fidelity observed by Gill (1978) of adult *N. viridescens* to breeding ponds over a three-year study of five ponds.

DISCUSSION

We studied life history parameters of two populations of partially migrating red-spotted newts over five years. We found considerable differences between residents and migrants in apparent survival probability, with higher winter survival for residents, and between the sexes in breeding probability, with females substantially more likely to skip breeding years. Our data also show that *N. viridescens* adults can switch migratory tactics over their lifespan. We found that newts are more likely to switch from residency to migrating than the reverse and males are more likely to remain as residents. Finally, we found strong support that density influenced the probability of remaining resident in the pond.

We did not find life history differences between residents and migrants that suggested the two tactics could have equal fitness over time. Our data highlight that winter survival of residents can be impacted by stochastic events, such as oxygen depletion in ponds under ice cover. A winterkill during our study decreased survival probability for residents, but the decrease was only to the level of apparent survival for migrants in the forest. Adriaensen and Dhondt (1990) observed a

PLATE 1. Adult red-spotted newts (*Notophthalmus viridescens*) migrating in the fall from a breeding pond to overwinter in the forest. Photo credit: H. M. Wilbur.

similar drop in survival of residents during the harshest winter in their five-year study on European Robins, but also only to the survival level of migrants. Across all years in this study, winter survival of residents was always higher than or equivalent to migrants. Our winter survival estimates were more variable and less precise for females compared to males; we attribute this difference to the lower number of female captures, resulting from lower capture probabilities and breeding frequencies.

In addition to survival benefits, male residents have a significant competitive advantage over migrant males for mating opportunities. Migrant males arrive at the breeding pond with reduced tail fins, which limits their success at capturing and courting female newts (Bloch and Grayson 2010). Our estimates of breeding probability suggest that the majority of migrant males return to breed the next year and resident males are more likely to remain residents, compared to females, to exploit their competitive breeding advantage. In contrast, fecundity was found to be similar between resident and migrant females within a breeding season, with differences only found in offspring size (Grayson and McLeod 2009). However, resident females often transition to the migrant state, and migrant females often skip one or more years of reproduction. Sex-based differences in breeding probability have been found in other studies of newts (Gill 1985) and ambystomatid salamanders (Church et al. 2007, Gamble et al. 2009), but the vast disparity between the sexes in our study is notable. These differences in breeding frequency suggest higher energetic costs of reproduction or a larger energetic investment required to initiate reproduction for females (Bull and Shine 1979). So, while resident and migrant females have similar reproductive outputs within a breeding season, resident females appear to have a reproductive advantage by having the resources to remain in the pond and breed again, while migrant females skip years in the terrestrial habitat before returning to the pond to mount a reproductive effort.

Thus, our survival and breeding frequency results support the hypothesis that migrants and residents can persist within a population due to conditional asymmetries. During the years of our study, we found higher fitness for resident males and females compared to migrants in two pond populations, even with a winterkill. Evidence for condition-dependent migration with higher payoffs for residents has also been found in avian studies (Adriaensen and Dhondt 1990, Gillis et al. 2008). Migrating and residency could have equal fitness benefits if winterkill in a pond occurred frequently enough to cause temporal fluctuations in the tactic with the highest winter survival. However, our small high-elevation ponds likely experience harsher winter conditions compared to low-elevation aquatic habitats or larger ponds and lakes. We expect winter conditions resulting in higher survival for migrants would need to occur frequently for temporal fluctuations to equalize fitness between migrants and residents over time. Theoretical models have highlighted the link between habitat quality, survival, and the proportion of a population that migrates (Taylor and Norris 2007). Our study shows empirically that overwinter survival plays a large role in determining the costs and benefits of migrating and residency.

When partial migration persists due to conditional asymmetries between migrants and residents, individuals are predicted to adjust their migration tactic based on attributes such as sex, age, social status, or condition (Lundberg 1988). As expected, we found that *N. viridescens* can change migratory tactic over their lifespan in natural populations. The mechanisms influencing individual migration decisions have largely been evaluated based on the demographics of migrant bird captures (e.g., Ketterson and Nolan 1976, Smith and Nilsson 1987, Boyle 2008), as opposed to multiyear data on the migratory decision of individuals (Jahn et al. 2010). Using our estimates of life history parameters in combination with previous experiments in the pond habitat, we find support for the dominance and arrival time hypotheses in our populations.

Support for the dominance hypothesis has been provided in avian systems with age-based migration, where older socially dominant adults remain as residents and migrant populations are composed of juveniles and socially inferior individuals (e.g., Smith and Nilsson 1987). These dominant adults are often larger and, in accordance with the body size hypothesis, have greater reserves for surviving the winter (Boyle 2008). Red-spotted newts are not known to have defined social hierarchies, and competitive ability is largely influenced by body size (Werner and Gilliam 1984). Repeated measures of individuals over the breeding season found that residents maintain higher body condition than migrants (M. A. Brians, H. D. McLeod, W. A. Hopkins, K. L. Grayson, *unpublished manuscript*). Migrants also end the breeding season with lower measures of body condition compared to residents in our study populations (K. Grayson, *unpublished data*). Our mark–recapture data indicate that once individuals become migrants, few switch back to being residents. Thus, individuals that remain in high condition appear able to compete for residency, while those in lower condition become migrants, supporting the resource competition mechanism postulated by the dominance hypothesis. Our higher estimates of survival for pond residents, combined with the body condition benefits from aquatic food sources and the ability to feed year-round (Morgan and Grierson 1932), suggest that residents are not physiologically limited by body size for survival overwinter in the pond, as suggested by the body size hypothesis.

The arrival-time hypothesis predicts that residency is more likely for the sex experiencing greater competition for breeding resources, where staying in the breeding habitat would result in larger gains in reproduction (Myers 1981). Several studies have shown intense competition between male *N. viridescens* for access to females and mating opportunities (e.g., Verrell 1983, Bloch and Grayson 2010). As predicted, we found that male newts were more likely to remain as residents both in an experimental setting (Grayson and Wilbur 2009) and based on our sex-specific estimates of transition probabilities between migratory states in the natural populations. Male biases are common in migration timing (earlier arrival; Morbey and Ydenberg 2001), distance (traveling shorter distances; Ketterson and Nolan 1983), and tactic (more likely to remain as residents; Adriaensen and Dhondt 1990). In our populations, sex-based differences in migration support the mechanism proposed by the arrival time hypothesis; higher rates of residency for males reflect the potential for larger reproductive gains.

Theoretical models of the conditions necessary for the evolution and maintenance of partial migration have also highlighted the importance of habitat quality and density dependence (Lundberg 1987, Kaitala et al. 1993, Taylor and Norris 2007). Empirical studies in fish and birds have found that the proportion of a population migrating can be influenced by density or food availability (e.g., Nilsson et al. 2006, Olsson et al. 2006, Brodersen et al. 2008). In accordance with these studies, our work demonstrates that density can strongly influence migration both in natural populations and in an experimental setting (Grayson and Wilbur 2009), indicating that partial migration can be a plastic response to environmental conditions.

In summary, we evaluated processes maintaining migration at the population level and assessed mechanisms influencing the decision to migrate at the individual level by determining the life history trade-offs of migration and residency. In our populations we found that partial migration can be maintained within a population through conditional asymmetries, with residents having higher fitness and inferior individuals migrating. Changes in the survival benefits of residency, through variation in the quality of the winter habitat, could alter the costs and benefits of the two tactics and would be predicted to change the proportion of the population migrating. The wide geographic and habitat range of the red-spotted newt makes it an ideal system for testing this prediction and future studies on migratory plasticity. On the individual level, our work found support for sex and resource competition as important mechanisms shaping the migration threshold for an individual, illustrating how migratory decisions can be influenced by a complex array of individual and environmental attributes.

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APPENDIX A

Study ponds at Mountain Lake Biological Station (*Ecological Archives* E092-103-A1).

APPENDIX B

Multistate mark–recapture model structure for newly captured individuals and constraints necessary for model identifiability, based on sampling methods (*Ecological Archives* E092-103-A2).

APPENDIX C

Model selection results for the complete model set fit to data from partially migrating red-spotted newts, *Notophthalmus viridescens* (*Ecological Archives* E092-103-A3).

APPENDIX D

Number of individuals captured in each state and season for male and female red-spotted newts, *Notophthalmus viridescens* (*Ecological Archives* E092-103-A4).

APPENDIX E

Phenology of fall and spring migrations for male and female red-spotted newts, *Notophthalmus viridescens* (*Ecological Archives* E092-103-A5).

APPENDIX F

The relationship between estimated pond and season-specific newt densities and transition probabilities between migratory states for male and female *Notophthalmus viridescens* (*Ecological Archives* E092-103-A6).

APPENDIX G

Estimates of apparent survival probability for adult male and female *Notophthalmus viridescens* during the breeding season (*Ecological Archives* E092-103-A7).