

A Review of the Life History and Ecology of the Eastern Newt

(Notophthalmus viridescens)

The rapid decline of the world's amphibian populations has spurred interest in their unique ecology. Nonetheless, little is known about most amphibian species. One exception is the eastern newt, *Notophthalmus viridescens*, which includes four morphologically distinct subspecies ranging across the eastern United States (Gabor and Nice 2004), the largest and most widespread of which is the red-spotted newt (*N. viridescens viridescens*). The eastern newt inhabits ponds and vernal pools in wooded areas (Gates and Thompson 1982) and is a key ecological player. Newts can significantly influence the organization and composition of these aquatic communities (Wilbur et al.; Morin 1986; Smith 2006). Furthermore, newt populations are important for conservation efforts since they may serve as indicators for forest fragmentation on account of their low population density and high migration rates (Gibbs 1998). In this review, I will focus on the main targets of recent newt research: its complex life history, keystone niche, metapopulation dynamics, and environmental sensitivity.

Like all other amphibians, it has an aquatic larval stage and a semiaquatic adult stage, but the most unique aspect of its life history is the terrestrial eft (juvenile) stage (Hulse et al. 2001). The evolutionary significance of the eft stage is contentious; some argue that it is a strategy for reducing intraspecific competition during maturation (Healy 1974, 1975) while others suggest that its primary application is increasing dispersal (Gill 1978, 1979). This allows the newt to occupy an ecological niche that affects both terrestrial and aquatic food webs. The eft stage preys exclusively on insects (Bishop 1941; MacNamara 1977; Hulse et al. 2001) but the aquatic adult

stage preys upon a wide variety of aquatic organisms and frequently (but not always) acts as a keystone predator in amphibian communities (Morin 1981; Wilber et al. 1983; Kurzara and Morin 1994; Smith 2006). Another layer of complexity stems from the structure of newt populations. Eastern newts exist in metapopulation mosaics that span a wide variety of ponds (Gill 1978). Source-sink dynamics as well as migration lead to significant temporal variation in newt population size (Gill 1978,1979; Harris et al. 1988). Finally, like many amphibians, newts are particularly vulnerable to environmental disturbance. They have highly permeable skin, which easily absorbs a variety of pollutants (Duelman and Trueb 1986; Wells 2007). Furthermore, the low population density and high dispersal rate of the newt make them sensitive to deforestation and habitat fragmentation (Gibbs 1998; Roe and Grayson 2008).

Life History

The larval stage of the eastern newt lasts 3 months (Hulse et al. 2001), during which mortality is high due primarily to predation by adult newts (Rohr et al. 2002) and other salamanders (Hulse et al. 2001) and pond desiccation (Bridges 2002). Such environmental conditions during the larval stage can slightly alter its length and affect many important developmental characteristics such as size and fecundity at maturity (Healy 1974). Larval density and intraspecific competition had a similarly dramatic affect on the development of newts (Bridges 2002). These details suggest that predation is a key determinant of ultimate fitness since predation tends to reduce intraspecific competition, increase growth rate, and decrease the length of the larval stage (Morin 1986) and thus increase size and fecundity at maturity. In summary, larval populations with predators tend to produce fewer individuals (Bridges 2002), but those that survive to the eft stage may be more likely to survive to sexual maturity.

As mentioned previously, eastern newts occasionally cannibalize larvae but this does not appear to be an important ecological relationship. Rohr et al. (2002) found that adult newts do not respond to larval alarm chemicals as a food source. However, alarm chemicals develop late in the larval stage and thus are relatively rare in natural populations (Rohr et al. 2002). However, further research is necessary to corroborate the ecological insignificance of cannibalization. If larval alarm chemicals are rare in natural populations, then selective pressures for recognizing such chemicals as food indicators would be weak.

Following the larval stage is the unique juvenile stage. The evolutionary significance of the stage has been a contentious subject. This purely terrestrial stage typically lasts 3-7 years (Hulse et al. 2001) but some coastal populations of the subspecies *N. v. dorsalis* omit the eft stage and reach sexual maturity at age 2 whereas inland populations with less variable environmental conditions do not (Healy 1974). Healy (1975) also showed that efts migrate out of ponds and establish a home territory of approximately 270 m², a size that was based on food availability rather than mobility constraints. Additionally, the movement patterns of efts are more wandering than those of migrating adults due to foraging activity (Roe and Grayson 2008). These findings led to the conclusion that the eft stage functions principally to reduce intraspecific competition and over-crowding in ponds as the newt matures. Furthermore, some populations omit the eft stage because mortality is too high in the surrounding terrestrial habitat and unstable environmental conditions favor a shorter life cycle.

The opposing theory uses the high migration rates and metapopulation structure of newts as evidence that the eft stage acts primarily to aid dispersal to new ponds. Since fine-scale local extinctions of newt subpopulations are common and the condition of shallow ponds fluctuate temporally (Gill 1978), a wide-ranging, terrestrial juvenile stage would significantly increase the

discovery of new ponds and subsequent dispersal. Gill (1979) also demonstrated that adults show high fidelity to breeding sites and thus adults probably do not discover uninhabited ponds often. Additionally, the life expectancy of sexually mature newts is conspicuously low (Gill 1978). Therefore, the long eft stage may have evolved to give individuals plenty of time to disperse while the life expectancy of adults is short to maintain a reasonable generation time. Overall, the spatial structure seems to be important when both hypotheses are considered; an eft stage will only be functional as a dispersal mechanism when habitable ponds exist at a reasonably high density.

After the eft stage, newts return to ponds and metamorphose into aquatic adults. These adults possess flattened tails and duller skin than the eft (Bishop 1941) and are important predators of amphibian larvae (Wilber et al. 1983; Morin 1986; Bridges 2002; Smith 2006). They can live as long as 13 years (Caetano and Leclair 1996). Despite its aquatic nature, adults are still capable of 0.4 km migrations between breeding and residence ponds (Gill 1979; Roe and Grayson 2008). Interestingly, neither type of pond seems to act as refugia because whenever habitat desiccation occurs, adults move to terrestrial refugia for several months before migrating to another pond in the fall or spring (Gill 1978). Adult females typically face higher mortality rates and later maturation than males (Caetano and Leclair 1996).

MATING

Newts become sexually polymorphic only during the breeding season with the males developing deeply keeled tails and visible bumps on the inside of thighs (Able 1999; Gabor 2000). Newts also have complex mating behaviors where males both ambush females (Bishop 1941) and employ a “hula” dance as a sexual display (Gabor 2000). However, the most

important dynamic in the newt's elaborate mating system is male-male competition, which is the evolutionary basis for the sexual polymorphisms. The deeply keeled tail is positively correlated with the probability of both amplexus and reproduction indicating that it improved locomotion during scramble competition and success during wrestling once amplexus is achieved (Able 1999; Gabor 2000). However, newts employ spermatophores to achieve insemination (Hardy and Dent 1988) and a deeply keeled tail was inversely related to the probability of insemination once amplexus has occurred (Able 1999).

Newt behavior also changes over the course of the breeding season. Throughout the season, males assess the sex ration of the pond through pheromones released by females and chemicals released by the cloacal gland of males (Rohr et al. 2004). The average sex ratio is 2.7 males to 1 female (Gill 1978) but both males and females avoid high male densities Early in the breeding season because the male-male wrestling exhausts both sexes (Rohr et al. 2004). As the season progresses, males become less selective about which reproductive opportunities to pursue (Rohr et al. 2004).

Keystone Niche

EFFECT ON COMMUNITY STRUCTURE

Adult eastern newts frequently prey upon the larvae of other amphibian species and act as keystone predators through differential predation. Competition is common in amphibian larval communities and negatively affects important life history characteristics like growth rate, size at metamorphosis and larval period length (Wilbur et al. 1983; Morin 1986). When newts are present, only the fastest-growing larvae escape predation and survive the larval stage; however, this high initial mortality may reduce later mortality because higher growth rates and larger size

at metamorphosis are both linked to adult fitness (Bridges 2002). Newt predation also has the broader effect of changing intraspecific and interspecific competitive relationships (Morin 1981,1986; Wilbur et al. 1983). Morin (1986) studied the predator-prey relationship between *N. viridescens* and *Hyla crucifera* and found that the newt was only slightly effective at regulating intraspecific competition. The tadpoles altered their microhabitat use so that predation rates were never high enough to counteract the negative affect of intraspecific competition on mass at metamorphosis. However, newts were much more significant regulators of interspecific competition. In the absence of newts, *Scaphiopus holbrooki* was the most dominant species. However, Wilbur et al. (1983) found that *S. holbrooki* had the lowest survivorship to metamorphosis. Finally, Kurzara and Morin (1994) found that two subspecies (*N. v. viridescens* and *N. v. dorsalis*) have different predation rates.

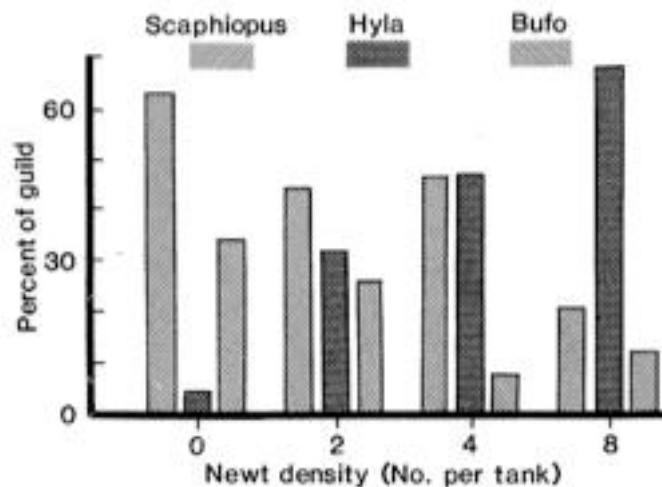


Fig 1: The effect of newt density on the relative abundances of three amphibian species. Percent composition is the mean calculated across 4 sample communities. Note the dramatic decline in Scaphiopus abundance with newt density and the correlated rise in Hyla abundance.

Recent research has revealed that eastern newts tend to combat invasive species in model populations studied so far (Smith 2006). Invasive species are differentiated from merely introduced species by the fact that they are competitively dominant over native species. Early studies of the synecological effects of newt predation revealed that a competitively dominant anuran tadpole, *Scaphiopus holbrooki*, was frequently the target of newt predation (Morin 1981, Wilber et al. 1983). Furthermore, the presence of newt predators altered the relative abundances of *S. holbrooki* and another two species (Morin 1981). This study suggests that *N. viridescens* should selectively prey on invasive species if they are competitively dominant. However, the keystone effect was not studied in invaded communities for several years. Smith (2006) found that newt predation almost completely eliminated interspecific competition from the invasive species *Osteopilus septentrionalis*. More importantly, newt predation even reduced sublethal effects of interspecific competition on the native species *B. terrestris* and *B. marinus* including growth rate and size at metamorphosis (Smith 2006). Thus, the eastern newt acts as a keystone predator in populations with a clear competitively dominant species, regardless of whether this dominant species is native or exotic.

Another significant effect of adult newts on amphibian tadpoles is the behavioral response to predation. Amphibian tadpoles respond to the presence of *N. viridescens* by dramatically reducing total activity level while increasing refugia use but do not decrease time spent feeding (Bridges 2002). Tadpoles also respond behaviorally to pond drying by accelerating development and increasing time spent feeding, but do not make these adjustments when predators are present (Bridges 2002). Therefore, newts could, theoretically, make natural larval populations more vulnerable to some threats (such as desiccation) while making them more resistant to others (such as predation later in life due to a large size at metamorphosis). Another

example of this effect occurs in frog populations infected by the fungus *B. dendrobatidis*. Parris and Beaudoin (2004) found that neither predation nor chytridiomycosis (the disease that accompanies infection) lengthened the larval period of gray tree frog larvae, but a predator-by-disease interaction slowed development by 12%. In conclusion, eastern newts occupy a predatory niche in amphibian communities with many keystone effects. *N. viridescens* as a predator fundamentally alters the demography, competitive interactions, and behavior of larval species while also affecting the species composition of the entire community.

PREDATORS AND MORTALITY

N. viridescens itself is generally not vulnerable to predation due to its toxic skin secretions and aposematic coloration (Duellman et al. 1986, Gill 1978, and Hulse et al. 2001). Snakes in the genus *Heterodon* are the most significant predator of the eastern newt while raccoons are occasional predators (Wells 2007). Gill (1978) also proposed that the toxic skin secretions might reduce leech parasitization (in addition to warding off predators), but this hypothesis has not yet been tested. Eastern newts also use alarm chemicals as a defense mechanism. All efts and adults produce alarm chemicals that individuals of both life stages respond to immediately (Rohr et al. 2002). Interestingly, the same compound appears to be an effective alarm chemical in both aquatic and terrestrial environments. Nonetheless, this makes evolutionary sense because adults and efts are syntopic whenever adults migrate or move to terrestrial refugia (Rohr et al. 2002). The defensive mechanisms of eastern newts are also able to affect the behavior of other species. Red salamanders (*Pseudotriton ruber*) exhibit Batesian mimicry of the eastern newt's defensive tail waving. Edible salamanders typically flee from

predators but *P. ruber* raises its tail like an eastern newt in order to enhance its similarity to *N. viridescens* (Brodie and Howard 1972).

Parasitization is the principal cause of mortality in red-spotted newts (Raffel et al. 2006). Leeches that carry a fungal parasite similar to *Ichthyophoris sp.* and/or an endoparasite, *Trypanosoma diemyctyli* often parasitize eastern newts (Gill 1978, Raffel et al. 2006). 12 of the 16 populations that Raffel et al. (2006) surveyed were infected. Large individuals and males were the most frequently parasitized (probably due to greater exposure). However, despite their increased rate of parasitization, males have an overall lower rate of mortality and longer life expectancy than females (Gill 1978).

Metapopulation Dynamics

The metapopulation structure of newts necessitates a mosaic of different ponds. Population size in each pond is widely ranging (from 6-2,800 individuals in Gill's study) and birth rates are greater than mortality rates only in the largest subpopulations (Gill 1978), i.e. only a few ponds are reproductively successful. Additionally, the largest subpopulations must also have to inhabit the largest ponds since adult population density is negatively correlated to larval density (Harris et al. 1988). Migration between ponds is common as adults return to the same pond each year to breed but disperse to live elsewhere throughout the year (Gill 1979). Female survivorship is highly density-dependent, so this annual dispersal is critical because it reduces crowding (Gill 1979). Therefore, a newt population typically inhabits ponds of many different sizes, some of which act as a population source but most of which act as a net population sink (Gill 1978). With these data, Gill (1978) suggested a new metapopulation model since traditional island biogeography did not adequately explain the high breeding site fidelity and consistent

reproductive failure of most ponds. Gill theorized that since newts always reproduce in the same pond each year, interdemographic gene flow is effectively 0 despite frequent migration. Furthermore, adult newts will return to their breeding pond even if it persistently functions as a population sink (Gill 1978). Therefore, rather than representing a newt metapopulation as a series of reproductive and interbreeding subpopulations, Gill views the newt as a colonizing species where most of the population is born in a handful of ponds then disperses to reduce density-dependent mortality. He also argues that efts must be the primary dispersal mechanisms because adult newts cannot act as true population founders since they will not reproduce in newly discovered pools. Finally, empirical evidence suggests that newts rapidly colonize new ponds; for example, Gill (1978) found inhabited ponds that were less than 10 years old.

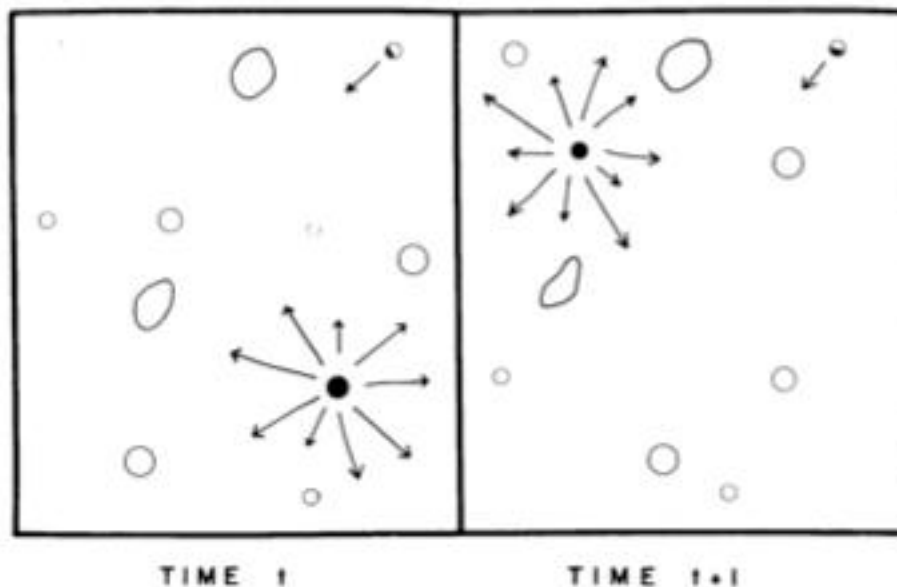


Fig 2: Schematic summary of Gill's (1978) metapopulation model. All ponds are inhabited but only the shaded ones are reproductively successful. Note that the "source" can shift from pond to pond over time.

Gabor and Nice (2004) examined the genetic basis for the current subspecies classifications but discuss how metapopulation dynamics may have affected local evolutionary

trajectories. Surprisingly, their calculations of genetic distance revealed that the current taxonomic classifications do not match the patterns of genetic variation of the species. More importantly, they found that two distinct clusters (a northern subpopulation and a southern subpopulation) had distinct genetic structures. Most of the variation in the northern population was correlated with distance, so Gabor and Nice concluded that gene flow is relatively limited. Meanwhile, among-population variation is higher than expected by distance alone in the southern subpopulation indicating that gene flow has almost completely ceased and each subpopulation is experiencing genetic drift or strong selection. In general, the metapopulation structure of *N. viridescens* probably predisposes the newt to forming genetically isolated subpopulations since efts tend to spread into new ponds rapidly but, once established, the gene flow outside of the metapopulation is virtually zero (Gill 1978).

Environmental Sensitivity

The recent decline of amphibian populations suggests that many species are highly sensitive to environmental perturbations and the eastern newt is no exception. The highly permeable skin of adults and larvae allows for regulation of internal water levels but also eases the absorption of pollutants (Hulse et al. 2001). However, many pesticides not only affect newt mortality, life history, and development but also can affect the ecological relationships between newts and prey species. For example, carbaryl, a widely used pesticide, reduced predation rates whenever either predator or prey was exposed (Bridges 1999).

However, habitat fragmentation may pose a greater threat to newt populations than pollution (Gibbs 1998, Harris et al. 1988, Roe and Grayson 2008). One characteristic that causes its susceptibility to habitat fragmentation low population density; efts are typically found at a

density of 0.03 per m² and adult population density varies from 0.8 to 4 per m² temporally (Harris et al. 1988). Furthermore newts require at least 50% cover to survive probably because leaf litter and shade slow desiccation (Gibbs 1998). The metapopulation structure of newts also makes them particularly vulnerable to habitat fragmentation. While newts can rapidly colonize new pools (Gill 1978), they depend on a relatively dense mosaic of ponds for successful dispersal and reproduction. Furthermore, migrating adults need similar terrestrial conditions as efts. Such migratory habits significant increase the newt's sensitivity to fragmentation (Roe and Grayson 2008) since roads can act as physical migration barriers and deforested areas may act as population sinks (Gibbs 1998). Worse still, the relatively long migrations observed by Roe and Grayson (2008) implies that standard wetland buffer areas may not be sufficient for protecting the eastern newt.

Conclusion

The eastern newt (*N. viridescens*) is one of few well-studied salamander species. Research has revealed its ecological significance both as a keystone predator in amphibian larval communities and as a valuable indicator of forest fragmentation while also exploring its unique population structure. Recent studies have taken the Gill's (1978) metapopulation study and examined the details of demography and migration in greater detail and Gabor and Nice (2004) have investigated regional patterns of genetic diversity, but no studies have looked at the organization of genetic variation at a finer scale. Gill (1978,1878) noted that the high breeding site fidelity of newts likely reduces the level of gene flow below what other island metapopulation models predict. However,

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