PLANNING COMMISSION EXHIBIT #167

Biological Delineation of Terrestrial Buffer Zones for Pond-Breeding Salamanders

RAYMOND D. SEMLITSCH

Division of Biological Sciences, 105 Tucker Hall, University of Missouri, Columbia, MO 65211-7400, U.S.A., email rays@biosci.mbp.missouri.edu

Abstract: *Many semi-aquatic organisms, such as salamanders, depend on both aquatic and terrestrial habitats to complete their life cycle and maintain viable populations. But current U.S. federal and state regulations protect only the wetland itself or arbitrarily defined portions of terrestrial habitat, if any. Part of the reason terrestrial habitats adjacent to wetlands are not protected is the lack of a clear understanding of the distances from shorelines that are biologically relevant to wetland fauna. Such information is critical for delineation of terrestrial "buffer zones" for wetlands, and thus for the conservation of semi-aquatic organisms. I summarized data from the literature on terrestrial habitat use by one group of pond-breeding salamanders, especially distances individuals traveled away from ponds. The results provide a basis for setting terrestrial buffer zones determined from actual habitat use by adult and juvenile salamanders. The mean distance salamanders were found from the edge of aquatic habitats was 125.3 m for adults of six species and 69.6 m for juveniles of two of these species. Assuming that the mean distance encompasses 50% of the population, a buffer zone encompassing 95% of the population would extend 164.3 m (534 ft) from a wetland's edge into the terrestrial habitat. Data from other amphibians suggest that this buffer zone is applicable to a range of species, but caution should be taken for taxa suspected to be more vagile. Wetland managers and policymakers must recognize the special needs of semi-aquatic organisms during their entire life cycle, not just during the breeding season. To maintain viable populations and communities of salamanders, attention must be directed to the terrestrial areas peripheral to all wetlands. Data on habitat use from salamanders and other semi-aquatic species make it increasingly apparent that maintaining the connection between wetlands and terrestrial habitats will be necessary to preserve the remaining biodiversity of our vanishing wetlands.*

Delineación Biológica de Zonas Terrestres de Amortiguamiento para Salamandras con Reproducción en Charcas

Resumen: *Muchos organismos semi-acuáticos, como son las salamandras, dependen tanto de hábitats acuáticos como terrestres para completar su ciclo de vida y mantener poblaciones viables. Sin embargo, las actuales regulaciones federales y estatales en los Estados Unidos protegen unicamente a los humedales o a porciones de hábitat terrestres (de ser posible). Parte de las razones por las cuales los hábitates terrestres adyacentes a humedales no son protegidos se debe a la carencia de un claro entendimiento de las distancias biológicamente relevantes partiendo de los bordes y que son utilizados por la fuana del humedal. Esta información es crítica para delinear zonas terrestres de "amortiguamiento" para humedales, y en consecuencia para la conservación de organismos semi-acuáticos. Resumo datos de la literatura sobre el uso de hábitat terrestre por un grupo de salamandras con reproducción en charcas, especialmente de distancias individuales viajadas hacia afuera de las charcas. Los resultados proveen las bases para establecer zonas terrestres de amortiguamiento determinadas a partir del uso actual del hábitat por salamandras adultas y juveniles. La distancia media a partir del borde de los hábitats acuáticos en la cual las salamandras fueron encontradas fue de 125.3 m para adultos de seis especies y de 69.6 m para juveniles de dos de estas especies. Asumiendo que la distancia media abarca un 50% de la población, una zona de amortiguamiento que abarque 95% de la población podría extenderse hasta los 164.3 m (534 pies) partiendo del borde del humedal hacia el hábitat ter-*

Paper submitted July 8, 1997; revised manuscript accepted December 10, 1997.

restre. Datos de ostros anfibios sugieren que esta zona de amortiguamiento es aplicable para un rango de especies, pero se deben tomar precauciones para taxes de los que se sospecha se desplazan mas. Manejadores de humedales y estructuradores de políticas deben reconocer las necesidades especiales de organismos semiacuáticos a lo largo de su ciclo de vida completo, no solo durante la temporada de reproducción. Se debe dirijir especial atención a las áreas terrestres periféricas a todos los humedales para mantener poblaciones viables y comunidades de salamandras. Datos de uso del hábitat por salamandras y otras especies semi-acuáticas hacen mas aparente la necesidad de mantener la conección entre humedales y hábitats terrestres para conservar la biodiversidad que aún queda en nuestros humedales en desaparición.

Introduction

An estimated 53% of original wetlands in the United States has been lost to human development during the past 200 years, likely resulting in the irreversible loss of habitat for a wide variety of plants and animals (Dahl 1990). Although U.S. federal regulations (e.g., Executive Order 11990, Protection of Wetlands) were established to protect the remaining natural wetland systems, such regulations generally encompass only aquatic habitats regularly holding water or those characterized by hydric soils (defined as saturated, flooded, or holding water long enough to develop anaerobic conditions in the upper part and hydrophytic vegetation; Dahl 1990). Although many semi-aquatic organisms such as insects, frogs, salamanders, snakes, and turtles depend on both aquatic and terrestrial habitats to complete their life cycle and maintain viable populations, protection for most species that inhabit wetlands stops at the water-land interface or upper shoreline. In response to the terrestrial needs of semi-aquatic organisms, states such as Massachusetts (Klein & Freed 1989) and Florida (Brown et al. 1990) are developing and implementing criteria for the delineation of terrestrial "buffer zones" for wetlands. Nevertheless, biological information remains sparse concerning use of terrestrial habitats adjacent to wetlands, the definition of biologically relevant distances from the shoreline, and the size of areas required during the life cycle of some species (but see Burke & Gibbons 1995).

Amphibians with complex life cycles, such as pond-breeding salamanders, depend on both aquatic and terrestrial habitats during their lifetime (Wilbur 1980) and would clearly be affected by the area of a terrestrial buffer zone (Semlitsch et al. 1996). Adult salamanders use aquatic habitats for reproduction (mating and oviposition) during specific seasons of the year, depending on the species and its geographic location. Some species spend only a few weeks breeding in aquatic habitats (e.g., 9–29 days for *Ambystoma maculatum*; Husting 1965) and then spend the remainder of the year on land in underground refuges. Aquatic larvae feed primarily on zooplankton and insects in wetlands and develop until metamorphosis is achieved (e.g., 122–172 days for *Ambystoma opacum*; Scott 1990). After metamorphosis, juveniles emigrate to terrestrial habitats, where they grow and develop to reproductive maturity. Some species reach maturity and return to the pond to breed for the first time after 3–6 months (e.g., 1-year-old *Ambystoma talpoideum*; Semlitsch et al. 1988) or after several years (e.g., 2- to 3-year-old *Ambystoma opacum*; Scott 1994). Adults can breed repeatedly during their lifetime (e.g., up to six times for *Ambystoma talpoideum*), returning to the same pond each time (Semlitsch et al. 1993). Thus, both aquatic and terrestrial habitats are critical to the reproduction and survival of resident salamander populations.

I summarize data from the literature on the use of terrestrial habitats by one group of pond-breeding salamanders, especially distances individuals travel away from ponds. I then calculate an average distance for these species and evaluate whether current laws adequately protect salamander populations. In addition, I recommend a biologically delineated terrestrial buffer zone that protects different portions of the population that is based on the terrestrial habitat actually used by salamanders, and I discuss the applicability of this buffer zone to other taxa of amphibians.

Methods

Reliable data were obtained from published literature and unpublished dissertations for six species of pond-breeding, ambystomatid salamanders in five states (Table 1). To maintain reliability of results, only data collected from direct monitoring of migratory activity (with radioactive tags or radiotransmitters) or from direct observation of marked—or, in one case, unmarked—individuals originating from a known breeding pond were included in the analysis. There were anecdotal observations of individuals found known distances from ponds, but there was no way of determining if the individual actually originated from the nearest pond or from some more distant unknown site. In addition, much of the literature reports "maximum" migratory distances, which are of interest but cannot be used to determine terrestrial habitat use by the majority of the population. These data were not included because of obvious ambiguities.

Table 1. Summary of terrestrial migration distances from breeding sites for six species of *Ambystoma* salamanders from several geographic locations.

Species and location	Average migration distance (m)[a] Adults	Juveniles	Data source
Ambystoma jeffersonianum			
Michigan	38.9[b] (22–108) $n = 6$	—	Wacasey (1961)[c]
Michigan	92.4[b] (15–231) $n = 45$	—	Wacasey (1961)[d]
Indiana	252.0 (20–625) $n = 86$	92.2 (3–247) $n = 13$	Williams (1973)[e]
Kentucky	250.0 $n = 10$	—	Douglas & Monroe (1981)[f]
Ambystoma maculatum			
Michigan	66.9[b] (26–108) $n = 2$	—	Wacasey (1961)[c]
Michigan	103.3[b] (15–200) $n = 14$	—	Wacasey (1961)[d]
Indiana	64.2 (0–125) $n = 7$	—	Williams (1973)[e]
Kentucky	150.0 (6–220) $n = 8$	—	Douglas & Monroe (1981)[f]
Michigan	192.0 (157–249) $n = 6$	—	Kleeberger & Werner (1983)[f]
New York	118.0 (15–210) $n = 8$	—	Madison (1997)[g]
Ambystoma opacum			
Indiana	193.7 (0-450) $n = 12$	—	Williams (1973)[e]
Kentucky	30.0[b] $n = 6$	—	Douglas & Monroe (1981)[f]
Ambystoma talpoideum			
South Carolina	178.0 (13–287) $n = 17$	47.0 (14–204) $n = 5$	Semlitsch (1981*a*)[e]
Ambystoma texanum			
Indiana	52.4 (0–125) $n = 10$	—	Williams (1973)[e]
Ambystoma tigrinum			
South Carolina	162.0[b] $n = 1$	—	Semlitsch (1983)[e]
New York	60.5 (0–286) $n = 27$	—	Madison & Farrand (1998)[g]
Mean (±1 S.D.)	125.3 ± 73.16 m	69.6 m	

[a]*Ranges of values are given in parentheses and sample sizes (n = number of individuals) are provided.*
[b]*Minimum estimate because searches were restricted to areas near the pond.*
[c]*Hand collecting of marked individuals.*
[d]*Hand collecting of unmarked individuals.*
[e]*Monitoring with radioactive tantalum-182 tags.*
[f]*Monitoring with radioactive cobalt-60 tags.*
[g]*Monitoring with implanted radiotransmitters.*
[b]*Minimum estimate because monitoring was prematurely terminated.*

In addition, data on distances traveled during homing studies were not included because they would clearly bias estimates of distances traveled away from ponds during natural emigration.

Direct observation of marked and unmarked individuals (either post-breeding or post-metamorphic) from mark-release-recapture studies in terrestrial habitats around known breeding or natal ponds provided reliable data, but these data usually consisted of only one observation per salamander (Wacasey 1961). In the past, monitoring the terrestrial migratory activity of individuals typically consisted of collecting post-breeding adults or metamorphosing juveniles at a pond, inserting a small radioactive wire tag (tantalum-182 or cobalt-60) under the skin, and subsequently locating the same individuals periodically with a portable scintillation counter as they emigrated into terrestrial habitats (Williams 1973; Douglas & Monroe 1981; Semlitsch 1981*a*, 1983). Detectability of tagged individuals was relatively high over short distances (<5 m), even when salamanders were underground, and radioactivity from tags was unlikely to affect migration behavior or ability (but see effects on growth and tag longevity; Semlitsch 1981*b*). More recently, individual monitoring was enhanced by small radiotransmitters (<2.0 g) surgically implanted into adult salamanders migrating to breeding ponds (Madison 1997; Madison & Farrand 1997). The salamanders were monitored periodically in the pond during the breeding period and during post-breeding emigration to terrestrial habitats. In other studies, information on use of terrestrial habitats, refuges, and time spent on land was also recorded (e.g., Shoop 1965; Douglas 1979; Semlitsch 1981*a*; Madison & Farrand 1997).

I summarized the data on average migration distances from the edge of the aquatic habitat for adults and metamorphosed juveniles of each species, from published values in the source reference when possible (Table 1). In one case, raw data from collections of unmarked individuals were estimated from a plot of localities around two ponds (Wacasey 1961, Fig. 13, p. 61). Estimates were derived by counting the number of individuals within each concentric circle around the ponds and multiplying the total by the mid-value of each circle (i.e., 100-foot [30.8-m] contour lines). Because the average migration distance derived separately for each pond was very similar among ponds, assuming all individuals came from one or the other pond, data were combined for the two ponds (Wacasey 1961).

Results

Adult salamanders ($n = 265$) of six species were found an average of 125.3 m from the edge of aquatic habitats, whereas juveniles ($n = 18$) of two species were found an average of 69.6 m from the edge (Table 1). Adult salamanders were found up to 625 m and juveniles up to 247 m from the edge of wetlands. All post-breeding adults and newly metamorphosed juveniles were found outside the probable, current federally delineated wetland boundary, and 76% of all individuals were found outside the extended terrestrial buffer zone recommended in some states (i.e., 30.8 m [100 ft]; Massachusetts and Florida). If we assume that the distances salamanders move from wetlands are a normal distribution (test of normality for data in Table 1; $W = 0.927$, $p = 0.2168$), then by definition the mean for adults of all species combined ($\bar{x} = 125.3$ m) represents a distance encompassing only 50% of the population. A buffer zone encompassing the majority (95% confidence limits = $\bar{x} \pm 2.13$ [$\alpha = 0.05$, df = 15] $\times$ standard deviation/$\sqrt{n}$) of the population would have to encompass the terrestrial habitat 164.3 m (534 ft) from a wetland's edge.

The length of time adults spent in aquatic habitats during the breeding season was 9–29 or 4–20 days for *A. maculatum* (Husting 1965; Shoop 1965); 29.7 and 19.4 days for male and female *A. jeffersonianum* (Douglas 1979); 51 days for *A. talpoideum* (Semlitsch 1981*a*); 38 days for *A. cingulatum* (Palis 1997); and 12.1 days for *A. tigrinum* (Madison & Farrand 1997). For these species the length of time adults spent in terrestrial habitats during the remainder, and majority, of their annual cycle was 336–356 or 345–361 days (92.1–97.5% or 94.5–98.9% of the year) for *A. maculatum*; 335.3–345.6 days (91.9–94.7%) for *A. jeffersonianum*; 313.8 days (85.9%) for *A. talpoideum*; 327 days (89.6%) for *A. cingulatum*; and 352.9 days (96.7%) for *A. tigrinum* (references cited above for each species.). In terrestrial habitats, adult salamanders were found primarily in closed-canopy habitat most often found in underground blind tunnels, burrows, or mammal runway systems (2.5–7.5 cm underground; Wacasey 1961; Semlitsch 1981*a*; Madison 1997; Madison & Farrand 1997). Salamanders feed primarily underground in such tunnel systems, and they also use them for winter (or summer) refuges.

Discussion

These analyses indicate that large terrestrial areas adjacent to wetlands are used by adult pond-breeding salamanders and newly metamorphosed juveniles throughout the majority of the year. The exclusion of these terrestrial areas from protection under wetland statutes would most likely reduce recruitment of juveniles into the breeding adult population, reduce adult survival, and therefore reduce the potential of the population to persist (Semlitsch et al. 1996). The widespread use of adjacent terrestrial habitats by other amphibians and semiaquatic species for various parts of their life cycle further underscores their importance (Dole 1965*a*, 1965*b*; Gill 1978; Bennett et al. 1980; Semlitsch & Moran 1980; Semlitsch et al. 1988; Berven & Grudzien 1990; Buhlmann et al. 1993; Burke & Gibbons 1995; Reese 1996) and suggests that these are critical habitats in need of protection.

Although there is variation in the size of terrestrial habitats used by salamander species, presumably related to life-history requirements, geographic variation in climate and habitat, or even among particular ponds because of topography, vegetation, and wetland size, a buffer zone cannot realistically be determined for each wetland and species. By combining all available data, it was my intention to suggest a general buffer zone that could be used for conservation purposes for most wetlands and species of ambystomatid salamanders. Because the data used in my calculations were from six species of ambystomatid salamanders in five states and were collected over a period of several decades, it is likely that the 164-m buffer zone I calculated for 95% of the population is robust to most sources of variation mentioned above. It is also important to note that some of the literature values used in this analysis were minimum estimates of mean distances traveled from ponds because of limited monitoring time or due to increased search area as the radius from the pond increased. Therefore, the measured values probably underestimate the actual buffer zone needed to encompass 95% of the population of some species of salamanders, so my recommended buffer zone of 164 m is an underestimate.

How applicable are these findings to other taxa of pond-breeding salamanders or anurans? Much of the salamander data not used in my calculations were collected indirectly or were the result of an incomplete duration of monitoring, so they are likely biased. Nevertheless, among other species of *Ambystoma*, these data show that my recommended buffer zone might encompass most adults and juveniles of *A. californiense* (Loredo et al. 1996) and some populations of western *A. tigrinum* (Gehlbach 1967; Gehlbach 1969; Webb & Roueche 1971), but it may be an underestimate of the habitat used by *A. cingulatum* (Means et al. 1996) and *A. mabeei* (Hardy 1969), which are thought to move hundreds of meters from their breeding ponds. Likewise for other taxa of pond-breeding salamanders, my recommended buffer zone would likely accommodate species such as *Eurycea l. longicauda* that disperse only short distances from water (Anderson & Martino 1966), as is common for most woodland salamanders (Plethodontidae; e.g., Madison 1969). Also, it is reported that most *Hynobius nebulosus tokyoensis* disperse less than 100 m from breeding ponds (Kusano & Miyashita 1984) and that 90% of *Taricha torosa granulosa* remain within 200 m of their pond (Pimentel 1960). The recommended buffer zone, however, may underestimate the size of terrestrial habitats needed for some species of the family Salamandridae in which greater dispersal distances are commonly reported (e.g., *Notophthalmus*; Healy 1974, 1975; Dodd 1996). For anurans it is also apparent that the recommended buffer zone is quite adequate for species like *Bufo japonicus* (Kusano et al. 1995), *Pseudacris t. triseriata* (Kramer 1973) and *Hyla andersoni* (Freda & Gonzalez 1986) but may be an underestimate of the terrestrial area needed for more vagile species (Dole 1965*a*; Berven & Grudzien 1990; Sinsch 1990).

These examples yield positive but mixed results for the adequacy of the recommended buffer zone and illustrate the need for more data based on direct monitoring techniques such as miniaturized radiotransmitters (e.g., Kusano et al. 1995; Madison 1997). I encourage further documentation of habitat requirements for these and other species, especially those in underrepresented geographic regions (e.g., montane and western United States), for species with special habitat requirements, and for species listed as endangered by U.S. federal and state governments. Nevertheless, my recommended buffer zone of 164 m, which can be easily defended on the basis of direct biological evidence, is more ecologically realistic than existing buffer zones and is a start in the right direction for initiating legislative change.

Finally, my results raise three important issues. First, do salamanders really need all this terrestrial habitat to maintain viable populations, or would they simply use whatever area was available? To my knowledge, there are no data to address this question directly by evaluating the dynamics of populations—reproduction and survival—constrained by different-sized buffer zones. But there is evidence to suggest that if the terrestrial density of juveniles or adults is increased, there will be a concomitant decrease in survival and reproductive potential (i.e., reduced body size at first reproduction and increased age at first reproduction) of some species (Pechmann 1994). Thus, it is likely that habitat quality such as density of food and underground refuges within the buffer zone is also important.

The second issue is whether such terrestrial areas are truly buffer zones as originally intended, zones of protection around critical habitat (Schonewald-Cox 1988). The biological significance of the buffer zones as shown here indicates they are more critical than the original term suggests. For salamanders as well as other semiaquatic amphibians, I suggest that the upland terrestrial habitat is more than just an area where individuals occasionally feed, stop, or wander. Rather, it is a "life zone," a critical habitat vital for feeding, growth, maturation, and maintenance of the entire juvenile and adult breeding population (e.g., Gill 1978; Semlitsch et al. 1988; Scott 1994). A buffer zone then by definition would serve to further protect populations (being larger than the recommended 164 m) by reducing the potential for edge effects that may penetrate up to 50 m (163 ft) into critical habitats (Murcia 1995; deMaynadier & Hunter 1996).

The last and perhaps most important issue is that, in recommending a terrestrial buffer zone for wetlands, I have focused on the conservation of local populations and have avoided the more complex issue of metapopulation dynamics and landscape-level processes (Brown & Kodric-Brown 1977; Pulliam 1988; Hanski & Gilpin 1991). It is critical for managers to realize that any application of the 164-m buffer zone protects only that specific population for as long as it remains viable (i.e., births equal or exceed deaths). Considering that many vernal pools and ponds used by salamanders are temporary over geological time, or possibly even over shorter periods of ecological time due to succession, inevitable extinction of local populations must be counterbalanced by colonization of new sites (e.g., Gill 1978). Thus, it is clear that a successful management plan must also protect additional terrestrial habitats for corridors of movement of salamanders from source ponds to new sites and for recolonization or rescue of extinct populations at old sites.

Wetland managers and policymakers must recognize the special needs of semi-aquatic organisms during their entire life cycle and not just during the most obvious portion, the breeding season. To maintain viable populations and communities of salamanders, attention must be directed to the terrestrial areas peripheral to all wetlands. Data from salamanders and other semi-aquatic species make it increasingly apparent that protection of wetlands should not stop at the water-land interface or upper shoreline, as U.S. federal regulations still allow. Maintaining the connection between wetlands and terrestrial habitats will be necessary to preserve the remaining biodiversity of our vanishing wetlands.

Acknowledgments

I thank D. Madison for access to manuscripts in press and R. Bodie, M. Boone, T. Bridges, V. Burke, W. Gibbons, J. Krenz, N. Mills, M. Parris, and T. Ryan for comments and criticisms on my manuscript. I especially thank J. Petranka for insightful additions to the original discussion and R. Bruce for facilities at the Highlands Biological Station, North Carolina, during the writing of this paper. This research was partially supported by Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.

Literature Cited

Anderson, J. D., and P. J. Martino. 1966. The life history of *Eurycea l. longicauda* associated with ponds. American Midland Naturalist 75:257-279.

Bennett, S. H., J. W. Gibbons, and J. Glanville. 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. American Midland Naturalist 103:412-416.

Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic structure. Evolution 44: 2047-2056.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Brown, M. T., J. Schaefer, and K. Brandt. 1990. Buffer zones for water, wetlands, and wildlife in east central Florida. CFW publication #89-07. Florida agricultural experiment stations journal series no. T-00061. University of Florida, Gainesville.

Buhlmann, K. A., J. C. Mitchell, and C. A. Pague. 1993. Amphibian and small mammal abundance and diversity in saturated forested wetlands and adjacent uplands of southeastern Virginia. Pages 1-7 in Eckles, S. D., A. Jennings, A. Spingarn, and C. Weinhold, editors. Proceedings of the conference on saturated forested wetlands in the mid-Atlantic region, 29-31 January, 1992. U.S. Fish and Wildlife Service, Annapolis, Maryland.

Burke, V. J., and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365-1369.

Dahl, T. E. 1990. Wetlands: losses in the United States 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, D.C.

deMaynadier, P. G., and M. L. Hunter, Jr. 1996. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230-261.

Dodd, C. K., Jr. 1996. Use of terrestrial habitats by amphibians in the Sandhills Uplands of north-central Florida. Alytes 14:42-52.

Dole, J. W. 1965*a*. Summer movements of adult leopard frogs, *Rana pipiens* Schreber, in northern Michigan. Ecology 46:236-255.

Dole, J. W. 1965*b*. Spatial relations in natural populations of the leopard frog, *Rana pipiens* Schreber, in northern Michigan. American Midland Naturalist 74:464-478.

Douglas, M. E. 1979. Migration and sexual selection in *Ambystoma jeffersonianum*. Canadian Journal of Zoology 57:2303-2310.

Douglas, M. E., and B. L. Monroe. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). Copeia 1981:460-463.

Freda, J., and R. J. Gonzalez. 1986. Daily movements of the treefrog, *Hyla andersoni*. Journal of Herpetology 20:469-471.

Gehlbach, F. R. 1967. Evolution of tiger salamanders (*Ambystoma tigrinum*) on the Grand Canyon rims, Arizona. Yearbook of the American Philosophical Society 1967:266-269.

Gehlbach, F. R. 1969. Determination of the relationships of tiger salamander larval populations to different stages of pond succession at the Grand Canyon, Arizona. Yearbook of the American Philosophical Society 1969:299-302.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145-166.

Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics. Academic Press, London.

Hardy, J. D., Jr. 1969. Reproductive activity, growth, and movements of *Ambystoma mabeei* Bishop in North Carolina. Bulletin of the Maryland Herpetological Society 5:65-76.

Healy, W. R. 1974. Population consequences of alternative life histories in *Notophthalmus v. viridescens*. Copeia 1974:221-229.

Healy, W. R. 1975. Terrestrial activity and home range in efts of *Notophthalmus viridescens*. American Midland Naturalist 93:131-138.

Husting, E. L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965:352-362.

Kleeberger, S. R., and J. K. Werner. 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. Journal of Herpetology 17:176-177.

Klein, K. C., and R. Freed. 1989. Implementing the Massachusetts Wetlands Protection Act: the local perspective. Pages 499-507 in D. W. Fisk, editor. Wetlands: concerns and successes. American Resources Association, Bethesda, Maryland.

Kramer, D. C. 1973. Movements of western chorus frogs *Pseudacris triseriata triseriata* tagged with Co-60. Journal of Herpetology 7: 231-235.

Kusano, T., and K. Miyashita. 1984. Dispersal of the salamander, *Hynobius nebulosus tokyoensis*. Journal of Herpetology 18:349-353.

Kusano, T., K. Maruyama, and S. Kaneko. 1995. Post-breeding dispersal of the Japanese toad, *Bufo japonicus formosus*. Journal of Herpetology 29:633-638.

Loredo, I., D. Van Vuren, and M. L. Morrison. 1996. Habitat use and migration behavior of the California tiger salamander. Journal of Herpetology 30:282-285.

Madison, D. M. 1969. Homing behavior of the red-cheeked salamander, *Plethodon jordani*. Animal Behavior 17:25-39.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology 31: 542-552.

Madison, D. M., and L. Farrand. 1997. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. Copeia 1998:402-410.

Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander (*Ambystoma cingulatum*). Conservation Biology 10:426-437.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58–62.

Palis, J. G. 1997. Breeding migration of *Ambystoma cingulatum* in Florida. Journal of Herpetology 31:71–78.

Pechmann, J. H. K. 1994. Population regulation in complex life cycles: aquatic and terrestrial density-dependence in pond-breeding amphibians. Ph.D. dissertation. Duke University, Durham, North Carolina.

Pimentel, R. A. 1960. Inter- and intrahabitat movements of the rough-skinned newt, *Taricha torosa granulosa* (Skilton). American Midland Naturalist 63:470–496.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Reese, D. A. 1996. Comparative demography and habitat use of western pond turtles in northern California: the effects of damming and related alterations. Ph.D. dissertation. University of California, Berkeley, California.

Schonewald-Cox, C. M. 1988. Boundaries in the protection of nature reserves. Bioscience 38:480–486.

Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology 71:296–306.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396.

Semlitsch, R. D. 1981*a*. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology 59:315–322.

Semlitsch, R. D. 1981*b*. Effects of implanted Tantalum-182 wire tags on the mole salamander, *Ambystoma talpoideum*. Copeia 1981: 735–737.

Semlitsch, R. D. 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Canadian Journal of Zoology 61:616–620.

Semlitsch, R. D., and G. B. Moran. 1980. Ecology of the redbelly snake (*Storeia occipitomaculata*) using mesic habitats in South Carolina. American Midland Naturalist 111:33–40.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184–192.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1993. Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influences. Journal of Animal Ecology 62:334–340.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217–248 in M. L. Cody, and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California.

Shoop, C. R. 1965. Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. Science 149:558–559.

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology, Ecology, and Evolution 2:65–79.

Wacasey, J. W. 1961. An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonianum*, in southern Michigan. Ph.D. dissertation. Michigan State University, Lansing.

Webb, R. G., and W. L. Roueche. 1971. Life history aspects of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan desert. Great Basin Naturalist 31:193–212.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

Williams, P. K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. dissertation. Indiana University, Bloomington.