

12-2014

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Article

The Importance of Maintaining Upland Forest Habitat Surrounding Salamander Breeding Ponds: Case Study of the Eastern Tiger Salamander in New York, USA

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External Editor: Deanna H. Olson

Received: 6 October 2014; in revised form: 2 December 2014 / Accepted: 2 December 2014 / Published: 9 December 2014

Abstract: Most amphibians use both wetland and upland habitats, but the extent of their movement in forested habitats is poorly known. We used radiotelemetry to observe the movements of adult and juvenile eastern tiger salamanders over a 4-year period. Females tended to move farther from the breeding ponds into upland forested habitat than males, while the distance a juvenile moved appeared to be related to body size, with the largest individuals moving as far as the adult females. Individuals chose refugia in native pitch pine—oak forested habitat and avoided open fields, roads, and developed areas. We also observed a difference in potential predation pressures in relation to the distance an individual moved from the edge of the pond. Our results support delineating forested wetland buffer zones on a case-by-case basis to reduce the impacts of concentrated predation, to increase and protect the availability of pitch pine—oak forests near the breeding pond, and to focus primarily on the habitat needs of the adult females and larger juveniles, which in turn will encompass habitat needs of adult males and smaller juveniles.

Keywords: *Ambystoma tigrinum*; tiger salamander; amphibians; radiotelemetry; buffer zone; conservation management; forested habitat

1. Introduction

Habitat loss due to development and resource acquisition, especially in or near wetlands, has increasingly become an issue linked with amphibian decline [1–3]. Over half the wetlands in the United States have been lost to development and poor mitigation practices [4–8]. As a result, many populations of amphibians are pushed into smaller areas with minimal protection. The occupation of both wetland and forested upland habitats by many amphibian species has exacerbated the situation, necessitating policies that include both wetlands and adjacent non-wetland habitats [4,7–12].

Studies that include both adult and juvenile amphibian movements are particularly critical because they provide insights into emigration (movements to and from breeding ponds) and dispersal (one-way movement from one breeding pond to another) behaviors [13], and habitat requirements in upland forests [4,7,8,10–14]. Details on survival and resource needs in upland habitat are often scarce, mainly because amphibians often live in forest floor refuges or tunnels throughout the nonbreeding period [14–21]. Some reports suggest the use of “buffer” or “life” zones to protect upland habitat [4,7–12,22], and many of these studies were initiated because of immediate necessity for buffer zone policies in order to offer at least some protection for amphibians in a growing number of permit applications and court cases involving land development. Unfortunately, for some amphibian species, accurate and localized guidelines encompassing the long-term habitat use and survival of all classes of individuals within populations are still needed. Even where upland data are becoming more available, additional solutions for long-term population maintenance are necessary [3,12,14,16,23–27].

Further complicating protection policy is the likelihood that the various sex and size classes within each species would have different resource needs [7,12,21,23,26–29]. Potential differences in adult male and female movements and space needs have not been studied in detail in most amphibian species. Some studies have suggested that females may move farther from breeding ponds than males following the breeding season [25,30–36]. Moreover, females tend to spend less time in breeding ponds than males, arriving later and emigrating earlier in the season [14,16,24,35,37,38]. These differences could potentially imply different selection pressures or resource needs between sexes. Furthermore, if females move farther than males within a particular species, the protection of adequate forested buffer zones around breeding habitat becomes even more critical.

Knowledge of juvenile recruitment and movement is also crucial to conservation planning. Without an understanding of the presumably most vulnerable group of individuals within a species, appropriate conservation recommendations cannot be developed. Due to the small size of juvenile amphibians, few studies have looked at juvenile survival, habitat use, and movement. Most studies of juveniles have used drift fence and mark-recapture techniques as opposed to radiotelemetry [3,12,20,27,29,30,39,40], but there have been some successful studies with smaller species of salamanders using powder tracking and PIT tags [41–43]. While drift fence methods can provide some information on the extent and direction of juvenile movement, radiotelemetry allows the collection of data on hourly-daily travel, exact foraging

areas, burrow use, number of movements, and predation. Potentially complicating the situation for juvenile emigrations are that juvenile body size and emergence can vary considerably with pond hydroperiod and water temperature [44,45]. One study on *Ambystoma tapoideum* suggested that the number of successful juveniles was related to the pond hydroperiod [46].

A model species for examining sex and size differences in habitat use and movement is the eastern tiger salamander (*Ambystoma tigrinum*). Adults and juveniles occupy both wetland and upland forested habitat, sexes have different resident times at breeding wetlands, and juveniles are large enough to follow using radiotracer implants [14,34,37,38,47]. This species is endangered in New York, USA, and at the time of this study, *A. tigrinum* was only consistently found in a few isolated populations on protected state, federal, and private lands in Suffolk County, Long Island, NY. The freshwater wetland act in New York includes regulation of an adjacent area extending 30 m perpendicular to the edge of the wetland, and only protects the wetland itself [48]. The New York State Department of Environmental Conservation (NYSDEC) also: (1) recommends 164 m buffer zones specifically for *A. tigrinum*, based on Semlitsch [4], and (2) suggests that no more than 50% of upland habitat within 305 m of the breeding wetland be converted to unsuitable habitat [49]. Unfortunately, the latter two guidelines are not legal mandates within New York.

Our first objective of this study was to observe the extent and timing of the movements and habitat use of adult and juvenile eastern tiger salamanders (*Ambystoma tigrinum*) throughout the annual cycle. Our second objective was to determine if existing buffer zone requirements and recommendations in New York pertaining to freshwater wetlands were adequate to protect the necessary forested habitat for both sex and size-age class of this species. To fulfill these objectives, we used radiotelemetry to observe movements and habitat use of eastern tiger salamanders. We hypothesized that adult female tiger salamanders would travel greater distances into the upland forested habitat during emigration than males, potentially biasing zones of protection that are based on averaging emigration distances across both sexes [25,30–36]. Second, we hypothesized that a percentage of juveniles would travel farther than the adults, since some juveniles disperse to other wetlands from the natal wetland, rather than simply emigrating, creating a need for safe dispersal routes connecting wetlands [50,51]. Third, we predicted that the distance moved by juveniles would vary by body size, because larger juveniles could have more energy reserves and be less vulnerable to dehydration during movement [52,53]. Fourth, we predicted that since habitat characteristics affect emigration movements [3,12,40], adult and juvenile tiger salamanders would select refugia within the forested pitch pine—oak forest.

2. Methods

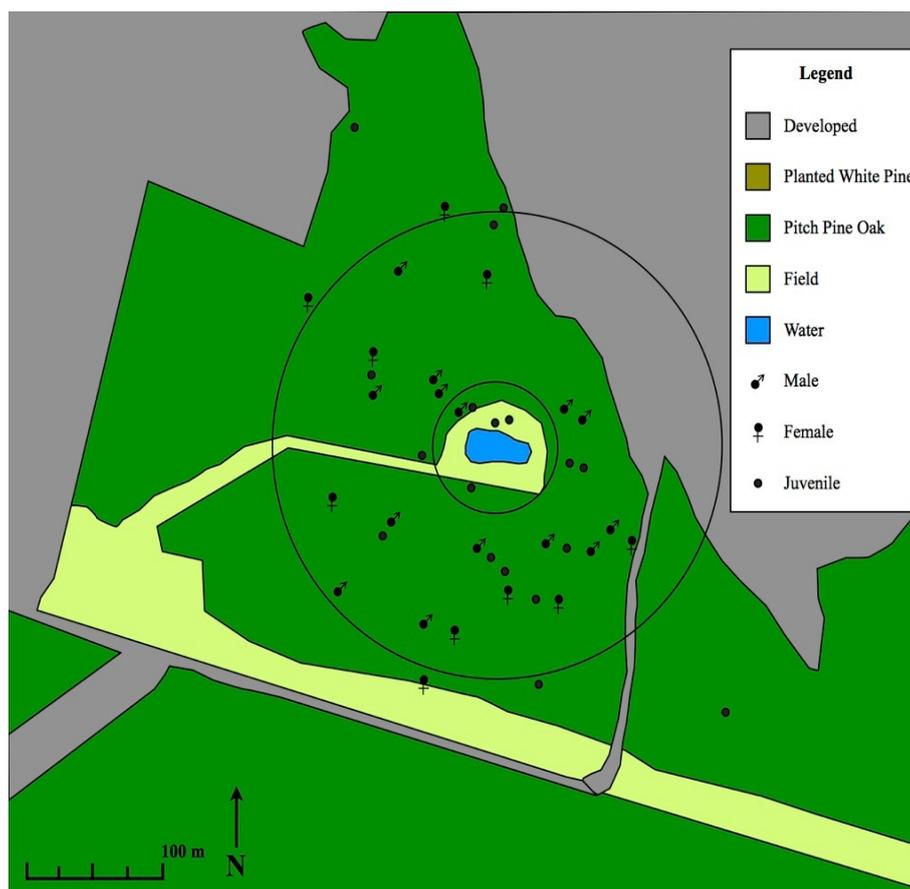
2.1. Study Site

Our study was centered around three focal breeding ponds (Figure 1) on the property of the United States Department of Energy's Brookhaven National Laboratory (BNL), Suffolk County, Long Island, NY from 2005 through 2008. This property falls within the Long Island Pine Barrens Region where the dominant habitat type is pitch pine—oak forest, with varying proportions of pitch pine (*Pinus rigida*) and one or more oak species (*Quercus coccinea*, *Q. rubra*, *Q. alba*, *Q. velutina*). The understory is dominated by ericaceous plants, such as huckleberry (*Gaylussacia baccata*), blueberry

(*Vaccinium pallidum*), wintergreen (*Gaultheria procumbens*), hudsonia (*Hudsonia ericoides*), and Pennsylvania sedge (*Carex pensylvanica*), with occasional patches of scrub oak (*Quercus ilicifolia*). Aside from the developed areas on the BNL property (buildings, parking lots, etc.), there are also several stands of planted white pine (*Pinus strobus*) with sparse understory, and open, grassy fields.

Pond L1 is maintained for aquatic wildlife, but collects untreated runoff from a ditch that runs behind buildings 350 m north of the pond (Figure 1a). We collected adult tracking data from this pond starting in February 2005 and juvenile tracking data starting in June 2005. Pond L3 was added as a focal pond for this study in the summer of 2005, following captures of a high number of larvae during inventory sampling of all BNL ponds (Figure 1b). We began tracking adults in March 2006. This pond is 1.1 km northeast of L1. Pond L7 is located 2.3 km east of L1 with fields, forest, and paved and gravel roads separating the two wetlands (Figure 1c). This pond is 1.9 km southeast of L3. Only open fields, firebreaks, and roads occur between L7 and L3. We began tracking adults in February 2005 and juveniles in July 2005.

Figure 1. Locations of males, females, and juveniles at each of the focal ponds, L1 (a); L3 (b); and L7 (c) at Brookhaven National Laboratory, Long Island, New York, USA from 2005–2008. Each location represents the maximum distance an individual was located from the edge of the breeding pond. The inner circle represents an average, mandated 30 m buffer from the edge of the pond in New York State, with the minimum distance from the edge of the pond being 30 m. The outer circle represents the recommended 164 m buffer from development in New York State based on Semlitsch [4].



(a)

Figure 1. Cont.



(b)



(c)

2.2. Radiotelemetry Equipment

The radiotransmitter implants were 1.8 g BD-2H units with internal helix antennas (Holohil Systems Ltd., Carp, ON, Canada). Radiotransmitter frequencies ranged from 149 to 152 MHz with a 14-week battery life. We used an R-1000 radio receiver (Communications Specialists, Inc., Orange, CA, USA) and a fold-up, 3-element Yagi antenna for signal detection and direction determination. Signal detection distance averaged about 60 m.

2.3. Trapping and Surgical Procedures

Animals for radiotracking were captured from the ponds using dip nets and seines, or by using drift fences and pitfall traps. Four, 6 m-long aluminum fences were constructed at the northeast, southeast, northwest, and southwest corners of each pond, 3 m in distance from the pond edge. Five-gallon buckets were placed on the ends and in the center of the fence line and on each side of the fence to detect movement direction.

We used surgical and tracking techniques as outlined in Madison *et al.* [54]. Radiotransmitters were implanted into the coelomic cavity of each animal (35 males, 27 females and 62 juveniles; 9 males, 7 females, and 3 juveniles were reimplanted at least once) [55]. Animals were anesthetized using MS-222 (3-aminobenzoic acid ester methanesulfate salt) dissolved into a 0.25% solution using distilled water, and buffered with sodium bicarbonate to a pH of 7 [54–57]. Animals were then rinsed with cool tap water to remove excess anesthetic and placed on a wet paper towel. Instruments and implants were sterilized in 95% ethanol. A 10 mm longitudinal incision was made in the left ventrolateral abdominal wall anterior to the left hind leg, an implant was inserted, and then a minimum of twelve sterile polyvioline sutures (LOOK 5-0) were used to close the incision.

2.4. Tracking Methods

Animals were released at dusk approximately 24 hours after surgery. Salamanders captured by drift fence sections were released on the opposite side of the fence in areas of high ground cover within 3 m of capture, giving the animal a choice of returning toward the pond or proceeding into upland habitat. Animals captured in the ponds were released in the water near the capture point.

After release, position checks were taken at least every 48 hours. Initial positions of salamanders were obtained by local triangulation [58], and exact underground positions were determined by direct overhead localization [14,54].

All salamanders were in burrow systems when we needed to retrieve them for radiotransmitter replacement or removal. To excavate animals, we made channel cuts entirely around the position of the animal with a small hand shovel about 0.5 m from the position to a depth of 6 to 15 cm [14]. If the animal did not emerge from its burrow into these channels, we carefully excavated above the signal down to the animal. Refuge use and overall post-operative condition were determined upon retrieving salamanders [14]. When possible, radiotransmitters were surgically replaced with new ones after 11–13 weeks. Salamanders were released at dusk 24 hours after surgery in vegetative shelter no more than 2 m from the capture point.

2.5. Data Analysis

The maximum net distance from the breeding pond was computed using the Hawth's Analysis Tools extension for ArcGIS 9 software [59]. Animals with a zero distance recorded were not included in the analyses ($N = 3$ adults; $N = 15$ juveniles). These animals were not located after an initial fix was obtained post-release. We used Kruskal-Wallis and Mann-Whitney U tests for the remaining animals ($N = 59$ adults; $N = 47$ juveniles) to compare the number of days we tracked each individual and the maximum distance from the edge of the pond because these data deviated from normal distributions and did not normalize with standard transformations. We grouped data by males, females, and juveniles to determine potential differences between breeding ponds and age and sex classes. We used a t -test to compare body size of males and females. To determine if body size contributed to the distance an animal moved from the edge of the pond, Pearson correlation was used to determine the relationship between adult and juvenile body size and distance moved. Fisher exact probabilities were used to examine the relationship between radiotransmitter recovery and the last known location of adult animals from the edge of the breeding pond. Mann-Whitney U tests were used to compare the distances juveniles moved from the edge of the breeding pond when grouped by radiotransmitter recovery *versus* radiotransmitter loss (lost signals). All statistics were run using StatPlus statistical software for Microsoft Excel (AnalystSoft 2009, Alexandria, VA, USA) and were performed with $\alpha = 0.05$.

3. Results and Discussion

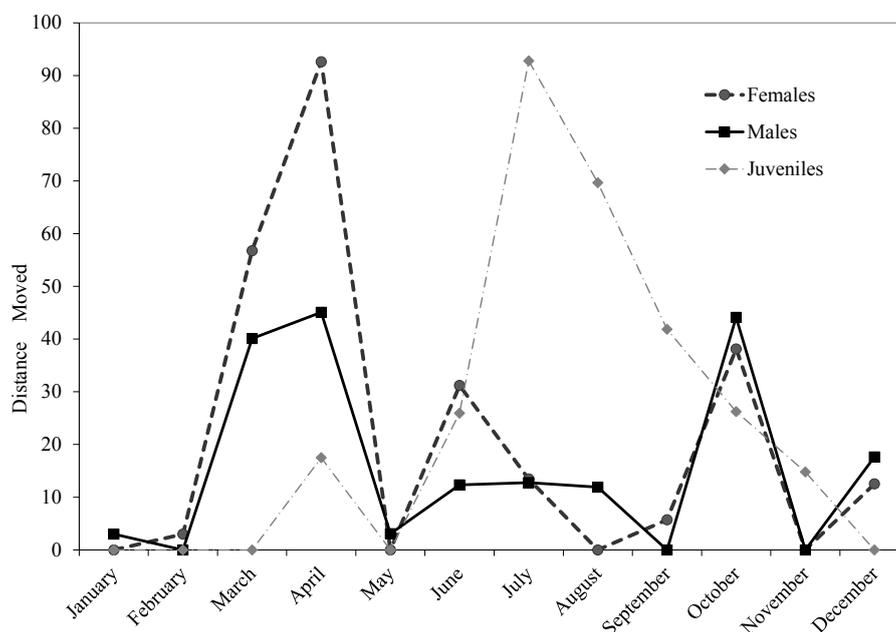
In general, movements occurred at night during or following rain, with most short movements occurring soon after release following radiotransmitter replacement. We observed that animals tended to avoid open fields, building areas, and roads (both paved and firebreaks) (Figure 1). All major adult movements (>1 m) appeared to be seasonally bimodal, occurring either in the late winter-early spring following breeding or in the fall prior to breeding (Figure 2). Most major juvenile movements (>1 m) occurred during the mid-late summer upon emergence (Figure 2).

For the salamanders radiotracked between 2005–2008, 33 males were monitored for an average of 68.6 ± 75.7 ($\bar{x} \pm SD$) days, 26 females were tracked for an average of 108.8 ± 133.2 days, and 47 juveniles were tracked an average of 45.8 ± 45.1 days (Table 1). All adults were captured at the breeding ponds in the winter-spring months during breeding with the exception of one male, which was found sharing a burrow with an already implanted male in July.

Table 1. Summary the number of days tracked and maximum distance from the breeding pond of 59 adult and 47 metamorphic tiger salamanders at Brookhaven National Laboratory, Long Island, New York, USA from 2005–2008.

Number of Days Tracked and Distance From Pond	Pond	Mean \pm SD			Range		
		Males	Females	Juveniles	Males	Females	Juveniles
		<i>n</i> = 15	<i>n</i> = 10	<i>n</i> = 16			
# Days Tracked	L1	90.5 \pm 88.4	147.4 \pm 186.6	34.1 \pm 28.8	26–394	28–402	5–196
Distance from Pond (m)		65.4 \pm 42.3	106.9 \pm 28.0	85.9 \pm 75.0	9.1–153.4	68.4–145.6	3.2–239.8
		<i>n</i> = 9	<i>n</i> = 7	<i>n</i> = 19			
# Days Tracked	L3	35.6 \pm 28.5	44.0 \pm 35.7	59.9 \pm 60.0	18–97	18–84	12–304
Distance from Pond (m)		28.9 \pm 13.9	84.0 \pm 16.4	141.5 \pm 86.0	12.6–59.3	72.2–108.5	5.7–282.1
		<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 12			
# Days Tracked	L7	70.1 \pm 79.4	116.2 \pm 98.8	39.1 \pm 29.8	3–371	6–401	10–96
Distance from Pond (m)		49.7 \pm 22.9	148.4 \pm 72.0	58.3 \pm 42.0	20.1–99.8	31.1–249.3	17.5–142.7
		<i>n</i> = 33	<i>n</i> = 26	<i>n</i> = 47			
# Days Tracked	Combined	68.6 \pm 75.7	108.8 \pm 133.2	45.8 \pm 45.1	3–394	6–402	5–304
Distance from Pond (m)		51.9 \pm 34.9	115.1 \pm 52.0	101.3 \pm 79.7	9.1–153.4	31.1–249.3	3.2–282.1

Figure 2. Pooled monthly timing and distances traveled by radiotracked adult male (black), female (dark gray), and juvenile (light gray) *A. tigrinum* at Brookhaven National Laboratory, Long Island, New York, USA from 2005–2008. Smaller movements that may have been due to radiotransmitter replacement were not included in this figure. The movements of males and females appear to be bimodal, with large movements in the spring following emigration from the breeding pond and shorter movements in the fall. The majority of large juvenile movements coincide with leaving the natal ponds beginning in mid-June and continuing through September.



Males from ponds L1 and L7 moved, on average, twice as far as males from pond L3 ($H = 6.783$, $P = 0.034$; Figure 1). In order to determine if the duration of tracking was a factor in this difference, we compared the number of days individual males were tracked from each pond. There was no difference in the values between each breeding pond ($H = 3.960$, $P = 0.138$; Table 1).

Most females from ponds L1 and L7 moved farther from the breeding pond than the females from pond L3, but these differences were not significant ($H = 4.713$, $P = 0.095$; Figure 1). The number of days females were tracked at each breeding pond did not appear to be a factor in the distances traveled from these ponds ($H = 2.767$, $P = 0.251$; Table 1).

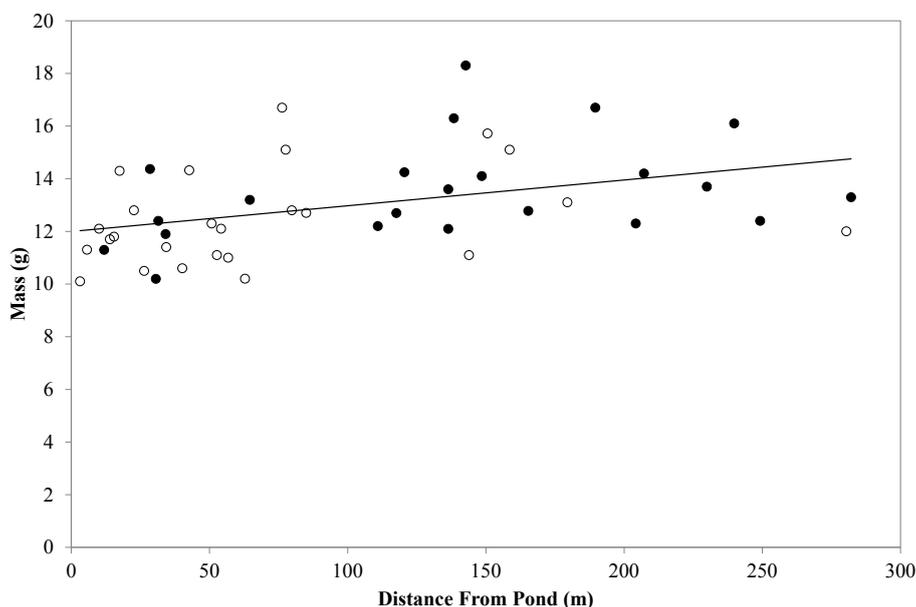
Due to the differences between ponds, we compared adult male and female movement at each pond separately. Females traveled farther than males at all breeding ponds (Table 2). Males and females from each pond were tracked a similar number of days (L1 $Z = 0.194$, $P = 0.846$; L3 $Z = 0.476$, $P = 0.634$; L7 $Z = 1.590$, $P = 0.112$). In order to determine whether adult body size varied with emigration distance, we compared body sizes of males and females and found no difference ($t = 2.002$, $P = 0.982$), nor was there a correlation between body mass and distance traveled (Pearson correlation coefficient = 0.137, $P = 0.300$).

Table 2. Movement distance comparisons between sex and age classes of eastern tiger salamanders at Brookhaven National Laboratory, Long Island, New York, USA from 2005–2008. Bold indicates significance, * denotes females moving significantly farther and ** denotes juveniles moving significantly farther.

Movement Distance Comparisons Between Sex and Age Classes	Pond		
	L1	L3	L7
Males vs. Females	Z = 2.946 * P = 0.013	Z = 3.334 * P = 0.001	Z = 2.782 * P = 0.005
Males vs. Juveniles	Z = 0.376 P = 0.707	Z = 3.025 ** P = 0.002	Z = 0.071 P = 0.943
Females vs. Juveniles	Z = 1.265 P = 0.206	Z = 1.937 ** P = 0.052	Z = 2.772 * P = 0.006

All juveniles were either captured by seine just prior to metamorphosis or by drift fence bucket upon emergence from the breeding ponds late June through September. Juveniles at pond L3 traveled greater distances than those at L1 and L7 ($H = 7.065, P = 0.029$) despite no difference in tracking time duration ($H = 2.767, P = 0.251$). Juveniles at pond L1 exhibited similar movement distances to both males and females (Table 2). At pond L3, juveniles moved significantly farther than the adult males and females (Table 2). Females, on average, moved farther than juveniles at pond L7, while juveniles did not differ from males at the same wetland (Table 2). This variation in juvenile movement prompted us to compare body size and distance traveled by juveniles. We observed a significant positive correlation between juvenile body size and the distance traveled ($t = 2.988, P = 0.005$; Figure 3).

Figure 3. Distance moved by juvenile eastern tiger salamanders in relation to their mass at Brookhaven National Laboratory, Long Island, New York, USA, from 2005–2008. There was a significant positive relationship between the distance traveled from the edge of the wetland and the size of the juvenile ($t = 2.988, P = 0.005$). White circles represent recovered radiotransmitters and black circles represent lost individuals.



After acquiring at least an initial emigration location, implant signals were eventually lost (and implants not recovered) for 49 animals (9 males, 18 females, 22 juveniles), while we recovered implants for 57 individuals (24 males, 8 females, 25 juveniles). Predation events were included in the numbers for radiotransmitter recovery. One adult male was depredated by a bullfrog (*Lithobates catesbeianus*) within a pond, one female was partially consumed about 23 m from the edge of the breeding pond by a raccoon (*Procyon lotor*), while moving in the direction of the breeding pond, and one female was found dead above her burrow with an eviscerated gut following a rain event, about 40 m from the breeding pond. We can attribute four juvenile losses to predation by a bullfrog (within the pond), a ribbon snake (*Thamnophis sauritus*) (20 m from the pond), a hognose snake (*Heterodon platirhinos*) (32 m from the pond), and a northern short-tailed shrew (*Blarina brevicauda*) (50 m from the pond). Live animals and bare radiotransmitters (no longer implanted in the salamander) were almost always found in burrows in forested pitch pine–oak forest with microhabitat characteristics similar to that described by Madison and Farrand [14] (*i.e.*, small mammal burrows or self-excavated burrows) (Figure 1). We recovered a greater proportion of radiotransmitters from males (72.7%, 24 of 33) than females (30%, 8 of 26), and therefore lost more transmitter signals from females (Fisher exact probability, $P = 0.001$). There were no significant differences between the numbers of radiotransmitters recovered ($N = 25$) versus lost ($N = 22$) for juveniles, but we were more likely to eventually recover a radiotransmitter from juveniles remaining close to the breeding pond ($Z = 2.750$, $P = 0.006$; Figure 3). Finally, we compared general distance or all individuals and transmitter recovery, and we found that we were more likely to recover a transmitter from an adult animal that stayed near the pond, regardless of sex or age ($Z = 2.392$, $P = 0.018$).

In order to compare our findings with current regulations, we plotted the final refugia for each male, female, and juvenile in relation to the buffer zone requirements in New York (Figure 1). There were no females found within the 30 m buffer. At ponds L1 and L7, only one male and 4 juveniles were found within the 30 m buffer. At pond L3, 7 males and 3 juveniles were found in forested refugia within the 30 m buffer. The majority of the total population at each pond fell within the 164 m buffer, however, 31% of females and 26% of juveniles exceeded this distance.

4. Conclusions

Our findings that eastern tiger salamander males, females, and different-sized juveniles migrate to different distances from the breeding ponds can be best explained by different selection pressures for each sex-size class.

Males remaining closer to the breeding ponds would benefit from more rapid return in spring to compete for the earliest arriving females [25,30–36]. The cost of sperm production is relatively low in most species [60], so it is likely that these males reproduce annually, as well [34,39]. In order to maintain the energy reserves necessary for reproduction, males likely benefit from high seasonal availability of invertebrate prey near the breeding ponds [61,62]. However, the cost of remaining close to the pond may be increased predation, as supported by the greater number of bare implants of the males close to the pond. Because our laboratory studies show no sloughing of implants [55], finding bare implants is assumed to be the result of active predation closest to the pond, hence greater predation rates among those males remaining near the breeding pond. Many terrestrial and fossorial predators, such as the northern short-tailed shrew (*Blarina brevicauda*), require moist environments [63,64], and due to the

sandy loam soil in this region, open canopy areas surrounding wetlands are optimal habitat for tunneling by shrews. Since the eastern tiger salamander has been shown to utilize small mammal burrows as refugia [14], there is an increased chance of depredation when salamanders use small mammal burrows. We observed at least one shrew predation event of a male tiger salamander by recovering a radio transmitter from a burrow within 50 m of the breeding pond with shrew tooth marks on the radio transmitter itself. Even with this predation risk, accessibility to incoming females and the low cost of sperm production, coupled with increased prey abundance near the breeding ponds, likely outweighs the energy expended on predator avoidance in male *A. tigrinum*. On the other hand, females may not reproduce every year [65,66], so moving further from the pond edge, avoiding potential increased burrow predation, and building resources over time may be a strategy as to why females choose refugia further from the breeding ponds.

Our observation that larger juveniles travel farther than smaller juveniles from the breeding ponds was expected. Smaller juveniles remaining closer to the breeding ponds upon emigration likely risk depredation (as discussed above) as a trade-off for higher prey availability. One study on *Ambystoma annulatum* observed that 23% of juveniles were depredated by anurans during the first night upon emigration [67]. Smaller juveniles may not have the water or fat reserves necessary to move great distances, so if individuals can survive staying closer to the breeding pond, the more abundant food availability would allow them to continue growing at a faster rate post-metamorphosis [52,53,61,62,68]. Larger juveniles are able to move larger distances from the breeding ponds upon emigration, likely due to higher body water and fat reserves (*i.e.*, lower surface area to volume ratio), and optimal time for larval development [52,53,68]. Body size of juvenile amphibians has been linked to the temperature and hydroperiod of a natal pond, indicating the importance of maintaining optimal wetland hydroperiods sufficient for full larval development [69]. If juveniles are able to feed and grow in optimal conditions, the chances of survival likely increase if they can emigrate far enough from the breeding pond to avoid depredation.

Traditionally calculated circular buffer zones appear to be an inadequate tool for suggesting the amount of land necessary to protect a viable breeding population of tiger salamanders on Long Island. The current legal standard of 30 m in New York would not protect any of the females we tracked in this study. Semlitsch [4], suggested that a minimum of 164 m as a buffer zone would be necessary to protect >95% of most populations. While New York recommends this distance to be used as a buffer for these populations, our data suggest that only about 80% of this population would be protected. These calculations do not take into consideration, however, the influence of disturbance along the edge of a buffer zone, or edge effects, which have been estimated to reach as far as 50 m into a buffer zone [70]. Using the recommended 164 m buffer zone and considering a 50 m depth of edge effects leaves a core zone of protection of only 114 m. This zone would only fully protect about 62% of the core upland habitat utilized by the females and juveniles from our study populations. This zone will also encompass unsuitable habitat at two of the ponds, as *A. tigrinum* utilized predominately pitch pine–oak forest and avoided open areas (e.g., fields, firebreaks), planted white pine stands, and developed areas. If zones were designed to encompass the maximum amount of suitable habitat and, preferably, a corridor allowing for dispersal to other wetlands, a majority of the population would be protected. Such forested corridors appear to exist for most of the Long Island tiger salamander populations and if maintained, can allow for population connectivity between breeding ponds [71], and additional modeling using

techniques such as kernel resistance measures [71–73] can provide improved recommendations for protection zones surrounding wetland habitats. Although Harper *et al.* [8] have simulated the effects of different buffers and the probability of extinction, exact numbers of each age and sex class needed to maintain a viable population cannot be determined in this study. It is essential to the survival of these populations to maintain a healthy number of breeding females and ensure juvenile survival to breeding age by managing for large tracts of native pitch pine—oak forests.

Our results support the need to manage large tracts of pitch pine—oak forests to maintain healthy eastern tiger salamander populations, especially to provide habitat for females and juveniles. Standard buffer zones may exclude significant areas of optimum habitat, while including some land that could be developed carefully as to minimize edge effects on the wetland itself. Creating buffer zones that encompass the maximum amount of viable habitat and creating corridors to allow for dispersal, while allowing for careful development in some areas, requires further research, but may end up protecting more viable upland habitat in the long run.

Acknowledgments

We would like to thank Al Breisch, John McDonald, Shannon Pederson Browne, and Jim Harding for comments on early versions of this manuscript. We would also like to thank the 2 anonymous reviewers for their helpful comments on this manuscript. This research was funded in part by State Wildlife Grant T-2–2 from the U.S. Fish and Wildlife Service (USFWS) to the New York State Department of Environmental Conservation (NYSDEC). This research was approved by Brookhaven National Laboratory IACUC #347 and New York State Department of Environmental Conservation Fish and Wildlife License #52.

Author Contributions

Valorie Titus was responsible for conceptualizing the study, data collection, analysis, and writing the manuscript. Dale Madison was responsible for procuring funding, conceptualizing and advising the study, and assistance with writing. Timothy Green was responsible for providing access to study site, procuring funding, conceptualizing and advising the study, and assistance with writing.

Conflicts of Interest

The authors declare no conflict of interest.

References and Notes

1. Knutson, M.G.; Sauer, J.R.; Olsen, D.A.; Mossman, M.J.; Hemesath, L.M.; Lanoo, M.J. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. *Conserv. Biol.* **1999**, *13*, 1437–1446.
2. Weyrauch, S.L.; Grubb, T.C. Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: An information-theoretic approach. *Biol. Conserv.* **2004**, *111*, 443–450.

3. Rittenhouse, T.A.G.; Semlitsch, R.D. Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders as a distinct habitat edge. *Biol. Conserv.* **2006**, *131*, 14–22.
4. Semlitsch, R.D. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conserv. Biol.* **1998**, *12*, 1113–1119.
5. Gibbs, J.P. Wetland loss and biodiversity conservation. *Conserv. Biol.* **2000**, *14*, 314–317.
6. Semlitsch, R.D. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conserv. Biol.* **2002**, *16*, 619–629.
7. Semlitsch, R.D.; Bodie, J.R. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conserv. Biol.* **2003**, *17*, 1219–1228.
8. Harper, E.B.; Rittenhouse, T.A.G.; Semlitsch, R.D. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: Predicting extinction risks associated with inadequate size of buffer zones. *Conserv. Biol.* **2008**, *22*, 1205–1215.
9. Burke, V.J.; Gibbons, J.W. Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina bay. *Conserv. Biol.* **1995**, *9*, 1365–1369.
10. Gibbons, J.W. Terrestrial habitat: A vital component for herpetofauna of isolated wetlands. *Wetlands* **2003**, *23*, 630–635.
11. Roth, E.D. Buffer zone applications in snake ecology: A case study using cottonmouths (*Agkistrodon piscivorus*). *Copeia* **2005**, *2005*, 399–402.
12. Veysey, J.S.; Babbitt, K.J.; Cooper, A. An experimental assessment of buffer width: Implications for salamander migratory behavior. *Biol. Conserv.* **2009**, *142*, 2227–2239.
13. Semlitsch, R.D. Differentiating migration and dispersal processes for pond-breeding amphibians. *J. Wildl. Manag.* **2008**, *72*, 260–267.
14. Madison, D.; Farrand, L. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. *Copeia* **1998**, *2*, 402–410.
15. Anderson, J.D.; Hassinger, D.D.; Dalrymple, G.H. Natural mortality of eggs and larvae of *Ambystoma tigrinum*. *Ecology* **1971**, *52*, 1107–1112.
16. Madison, D.M. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *J. Herpetol.* **1997**, *31*, 542–551.
17. Petranka, J.W. *Salamanders of the United States and Canada*; Smithsonian Institution Press: Washington, DC, USA, 1998.
18. Biek, R.; Funk, W.C.; Maxell, B.A.; Mills, L.S. What is missing in amphibian decline research: Insights from ecological sensitivity analysis. *Conserv. Biol.* **2002**, *16*, 728–734.
19. Vonesh, J.R.; de la Cruz, O. Complex life cycles and density dependence: Assessing the contribution of egg mortality to amphibian declines. *Oecologia* **2002**, *133*, 325–333.
20. Trenham, P.C.; Shaffer, H.B. Amphibian upland habitat use and its consequences for population viability. *Ecol. Appl.* **2005**, *15*, 1158–1168.
21. Orloff, S.G. Movement pattern and migration distances in an upland population of California tiger salamander (*Ambystoma californiense*). *Herpetol. Conserv.* **2011**, *6*, 266–276.
22. Calhoun, A.J.K.; Klemens, M.W. *Best Development Practices: Conserving Pool-Breeding Amphibians in Residential Developments in the Northeastern United States*; MCA Technical paper No. 5; Metropolitan Conservation Alliance, Wildlife Conservation Society: Bronx, NY, USA, 2002; p. 57.

23. Richter, S.C.; Young, J.E.; Siegel, R.A.; Johnson, G.N. Postbreeding movements of the dark gopher frog, *Rana sevosia* Goin and Netting: Implications for conservation and management. *J. Herpetol.* **2001**, *35*, 316–321.
24. Trenham, P.C. Terrestrial habitat use by adult California tiger salamanders. *J. Herpetol.* **2001**, *35*, 343–346.
25. Faccio, S.D. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *J. Herpetol.* **2003**, *37*, 479–489.
26. Porej, D.; Micacchion, M.; Hetherington, T.E. Core terrestrial habitat for conservation of local populations of salamanders and woo frogs in agricultural landscapes. *Biol. Conserv.* **2004**, *120*, 399–409.
27. Searcy, C.A.; Shaffer, H.B. Calculating biologically accurate mitigation credits: Insights from the California tiger salamander. *Conserv. Biol.* **2008**, *22*, 997–1005.
28. Castelle, A.J.; Johnson A.W.; Conolly, C. Wetland and stream buffer size requirements—A review. *J. Environ. Qual.* **1994**, *23*, 878–882.
29. Pittman, S.E.; Osbourn, M.S.; Semlitsch, R.D. Movement ecology of amphibians: A missing component for understanding population declines. *Biol. Conserv.* **2014**, *169*, 44–53.
30. Pilliod, D.S.; Peterson, C.R.; Ritson, P.I. Seasonal migration of Columbia spotted frogs (*Rana lutiventris*) among complementary resources in a high mountain basin. *Can. J. Zool.* **2002**, *80*, 1849–1862.
31. Regosin, J.V.; Windmiller, B.S.; Reed, J.M. Terrestrial habitat use and winter densities of the wood frog (*Rana sylvatica*). *J. Herpetol.* **2003**, *37*, 390–394.
32. Bartelt, P.E.; Peterson, C.R.; Klaver, R.W. Sexual Differences in the Post-Breeding Movements and Habitats Selected by Western Toads (*Bufo boreas*) in Southeastern Idaho. *Herpetologica* **2004**, *60*, 455–467.
33. Schabetsberger, R.; Jehle, R.; Maletzky, A.; Pesta, J.; Sztatecsny, M. Delineation of terrestrial reserves for amphibians: Post-breeding migrations of Italian crested newts (*Triturus c carnifex*) at high altitude. *Biol. Conserv.* **2004**, *117*, 95–104.
34. Steen, D.A.; Smith, L.L.; Miller, G.J.; Sterrett, S.C. Post-breeding terrestrial movements of *Ambystoma tigrinum* (eastern tiger salamander). *Southeast. Nat.* **2006**, *5*, 285–288.
35. Fellers, G.M.; Kleeman, P.M. California red-legged frog (*Rana draytonii*) movement and habitat use: Implications for conservation. *J. Herpetol.* **2007**, *41*, 276–286.
36. McDonough, C.; Paton, P.W.C. Salamander dispersal across a forested landscape fragmented by a golf course. *J. Wildl. Manag.* **2007**, *71*, 1163–1169.
37. Semlitsch, R.D. Terrestrial movements of an eastern tiger salamander, *Ambystoma tigrinum*. *Herpetol. Rev.* **1983**, *14*, 112–113.
38. Madison, D.M. Habitat-contingent reproductive behavior in radio-implanted salamanders: A model and test. *Anim. Behav.* **1998**, *55*, 1203–1210.
39. Loredó, I.; van Vuren, D.; Morrison, M.L. Habitat use and migration behavior of the California tiger salamander. *J. Herpetol.* **1996**, *30*, 282–285.
40. Vasconcelos, D.; Calhoun, J.K. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *J. Herpetol.* **2004**, *38*, 551–561.

41. Connete, G.M.; Semlitsch, R.D. Successful use of a passive integrated transponder (PIT) system for below-ground detection of plethodontid salamanders. *Wildl. Res.* **2012**, *39*, 1–6.
42. Pittman, S.E.; Semlitsch, R.D. Habitat type and distance to edge effect movement behavior of juvenile pond-breeding salamanders. *J. Zool.* **2013**, *291*, 154–162.
43. Ousterhout, B.; Ousterhout, R.; Semlitsch, R.D. Measuring terrestrial movement behavior using passive integrated transponder (PIT) tags: Effects of tag size on detection, movement, survival, and growth. *Behav. Ecol. Sociobiol.* **2014**, *68*, 343–350.
44. Gahl, M. Bates College, Lewiston, ME, USA. Personal Communication, 2011.
45. Titus, V.R. Green Mountain College, Poultney, VT, USA. Unpublished data, 2013.
46. Semlitsch, R.D.; Wilbur, H.M. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. *Copeia* **1988**, *1988*, 978–983.
47. Madison, D.; Andrus, R. *Tiger Salamander Habitat Use*; Final Progress Report to NYS DEC. 76; Albany, NY, USA, 1993; pp. 1–137.
48. New York State Department of Environmental Conservation. *Article 24 Freshwater Wetlands Title 23 of Article 71 of the Environmental Conservation Law*; New York State Department of Environmental Conservation: Albany, NY, USA, 1997.
49. Rosenblatt, D. New York State Department of Environmental Conservation, Albany, NY, USA. Personal Communication, 2012.
50. Gamble, L.R.; McGarigal, K.; Jenkins, C.L.; Timm, B.C. Limitations of regulated “buffer zones” for the conservation of marbled salamanders. *Wetlands* **2006**, *26*, 298–306.
51. Gamble, L.R.; McGarigal, K.; Compton, B.W. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biol. Conserv.* **2007**, *139*, 127–257.
52. Peterman, W.E.; Locke, J.L.; Semlitsch, R.D. Spatial and temporal patterns of water loss in heterogeneous landscapes: Using plaster models as amphibian analogues. *Can. J. Zool.* **2013**, *91*, 135–140.
53. Osbourn, M.S.; Connette, G.M.; Semlitsch, R.D. Effects of fine-scale forest habitat quality on movement and settling decisions in juvenile pond-breeding salamanders. *Ecol. Appl.* **2014**, *24*, 1719–1729.
54. Madison, D.M.; Titus, V.R.; Lamoureux, V.S. Movement patterns and radiotelemetry. In *Amphibian Conservation and Ecology: A Handbook of Techniques*; Dodd, C.K., Ed.; Oxford University Press: Oxford, UK, 2010; pp. 185–202.
55. Titus, V.R. Movements, connectivity, and management: Conserving the New York State endangered eastern tiger salamander. Ph.D. Thesis, Binghamton University, Binghamton, NY, USA, 2013.
56. Cecala, K.K.; Price, S.J.; Dorcas, M.E. A comparison of the effectiveness of recommended doses of MS-222 (tricain methanesulfonate) and Oragel (benzocaine) for amphibian anesthesia. *Herpetol. Rev.* **2007**, *38*, 63–66.
57. Peterman, W.E.; Semlitsch, R.D. Effects of tricaine methanesulfonate (MS-222) concentrations on anesthetization and recovery in four plethodontid salamanders. *Herpetol. Rev.* **2006**, *37*, 303–304.
58. Mineau, P.; Madison, D. Radio-tracking of *Peromyscus leucopus*. *Can. J. Zool.* **1977**, *55*, 465–468.

59. Beyer, H.L. Hawth's Analysis Tools for ArcGIS 2004. Available online: <http://www.spatial ecology.com/htools> (accessed on 16 July 2008).
60. Trivers, R. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971*; Campbell, B., Ed.; Aldine Press: Chicago, IL, USA, 1972; pp. 139–179.
61. Zimmer, K.D.; Hanson, M.A.; Butler, M.G. Factors influencing invertebrate communities in prairie wetlands: A multivariate approach. *Can. J. Fish Aquat. Sci.* **2000**, *57*, 76–85.
62. Neckles, H.A.; Murkin, H.R.; Cooper, J.A. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshw. Biol.* **1990**, *23*, 311–322.
63. Chew, R.W. The water exchange of some small mammals. *Ecol. Monogr.* **1951**, *21*, 215–225.
64. Getz, L.L. Factors influencing the local distribution of shrews. *Am. Midl. Nat.* **1961**, *65*, 67–88.
65. Trenham, P.C.; Shaffer, H.B.; Koenig, W.D.; Stromberg, M.R. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* **2000**, *2000*, 365–377.
66. Church, D.R.; Bailey, L.L.; Wilbur, H.M.; Kendall, W.L.; Hines, J.E. Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* **2007**, *88*, 891–903.
67. Pittman, S.E.; Osbourn, M.J.; Drake, D.L.; Semlitsch, R.D. Predation of juvenile ringed salamanders (*Ambystoma annulatum*) during initial movement out of ponds. *Herpetol. Conserv. Biol.* **2013**, *8*, 681–687.
68. Whiteman, H.H.; Wissinger, S.A.; Brown, W.S. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evol. Ecol.* **1996**, *10*, 429–442.
69. Phillips, C.A.; Johnson, J.R.; Drezlik, M.J.; Petzing, J.E. Effects of hydroperiod on recruitment of mole salamanders (Genus *Ambystoma*) at a temporary pond in Vermillion County, Illinois. *Trans. Ill. Acad. Sci.* **2002**, *95*, 131–139.
70. Murcia, C. Edge effects in fragmented forests: Implications for conservation. *Trends Ecol. Evol.* **1995**, *10*, 58–62.
71. Titus, V.R.; Bell, R.C.; Becker, C.G.; Zamudio, K.R. Connectivity and gene flow among eastern tiger salamander (*Ambystoma tigrinum tigrinum*) populations in highly modified anthropogenic landscapes. *Conserv. Genet.* **2014**, *15*, 1447–1462.
72. Compton, B.W.; McGarigal, K.; Cushman, S.A.; Gamble, L.R. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv. Biol.* **2007**, *21*, 788–799.
73. Greenwald, K.R.; Gibbs, H.L.; Waite, H.A. Efficacy of land-cover models in predicting isolation of marbles salamander populations in a fragmented landscape. *Conserv. Biol.* **2009**, *25*, 1232–1241.