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Sex and seasonal differences in the spatial terrestrial distribution of gray treefrog (*Hyla versicolor*) populations

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ABSTRACT

Fragmentation of terrestrial landscapes has exacerbated the need to understand the spatial requirements of organisms, especially those that undergo seasonal migrations, such as pond-breeding amphibians. Pond-breeding amphibians spend much of their lives in terrestrial habitat at some distance from aquatic breeding sites. The terrestrial habitat required by a particular individual encompasses the area adjacent to a breeding pond that is used for activities such as foraging or overwintering, as well as the expanses of habitat through which it moves. To elucidate amphibian spatial habitat requirements, we monitored gray treefrog (*Hyla versicolor*) movements through terrestrial habitat adjacent to breeding ponds using radiotelemetry and mark–recapture along transects of artificial refugia. Results indicate that gray treefrogs frequently make migrations between foraging grounds, overwintering sites, and breeding ponds of 200 m or more, with a maximum-recorded movement distance of 330 m. Additionally, females travel farther than males for reasons independent of body size, and the distribution of males during the breeding season is biased towards breeding ponds relative to the non-breeding season. The data illustrate the importance of habitat directly adjacent to breeding sites for males, and indicate that habitat loss resulting in small patches may have a greater negative impact on females than males, and consequently may have disproportionately large effects on population persistence. These results emphasize that effective management of amphibian breeding locations via protection of both aquatic and adjacent upland terrestrial resources likely requires detailed information regarding variation in movements between the sexes and among seasonal activity periods.

1. Introduction

The importance of studies investigating the spatial dynamics of populations is increasing as formerly continuous landscapes become fragmented by habitat loss and modification. Alteration of population dynamics resulting from habitat modification can occur at both local and regional scales and affect the persistence of populations and associations of populations (i.e., metapopulations). Concern regarding amphibian population declines (Houlahan et al., 2000; Stuart et al., 2004) emphasizes the importance of investigations on the effects of habitat modification. At the regional scale, habitat modification that negatively affects movements among populations (i.e., dispersal) has been shown to influence amphibian species distributions (Hecnar and M'Closkey, 1996; Houlahan and Findlay, 2003; Laan and Verboom, 1990;

Lehtinen et al., 1999). At the local scale, habitat modification likely directly affects daily and seasonal activities for migratory species. Many pond-breeding amphibians spend relatively little time at breeding sites and migrate some distance to terrestrial non-breeding habitat for foraging, summering, and wintering (reviewed by, Marsh and Trenham, 2001; Semlitsch, 2000). Furthermore, interruption of the movements that connect seasonally important habitats may also affect the persistence of local populations (e.g., Pope et al., 2000).

It is important to distinguish between the effects of habitat modification on migration (i.e., seasonal movements among resources such as foraging grounds and breeding sites) and dispersal (i.e., permanent departure from a breeding population and immigration to another) because each likely influences local and regional extinction probabilities differently, and therefore necessitate independent management strategies (Marsh and Trenham, 2001; Semlitsch, 2008). For example, habitat through which individuals disperse between populations need not provide resources for daily activities such as foraging and overwintering, but simply suitable conditions for overland travel. While long distance dispersal between populations can be critical for long-term persistence at the landscape level (Sjogren-Gulve, 1994; Smith and Green, 2005), local resource availability within the range of seasonal migrations is critical to the persistence of local populations (Semlitsch, 2000, 2008). However, for many amphibian taxa (particularly arboreal anurans), critical data regarding the use of non-breeding habitat adjacent to breeding sites is lacking (Lemckert, 2004) and uncertainty regarding the scale of movements adds to the difficulty in predicting the effects of habitat modification on populations (Trenham and Shaffer, 2005).

It is difficult to distinguish between movements at the local scale (i.e., seasonal migrations within population 'boundaries') and those at the regional scale (i.e., permanent dispersal between local populations) without explicit knowledge of population-level spatial distributions resulting from the movements of individuals among the habitat types they require throughout their life history. Estimates of core habitat used during local migrations, and non-breeding season behavior for some amphibian taxa are improving our ability to understand the spatial habitat requirements of local populations (e.g., Johnson and Semlitsch, 2003; Semlitsch, 1998) and terrestrial movement behavior of individuals (Rittenhouse and Semlitsch, 2006; Rothermel, 2004; Rothermel and Semlitsch, 2002). However, additional data regarding potential differences in the pattern and extent of amphibian movements with respect to size and sex are necessary to improve strategies that preserve natural amphibian population dynamics.

In our study, we combine the use of artificial arboreal refugia, mark–recapture, and radiotracking to determine the spatial extent of terrestrial habitat requirements for the gray treefrog (*Hyla versicolor*). We determine the spatial terrestrial distributions of adult gray treefrogs during the breeding and non-breeding seasons, and evaluate hypotheses regarding differential habitat-use based on an individual's sex and size. We discuss the implications of alteration of core habitat for amphibian populations, and provide recommendations regarding protection of upland core habitat surrounding amphibian breeding ponds.

2. Methods

2.1. Artificial arboreal refugia

We monitored three gray treefrog (*H. versicolor*) breeding sites located within the Thomas Baskett Wildlife Research Area, Boone County, Missouri from 2002 to 2004. A total of seven transects (two transects at Pond A and Pond B; three transects at Pond C) were established around the breeding ponds in secondary growth (~100 yr old) oak/hickory (*Quercus* spp., *Carya* spp.) forest with a sugar maple (*Acer saccharum*) understory. Each transect extended from a breeding pond into the forest with artificial refugia (see description below) attached to large diameter deciduous trees at intervals of 1, 5, 15, 35, 60, 100, and 200 m. We placed two refugia (on adjacent trees) at each of the seven sampling intervals, in each of the seven transects, for a total of 98 artificial arboreal refugia. Two refugia were placed at each interval in each transect to increase sampling effectiveness. Treefrogs were captured in artificial arboreal refugia with an upper opening 3 m above the ground. Each arboreal refuge consisted of 60 cm long sections of 3.8 cm inside diameter, black acrylonitrile–butadiene–styrene (ABS) pipe attached to trees with bungee cords (Johnson, 2005a). Refugia were sealed at the bottom to allow rainwater to fill to 15 cm deep. Water levels remained constant during monitoring because an inside pipe sits loosely within the bottom capped portion to allow draining of excess water (Johnson, 2005a). Frogs entered and left pipe-traps freely at the upper opening. Refugia were checked during daylight hours for the presence of treefrogs at varying intervals throughout each year.

For each treefrog, we measured snout-vent length with a plastic ruler at least once per season, and body mass with a Pesola spring scale starting in the spring of 2004. If not previously marked at breeding ponds (see below), toes were excised to produce unique toe-clip identifications. After processing, frogs were returned to the pipes, which were then placed back on the tree. Additionally, we performed nocturnal monitoring of the three breeding ponds from which the transects extended to help identify the exact breeding location of individuals captured in artificial refugia. At the breeding ponds, frogs were captured by hand and processed in the same manner as described above for the artificial refugia.

Toe excision did not appear to greatly affect the frog's ability to grip and climb even smooth vertical surfaces (e.g., plastic containers, glass aquaria), and we observed only a few instances of redness at excision sites. Furthermore, the total number of toes excised from an individual (range: 2–7) had no apparent effect on the total number of times an individual was recaptured in artificial refugia (males $[F_{5,66} = 1.28, P = 0.288]$ females $[F_{5,41} = 0.59, P = 0.705]$) using ANOVA.

2.2. Radiotelemetry

From July to October 2003 and 2004 during the post-breeding seasons, a subset of individuals captured in artificial refugia were implanted with radiotransmitters and tracked during migration to their overwintering sites. We conducted the

radiotelemetry portion of this study to verify that late-fall arboreal retreat captures could be used to approximate the final distance between breeding ponds and overwintering sites, and would not underestimate the total distance traveled. For both years combined, we implanted radiotransmitters in 22 adult (10 male and 12 female) treefrogs captured in arboreal refugia. We selected individuals based on capture date (~25 d prior to the first freezing temperature) and body mass (>8.5 g). We used radiotransmitters (Model BD2, 0.85 g, $14 \times 6.5 \times 3.5$ mm) with internal helical antennae (Holohil Systems Ltd., Carp, Ontario, Canada K0A 1L0) that had an expected battery life of at least 25 days. Transmitters did not exceed 10% of an individual's mass (Richards et al., 1994). Individuals were released ~24 h post-implantation at the point of capture and tracked for the duration of the transmitter battery life. Prior to release, the behavior (i.e., body posture, avoidance behavior) of each animal had returned to normal (Johnson, 2006). Kernel density estimates were generated for radiotracked individuals at Ponds A and B with the animal movements extension (Hooge and Eichenlaub, 2000) in ArcView using least-squares cross-validation to determine smoothing factors (Worton, 1989) for all relocations of each individual. We did not generate a population-level space-use estimate for Pond C due to small samples size. Transmitters were removed following tracking (Johnson, 2006) and treefrogs were returned to their last site of capture.

2.3. Simulation of random spatial distribution

Simulated migration events were generated using Resampling Stats (v. 5.2, Resampling Stats Inc.) to assess whether treefrog migration distances from the mark–recapture study were randomly distributed. The mean and standard deviation of individual daily movements were calculated from the radiotelemetry data only. Using these values to parameterize the simulation, 300 "individuals" were allowed to migrate randomly from the center of a "pond". Each individual was allowed to move in any direction each day and the distance moved was randomly chosen from a normal distribution with a mean and standard deviation identical to that calculated from the telemetry movement data. The simulated movements were terminated when the mean distance from the pond of individuals was equal to that of the observed data from individuals captured in refugia.

Upon termination of the simulation, the number of individuals at each sampling distance (1, 5, 15, 35, 60, 100, and 200 m) was recorded. Because equal numbers of arboreal refugia were used to recapture individuals at different distances during the mark–recapture study, we applied a correction factor. Due to the radius of the simulated breeding pond (6 m), the circumference at 100 m from the pond edge (106 m) is 15.1 times greater than it is at 1 m from the pond edge (7 m). Consequently, only 6.6% of the simulated individuals at 100 m were considered as recaptures relative to the simulated recaptures at 1 m. The percent of total recaptures at each sampling distance was calculated from these data. The simulation and sampling processes were repeated 1000 times and a mean percentage of recaptures was calculated for each distance. We compared the simulated frequency distribution to the observed number of captures at each distance using

Kolmogorov–Smirnov (KS) tests to determine if the distribution from the mark–recapture data was different than a Brownian motion (i.e., random) model of migration.

We also used SPSS (v. 11.0.1, SPSS Inc.) to perform KS tests to compare observed distributions of total captures and unique captures of males and females during both the breeding and non-breeding seasons. Additionally, we compared mean average distance from breeding ponds for males and females with a Wilcoxon Rank-Sum test, and performed simple linear regressions to test the relationship of SVL, mass, and length-specific mass (mg/mm) with distance.

3. Results

3.1. Artificial arboreal refugia

During the breeding seasons of 2003 and 2004 we marked 651 adult (577 male and 74 female) treefrogs and recorded a total of 700 individual recaptures (total N = 1351 total captures) at the three breeding ponds. Of these individuals captured and marked during the nocturnal monitoring at the breeding ponds, only 33 (5.1%) were subsequently recaptured in our artificial refugia. Combined with treefrogs never captured at breeding ponds (i.e., caught in refugia only), we captured a total of 109 adult frogs and 43 juveniles in artificial refugia and recorded 595 recaptures (total N = 704). Therefore it is possible assign a breeding location to only 30% of artificial refugia captures. Although we had expected much higher recapture rates in artificial refugia given our marking efforts at the breeding sites, we do not believe unmarked new captures at refugia represent individuals that had bred elsewhere. While movement between breeding sites was possible, we observed such events with low frequency (N = 7 individuals were observed at multiple ponds) in our study. A concurrent study at an adjacent treefrog breeding site (~500 m distant) observed only one individual of ~330 amplectant pairs bearing a mark from our study (N. Gordon pers. comm.). Furthermore, using the program CAPTURE (White et al., 1978) we estimated that we marked between 40% and 54% of the population at each pond in each year, indicating that perhaps it is no surprise that we captured many individuals for the first time in our artificial refugia. The sex ratio of individuals captured in artificial refugia was 67:42 (male:female), with males representing 61.5% of individuals captured. Twenty-six individuals (18 males, 8 females) were captured only once in refugia and were considered to be migrating (or dispersing) to locations unknown. Of the 43 individuals captured and initially marked as juveniles, during the course of the study 11 matured into males and five matured into females.

We combined the captures recorded in each of the paired artificial refugia at each sampling distance within transects due to high frequencies of movements among them. We also partitioned the activity period of treefrogs into four seasons: (1) after overwintering and before chorus formation (pre-breeding season), (2) during chorusing (breeding season), (3) after chorusing had ceased and before overwintering (post-breeding season), and (4) the period in which frogs were absent from refugia (overwintering season). We found that 80 individuals returned to the same artificial refuge during at least two seasons, suggesting foraging site fidelity. Excluding

the overwintering season, some individuals used the same refuge for six consecutive seasons. If we consider only treefrogs that were captured more than once and exclude frogs captured only during the final major monitoring season of the study (summer 2004), 98.8% of individuals exhibited site fidelity to particular artificial refugia. We considered treefrogs to exhibit site fidelity if individuals were captured and subsequently recaptured at the same refuge location separated by a prolonged (i.e., several months) absence for overwintering or temporary absence (i.e., several weeks for males, and several days for females) during the breeding season.

The overall distribution of captures was not significantly different from a uniform distribution (i.e., equal number of captures) throughout the seven distances (Fig. 1), when considering total captures ($D = 0.753$, $P = 0.621$) or when omitting recaptures (i.e., including only the single most distant capture location of an individual; $D = 0.532$, $P = 0.940$). However, when total capture data were separated by sex, we found that females were distributed at farther distances, and males were located nearer to ponds ($D = 2.907$, $P < 0.001$). Additionally, the average capture distance from breeding ponds was significantly less for males than for females when using either total captures ($Z = 4.943$, $P < 0.001$) or omitting recaptures ($Z = 2.928$, $P = 0.003$; Fig. 2). Eighty-five percent of all juvenile recaptures and 82% of all juvenile individuals were recorded within 35 m of breeding ponds (Fig. 3). We observed a decrease in abundance of juveniles as distance from the pond increased, with only 6% of recaptures and 11% of individuals captured beyond 100 m. Similarly, Roble (1979) recorded post-breeding season movements of juvenile gray treefrogs only within 125 m from breeding ponds.

During breeding seasons we recorded 146 total captures of 60 individuals in arboreal refugia. The overall spatial distribution of these captures encompasses the same range as that of combined yearly data. However, when comparing females and males, we found that the spatial distribution of females was the same during the breeding and non-breeding seasons
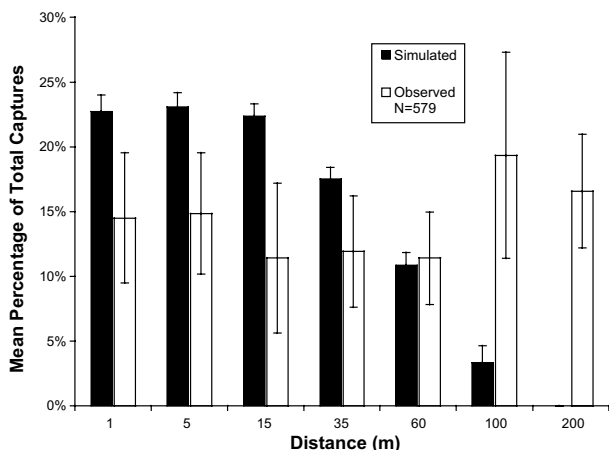

Fig. 1 – Average percentage of total adult recaptures in artificial arboreal refugia at each sampling interval compared to 1000 iterations of simulated distributions comprised of random-walk movements. Error bars represent ± SE across all seven transects and all model iterations, respectively.
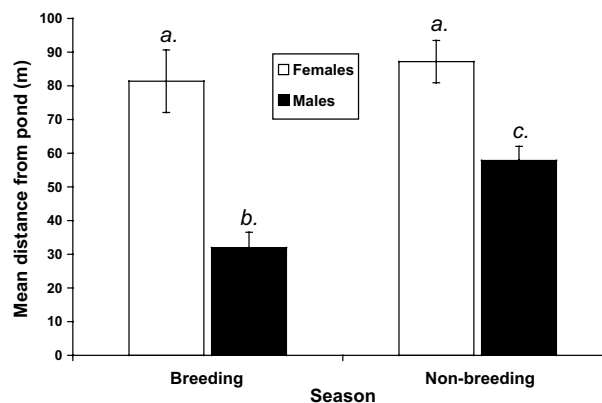

Fig. 2 – Comparison of male and female average distance from breeding sites during the breeding and non-breeding seasons based on total recaptures in artificial arboreal refugia. Letters denote significant differences between means as measured by a Wilcoxon Rank-Sum tests. Error bars represent ± SE for each sex.
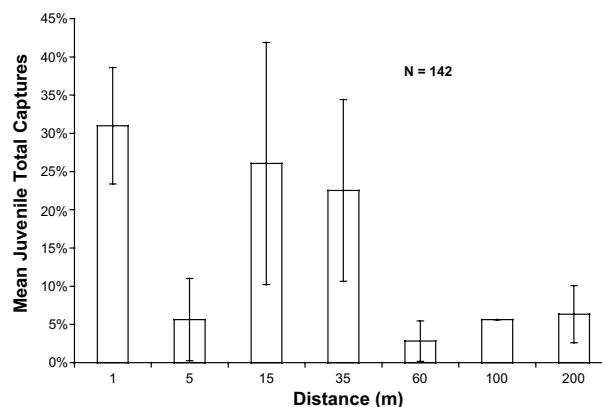

Fig. 3 – Average percent abundance of total recaptures of juvenile gray treefrogs for all seasons combined. Error bars represent ± SE across all seven transects.

($D = 0.923$, $P = 0.362$; Fig. 4a), but males were distributed nearer to the pond during the breeding season than during the non-breeding season ($D = 1.843$, $P = 0.002$; Fig. 4b). Among all adult captures, neither SVL ($F_{1,47} = 0.003$, $P = 0.958$) nor mass ($F_{1,47} = 1.245$, $P = 0.270$) of treefrogs appeared to have an effect on distance from breeding sites in pipe refugia. Males and females differed in length-specific mass (mg/mm; $t_{2\text{-tail}} = 9.4$, df = 25, $P < 0.001$), but we found no effect of length-specific mass on capture distance of males ($F_{1,28} < 0.001$, $P = 0.990$) or females ($F_{1,17} = 1.670$, $P = 0.214$).

3.2. Radiotelemetry

Two of the 22 individuals implanted with radiotransmitters were omitted from all analyses due to low numbers of relocations ($N = 1$ or 2). We relocated the remaining 20 individuals an average of 24 times (±0.9 SE) each, for a total of 485 relocation points. The average maximum distance from breeding
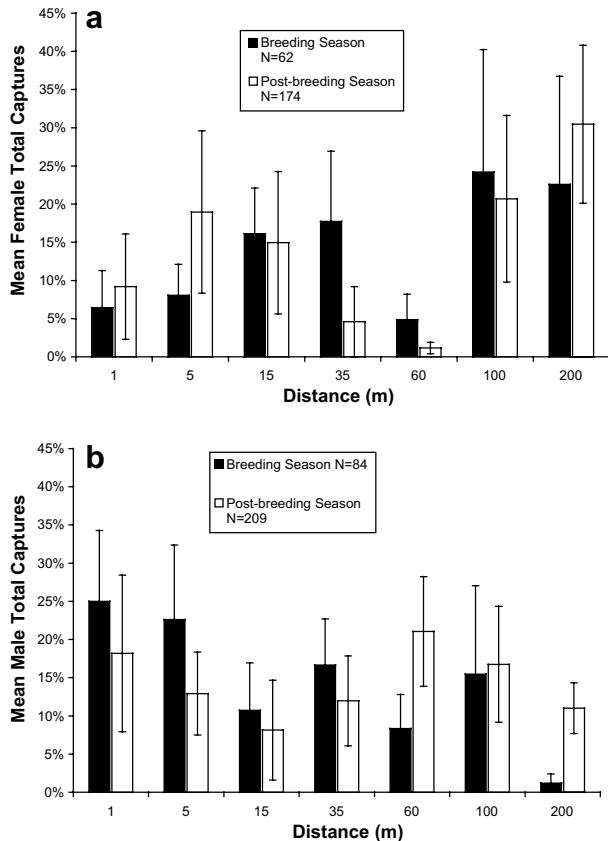
Fig. 4 – Average percent abundance of total recaptures during the breeding and post-breeding season for (a) females and (b) males. Error bars represent ± SE across all seven transects.
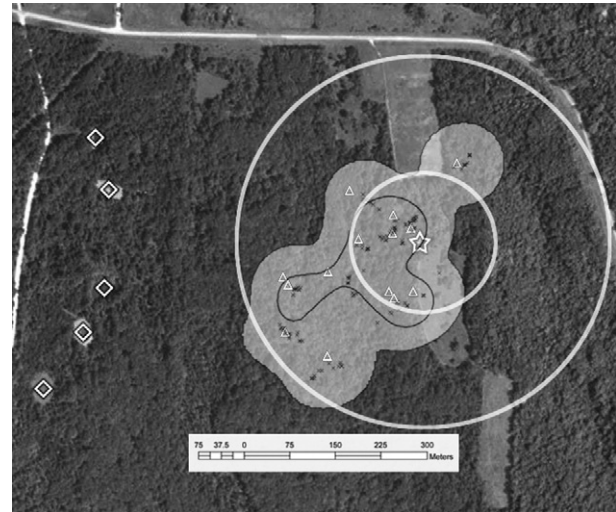

Fig. 5 – Aerial photograph of study site, illustrating distance among adjacent potential breeding locations (diamonds), core habitat area estimates that contain 95% and 50% of transmittered animal relocations (300 m and 100 m radii circles, respectively), and population-level space-use estimates (shaded area [outer, 95% kernel estimate and inner, 50% kernel estimate]) based on relocation points ('×') of all individuals (N = 14) at Ponds A and B combined (star). Triangles represent original capture location of each radiotracked individual.

3.3.   Simulation of random spatial distribution

The distribution of computer simulated random movements and application of capture probabilities that approximated our transect sampling scheme was significantly different from the observed distribution of total captured treefrogs in artificial refugia ($D = 5.008$, $P < 0.001$; Fig. 1). Recaptured individuals were found at a higher frequency at greater distances than expected from the simulation data, and indicated directed movement away from the pond and increased use of terrestrial habitats at greater distances from breeding ponds than predicted assuming random movements.

4.   Discussion

4.1.   Spatial distribution of habitats

The delineation of all habitats used by individuals within local populations is a necessary component of any attempt to understand landscape complementation (Dunning et al., 1992) and its importance for effective conservation planning for amphibians. Because treefrogs exhibit a complex life cycle, with a larval aquatic phase and a terrestrial adult phase, both habitats are essential for completion of the life cycle. Previous work demonstrated that treefrogs use two distinct terrestrial habitats beyond the breeding pond during the non-breeding season: (1) mature oak trees that provide cavities such as knot-holes and serve as foraging sites (Mahan and Johnson, 2007), and (2) leaf litter on the forest floor for

ponds of radiotracked treefrogs was 172.4 m (±28.8 SE), and was not significantly different than the average distance of final overwintering sites from breeding ponds (169.6 ± 28.5 SE; $t_{2\text{-tail}} = 2.02$, df = 38, $P = 0.95$). Overwintering migration distances (i.e., from the breeding pond edge to the overwintering location) were similar for both males (214.8 ± 56.2 SE) and females (136.6 ± 24.5 SE; $t_{2\text{-tail}} = 1.27$, df = 11, $P = 0.230$). The maximum distance traveled by any individual treefrog from its known breeding location (N = 6) was 270.9 m. While the maximum distance from the nearest potential breeding pond that was reached by any treefrog originally captured within the artificial refuge (i.e., for which the breeding location was unknown; N = 14) was 331.9 m. Only three frogs chose overwintering locations that were closer to adjacent breeding ponds than our study ponds, and the average distance from treefrog overwintering locations to non-study ponds was 369.5 m (±33.5 SE). The kernel density estimate for the 95% population-level space-use estimate was 340 m, illustrating the extent of terrestrial habitat adjacent to ponds used by the treefrogs in our study (Fig. 5). However, this space-use estimate could be an underestimate because our sample of radiotracked treefrogs was drawn solely from individuals captured in our artificial refugia and therefore may have already chosen post-breeding season foraging habitat located within 200 m of the breeding ponds.

overwintering (Johnson, 2005b). Data from our study reveal that foraging and overwintering habitats are distributed around the breeding pond and are used by treefrogs non-randomly at distances up to (and most likely beyond) 340 m away from ponds. In continuous habitat, these boundaries may be important only to distinguish between within- and among-population dynamics (Smith and Green, 2005), but in fragmented landscapes knowledge of habitat-use patterns can be used to determine the suitability of existing habitat patches (i.e., fragments) and the appropriate scale at which to preserve terrestrial habitat to protect local populations.

Based on captures within artificial arboreal refugia, we found that adult gray treefrogs were evenly distributed throughout the terrestrial habitat surrounding aquatic breeding sites up to at least 200 m (Fig. 1). The significant difference between the observed and simulated distribution of random movements away from breeding sites indicates that individual movements are directed away from breeding ponds. However, males and females did not exhibit the same spatial patterns across this range. Radiotelemetry data illustrate that individuals may move even farther (e.g., mean = 271 m) into forested terrestrial habitat during non-breeding seasons to reach preferred foraging and overwintering locations. These distances overlap completely with those summarized for other anurans (Semlitsch and Bodie, 2003). We do not contend to have determined precisely the distant tail of the treefrog migratory distribution because mark/recapture-release efforts stopped at 200 m, but rather to have illustrated that terrestrial habitat-use by treefrogs is extensive and non-randomly distributed. It is likely that adult gray treefrog terrestrial habitat-use continues beyond the 200 m in which our artificial refugia were placed, considering the approximately uniform distribution of males and increasing distribution of females we observed (Fig. 4), and data for other treefrogs (e.g., Carlson and Edenhamn, 2000; Pellet et al., 2006).

Using the radiotelemetry data, we have delineated the terrestrial habitat utilized at our study sites to extend 340 m from breeding ponds (Fig. 5). However, within the vicinity of our study sites, the average distance among clusters of breeding ponds was 491.8 m (±48.8 SE). Therefore, terrestrial habitat radii extending towards adjacent breeding pond clusters overlap, and individuals could reasonably move between breeding sites during subsequent breeding seasons in the absence of strong breeding site fidelity. When the 'boundaries' of local habitat patches overlap, dispersal events between patches are likely common. Our results are similar to those of Carlson and Edenhamn (2000) for *Hyla arborea*, in which an average interpond distance of 441 m resulted in a system of ponds that was unaffected by local extinctions, due to immediate recolonizations. Therefore, our results support the views of Marsh and Trenham (2001) that local populations can contain multiple breeding ponds and that a "ponds as patches" view of amphibian metapopulations is not always appropriate. Furthermore, our results support the contention of Smith and Green (2005) that not all pond-breeding amphibian populations exhibit metapopulation dynamics because the vagility of amphibians may be greater than generally assumed.

4.2. Sexual differences in spatial distributions

Sexual differences in morphology and behavior are prevalent throughout nature, and can be the result of sexual selection or niche divergence (Shine, 1989). When the size of females exceeds that of males, ecological causes, such as resource competition resulting in niche divergence, have been used to explain the differences between the sexes (Shine, 1989). We found that male size was significantly smaller than female size, and females migrated to locations more distant from ponds than males (Fig. 2). Females have recently been found to migrate longer distances than males in other anurans (Bartelt et al., 2004; Muths, 2003; Pilliod et al., 2002), and this behavior may be attributable to a variety of reasons. Females may travel farther to reach foraging locations that have higher densities of prey or more preferred prey species, which maximize energetic resources used to increase egg number, egg quality, or clutch frequency. But, if the distribution of insect prey is uniform, females may still seek locations distant to breeding sites with reduced densities of conspecific competitors, to increase the relative abundance of prey available to them. Furthermore, females generally arrive at breeding sites after males have established choruses, and Sinsch (1992) found that females are less philopatric to breeding sites than males. Females may benefit from the opportunity to choose a breeding site based on chorus characteristics, and by positioning themselves at greater distances from breeding sites, should increase their ability to assess multiple breeding choruses. Males may not benefit from traveling greater distances, because the ability to reach breeding sites quickly may be more beneficial for the acquisition of a desirable territory and increased opportunities to encounter females (Fellers, 1979).

However, the observed differences between the distributions of males and females do not appear to be the result of size differences alone. Although the length specific mass (mg/mm) of females was significantly larger than males, no overall relationship of capture distance and size was detected for either males or females. This indicates that size-independent factors are driving females to move farther than males, rather than morphological (i.e., locomotor) limitations of males. Regardless of the underlying cause of the distributions, the result is that females are located on the periphery of the population spatial distribution and more likely to exist along the border of the habitat patch. Thus, any reduction in patch size due to land-use may have severe impacts on the probability of population persistence not only by reducing the number of individuals that a patch can support, but by potentially eliminating a higher proportion of females than males. For example, removal of the sample of treefrogs from all 200 m arboreal refugia in our study would directly affect 51.5% of female individuals (or 26.8% of total female recaptures), but only 13.2% of male individuals (or 7.0% of total male recaptures) would be directly affected. However, our observed percentage of females lost from such a 50% reduction in patch size is most likely a very conservative estimate due to our sampling scheme, as we only have one sampling location beyond the 100 m arboreal refugia location.

It may be premature to suggest that modification of habitat along the periphery of populations leads to direct mortality of the individuals that once resided there, but increased densities resulting from decreased available habitat or potentially increased dispersal to adjacent patches certainly have the capacity to affect local population demographics. Our data indicate that females would be more likely to experience increased densities through truncation of typical migration distances or perhaps be more likely to move through altered habitat in search of more appropriate habitat.

4.3. Seasonal variation in spatial distributions

Similar to many species of amphibians, gray treefrogs are classified as prolonged-breeders and typically breed over several months. Past research has suggested that breeding chorus tenure affects the reproductive success of individuals, such that males spending more time calling at breeding sites mate more frequently than males that are absent or not actively calling (Godwin and Roble, 1983; Murphy, 1994; Ritke and Semlitsch, 1991; Sullivan and Hinshaw, 1992). However, calling is energetically costly and even the 'best' males must leave the chorus occasionally to forage (Murphy, 1994). What remained unknown was how far males ventured into surrounding terrestrial habitat to acquire food resources and replenish energetic reserves.

We found that the spatial distribution of males in arboreal retreat sites during the breeding season (i.e., while other males are calling at breeding sites) was significantly constricted towards the pond relative to the distribution of males during the non-breeding seasons (Fig. 4B). Thus, some males do not move as far to replenish energy reserves in between calling bouts as they do after the breeding season is finished. Therefore, maintaining appropriate terrestrial habitat adjacent to breeding sites may be particularly important to the duration of the breeding season, chorus tenure, and breeding success by allowing only short absences of males from choruses. In contrast, females spend very little time at breeding ponds during any portion of the year, usually no more than 48 h (pers. obs.) and maintain a relatively constant and more distant spatial distribution surrounding breeding sites (Fig. 4A). When females do migrate to breeding sites, the trips last just long enough to breed (Sullivan and Hinshaw, 1992) and return to their terrestrial foraging grounds. For example, one female in our study (#0769; Johnson, 2006) was observed in a 100 m artificial arboreal retreat during the day, then in amplexus at a breeding pond the following night, and then back in the same arboreal retreat the next day (200 m round-trip in 24 h).

While males rely on habitat immediately adjacent to breeding ponds during the breeding season, females rely on more distant habitat. If terrestrial habitat adjacent to ponds was lost, it may be true that males would simply move farther from breeding ponds because some short distance (~60 m) movements of adults through non-forest habitat have been observed in a separate study (Johnson, 2005b). However, what remains to be determined are the costs of migrating through non-forest habitat and the consequences of overlapping male and female spatial distributions in habitat fragments that are too small to allow the sexes to achieve niche separation. In non-altered habitats, the absence of conspecific male competitors at distant foraging sites could allow females to forage more effectively and produce higher quality eggs, or produce multiple clutches during the breeding season (Perrill and Daniels, 1983).

5. Conservation implications

Investigations of amphibian terrestrial migrations and upland habitat use have illustrated that current buffer zone guidelines for riparian habitat (see Lee et al., 2004 for review of US and Canada guidelines) do not contain the extent of terrestrial habitat utilized by amphibians during the non-breeding season. Therefore, non-breeding habitats that support foraging and overwintering/oversummering are largely unprotected from land-use (Semlitsch and Bodie, 2003). We believe estimates of the spatial extent of upland habitat used by pond-breeding amphibian populations are an appropriate metric upon which to base decisions regarding habitat protection requirements. In addition, buffer zones extending beyond the perimeter of these core areas could protect the life history activities of individuals along the periphery from edge effects (Murcia, 1995). We suggest that protection of terrestrial habitat adjacent to gray treefrog breeding sites extend greater than 200–300 m given the large proportion of captures recorded at 200 m artificial refugia and evidence for the use of distant habitat for overwintering. However, we do not suggest generalizing these recommendations to amphibian taxa that may differ in their terrestrial behavior and movement capabilities, and further caution that extension of protection perimeters to similar species requires information regarding niche separation of males and females to adequately determine the relative impact of land use on effective population size and reproductive success of local populations.

As more information regarding the terrestrial distributions of amphibians becomes available it is increasingly clear that we have a poor understanding of the distant tail of amphibian migration and dispersal distances due to the difficulty in detecting uncommon long-distance movements (Smith and Green, 2005). Therefore, effective conservation initiatives aimed at protection of both local and landscape-level pond-breeding amphibian population dynamics would benefit from the incorporation of (1) mark–recapture studies that elucidate terrestrial habitat requirements for local populations and (2) genetic approaches used to infer gene flow (Wright, 1965) and to estimate dispersal and immigration (Manel et al., 2003) across a landscape.

Acknowledgements

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