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## Defining core habitat of local populations of the gray treefrog (*Hyla versicolor*) based on choice of oviposition site

Received: 4 March 2003 / Accepted: 4 June 2003 / Published online: 17 July 2003  
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**Abstract** Concern over amphibian population declines and loss of terrestrial and aquatic habitat have emphasized the need to define habitat requirements for each stage in a species' life history. The realization that pond-breeding amphibians spend most of their lives in the terrestrial environment suggests the need to protect terrestrial as well as aquatic habitat. Many studies on amphibian populations have focused on emigration from breeding sites to define habitat use; however these studies do not typically elucidate terrestrial activities of adults within the breeding season. We measured colonization rates of artificial pools by gray treefrogs (*Hyla versicolor*) at multiple distances from natural breeding ponds. We found a non-random distribution of egg deposition among distances, with 95% of eggs deposited within 15 m of the breeding pond. Additionally, we found that the time to first colonization of artificial pools increased with respect to distance. Our results indicate that adult gray treefrogs may travel up to 200 m within a breeding season, and that multiple breeding ponds may be considered part of a single population. We suggest that a minimum core terrestrial habitat of 60 m surrounding breeding sites is appropriate for protection of local populations of gray treefrogs.

**Keywords** Amphibian · Colonization · Core Habitat · *Hyla* · Metapopulation

### Introduction

Concern over the loss and fragmentation of natural habitat has led to increased interest in metapopulation dynamics in the field of conservation biology (e.g., Pulliam 1988; Hanski and Gilpin 1991). Conservation-oriented meta-

population studies of amphibians are of particular importance due to widespread concern over population declines and local extinctions (e.g., Houlihan et al. 2000). Additionally, populations of pond-breeding amphibians are naturally spatially clumped due to their dependence on aquatic habitat for breeding and larval development, and are well suited for investigation of metapopulation dynamics (e.g., Gill 1978). The preservation of metapopulation dynamics is a critical aspect of conservation plans because recolonization of extinct patches is important for long-term preservation of metapopulations (e.g., Semlitsch 2000, 2002). The probability of extinction increases as the probability of recolonization of unoccupied habitat patches decreases with loss and fragmentation of natural habitat.

The historical view of amphibian populations considered each breeding site as a discrete population (Gill 1978; Sjøgren 1991; Sjøgren-Gulve 1994). This view of amphibian populations facilitated the application of simple metapopulation models similar to those envisioned by Levins (1970), in which each subpopulation consisted of a discrete aquatic breeding habitat patch and movement between any two breeding sites was interpreted as a dispersal event. This 'ponds as patches' view has traditionally been accepted because the aquatic habitat of pond-breeding amphibians can easily be characterized and defined (Marsh and Trenham 2001), and because amphibians are typically assumed to exhibit natal pond philopatry and limited dispersal ability (e.g., Berven and Grudzien 1990). However, direct monitoring of individual movements and indirect estimates of movements from molecular markers suggest that individuals of some amphibian species can move between two or more adjacent breeding sites (Breden 1987; Sinsch 1992, 1997; Trenham et al. 2001). Thus, the 'ponds as patches' model may not adequately characterize all amphibian populations. The development of realistic metapopulation models requires information on spatial dimensions of subpopulations as defined by movements in the terrestrial environment adjacent to breeding sites. Determination of the local patch size is an important step in delineating the

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critical terrestrial habitat area necessary for long-term survival of populations through maintaining dispersal and recolonization processes.

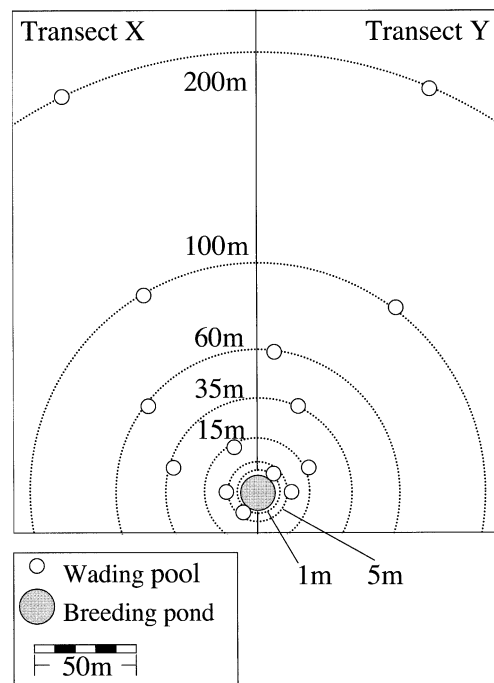
In our study, we identified the area around breeding ponds used by adult gray treefrogs (*Hyla versicolor*) during a single breeding season by monitoring colonization of artificial ponds at multiple distances from natural breeding sites. The terrestrial environment may be especially important to the gray treefrog because it breeds over a period of several months (Ritke et al. 1990; Johnson 2000). During the breeding season, gray treefrogs use the terrestrial habitat for shelter and foraging between breeding bouts, as well as for arboreal calling sites surrounding the breeding pond. Previous studies have reported that movements of *H. gratiosa* (Murphy 1994) and *H. chrysoscelis* (Ritke et al. 1991) between breeding sites within a breeding season are rare. However, most previous studies providing data on within-breeding-season movements of hylids (Jameson 1957; Harris 1975; Perrill 1984; Freda and Gonzalez 1986) have not been aimed at providing a relevant end-point to individual movements in the context of population biology, or in identifying the importance of the terrestrial environment for amphibians. Our study provides direct evidence of within-breeding-season movements through the terrestrial environment that result in reproduction. Identification of oviposition events outside the natural breeding site will help to quantify the spatial dimensions of gray treefrog subpopulations and aid in determination of appropriate protection guidelines for core habitat adjacent to amphibian breeding sites.

## Materials and methods

### Study species

The gray treefrog breeds in ephemeral or fishless ponds from early April to early July in Missouri (Johnson 2000). Gray treefrogs have been used in other studies using artificial ponds because females readily deposit eggs in small pools (Resetarits and Wilbur 1989; Ritke et al. 1990; Ritke et al. 1991; Ritke and Semlitsch 1991). Males have been observed to call from the edge of artificial ponds and attract females to the pool (Resetarits and Wilbur 1991). Females deposit multiple batches of 20–90 eggs until the full compliment has been laid (Ritke et al. 1990), and eggs float on the surface of the water for approximately 24 h, or until they are disturbed. Eggs hatch in 4–5 days (Johnson 2000) depending on the temperature, and larvae are free-swimming shortly after.

Other amphibians that occur at our study sites are the spotted salamander (*Ambystoma maculatum*), smallmouth salamander (*A. texanum*), southern leopard frog (*Rana sphenoccephala*), green frog (*R. clamitans*), bullfrog (*R. catesbeiana*), chorus frog (*Pseudacris triseriata*), spring peeper (*P. crucifer*), cricket frog (*Acris crepitans*), and American toad (*Bufo americanus*). Most of these species do not breed at the same time as gray treefrogs and the eggs of those that do are easily distinguished from gray treefrog eggs. Only three juvenile individuals of one other species (green frog) were found in the treatment pools during the course of our study.



**Fig. 1** Schematic drawing of a breeding site divided into staggered transects. All three breeding sites were divided into two transects and pools were arranged in a similar fashion. See Table 1 and 2 for average distances between wading pools as determined by GPS coordinates. Breeding pond and wading pools are not drawn to scale

### Study design

We placed two experimental transects composed of seven (1.52 m diameter, 30 cm deep) plastic wading pools in the terrestrial habitat surrounding each of three natural breeding ponds located at the Baskett Wildlife Research Area in Boone County, Missouri. Ponds A and B are within 60 m of each other, and pond C is separated from ponds A and B by 1 km. All three natural breeding ponds are at least 500 m away from other breeding sites and all wading pools were at least 300 m away from breeding sites not included in the study. All three breeding ponds are fishless and have variable hydroperiods; pond B dried and filled several times throughout the study. We do not believe that pond drying influenced our results, as Ritke et al. (1991) reported that drying of breeding sites did not stimulate dispersal of *H. chrysoscelis*. The terrestrial habitat surrounding all three ponds consists of secondary growth oak/hickory canopy (*Quercus* spp./*Carya* spp.) with maple/cedar understory (*Acer* spp./*Juniperus* spp.). Plastic wading pools were placed at 1, 5, 15, 35, 60, 100, and 200 m from the breeding ponds (Fig. 1). Wading pools were arranged in a staggered fashion to maximize the distance between experimental pools both within and between transects and limit movement from pool to pool (Table 1, 2). Distances between wading pools were maximized both within and between adjacent transects, while maintaining the appropriate distance from the breeding pond. All pools were placed at a level location to avoid confounding slope and distance. Each pool was also placed at the base of a large-diameter (mean=30.9 cm) oak, maple, or hickory tree to provide elevated refuges and foraging sites for adult treefrogs.

Wading pools were placed at the study sites on 23 May 2001 after the breeding season had begun, and adult gray treefrogs were seen and heard at all three breeding ponds. All wading pools were filled by a garden hose from a tank truck using tap water and rainwater to approximately 20 cm deep. After all pools in a transect were filled, wading pools were checked daily until the first

**Table 1** Average distance between wading pools within each transect ( $n=6$ )

Distance	1 m	5 m	15 m	35 m	60 m	100 m	200 m
1 m	0	13	21	43	66	108	196
5 m	13	0	13	36	57	100	188
15 m	21	13	0	24	48	90	179
35 m	43	36	24	0	30	72	160
60 m	66	57	48	30	0	50	135
100 m	108	100	90	72	50	0	91
200 m	196	188	179	160	135	91	0

**Table 2** Average distance between wading pools between adjacent transects within study sites ( $n=3$ )

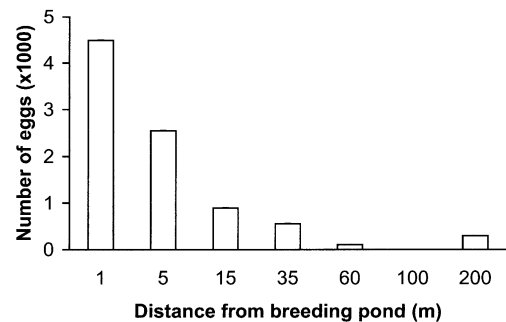
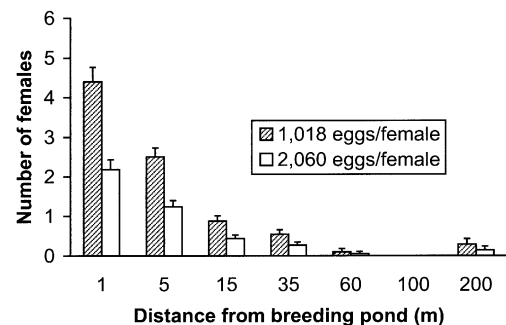
Distance	1 m	5 m	15 m	35 m	60 m	100 m	200 m
1 m	13	22	26	46	71	114	205
5 m	19	25	31	49	72	118	207
15 m	29	33	37	48	71	119	206
35 m	49	50	51	51	70	120	202
60 m	72	70	67	59	71	120	196
100 m	113	109	105	90	88	127	184
200 m	197	191	186	168	155	174	188

oviposition event occurred. Subsequently, wading pools were monitored every 3 days and all eggs found in each pool were counted. Eggs were counted individually in small containers, after which they were returned to the corresponding natural breeding pond. Occasionally, not all eggs were detected and newly hatched tadpoles were found upon subsequent monitoring. Tadpoles were assigned to that pool's egg count from the previous monitoring day if newly hatched with yolk sac or to the second previous monitoring day if larger and without yolk sac. Eggs, rather than tadpoles, were counted to avoid the biases of hatching mortality and insect predation on tadpoles. No attempt was made to remove insect predators from the pools, but vegetative debris that had fallen into the pools was removed each time they were checked. We assumed that females depositing eggs came from the closest natural breeding pond and the adjacent forest. Monitoring of wading pools ceased on 9 August 2001 after a period of 18 days with only two oviposition events.

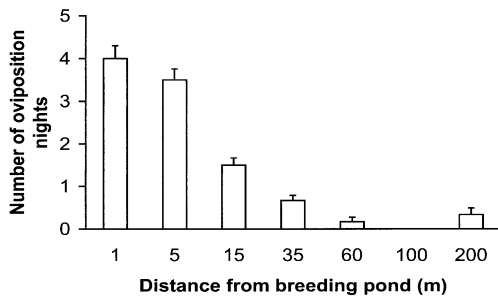
We calculated two estimates of the number of females ovipositing eggs based on average female clutch size from western Tennessee (2,060 eggs; Ritke et al. 1990) and central Missouri (1,018 eggs; S. James unpublished data), because we did not attempt to directly observe females depositing eggs in the pools. We performed Kruskal-Wallis tests with a correction for tied ranks to determine if the number of eggs deposited, number of females ovipositing, and number of oviposition events differed among treatment distances. We also performed survival data analyses in which survival time is defined as the time to the occurrence of an event. In our study, the 'event' was the time to first colonization of wading pools. These 'time-to-colonization' curves were compared to determine if the number of days to first colonization varied among treatment distances.

## Results

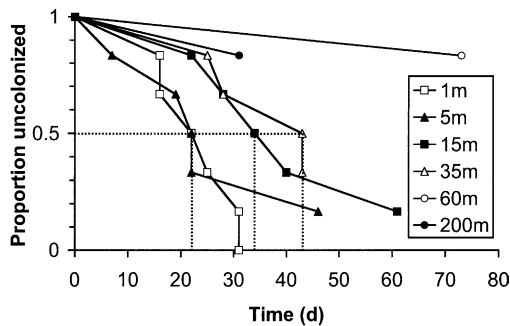
A total of 52,102 eggs and tadpoles were counted in pools from 23 May through 6 August 2001. There were 60 separate oviposition events occurring on 57 different nights. The first oviposition event occurred in a 5-m pool after 7 days. Kruskal-Wallis tests for each transect show that the average number of eggs deposited ( $H_c=15.68$ ,  $df=5$ ,  $P<0.01$ ), number of females ovipositing ( $H_c=15.68$ ,  $df=5$ ,  $P<0.01$ ), and number of nights with oviposition events ( $H_c=15.51$ ,  $df=5$ ,  $P<0.01$ ) differed across treatment

**Fig. 2** Average number of *Hyla versicolor* eggs (+SE) counted at each pool in relation to distance from natural breeding pond**Fig. 3** Estimated average number of female *Hyla versicolor* depositing eggs (+SE) in wading pools at each distance from natural breeding ponds based on average female clutch size from western Tennessee (2,060 eggs) and central Missouri (1,018 eggs)

distances. Figures 2, 3, and 4 indicate that the average number of eggs deposited, estimated average number of females ovipositing, and average number of nights with oviposition events at each site decrease with distance from the breeding ponds. Analysis of 'time-to-colonization' data using a Generalized Wilcoxon test (Lee 1992) revealed that the time to first colonization differed among



**Fig. 4** Average number of nights (out of 78) in which an oviposition occurred at each distance (+SE) from the natural breeding site



**Fig. 5** Number of days until first colonization of wading pools by *Hyla versicolor* represented as survival curves. Ponds that were never colonized were censored and included in the analysis. Dotted lines indicate the median time-to-colonization for each of the curves for which multiple comparisons were made (Table 3)

**Table 3** Multiple comparisons of 'time-to-colonization' curves based on the Kruskal-Wallis Test. Colonization events at 60 m, 100 m, and 200 m distances were omitted because of low sample sizes

Comparison	P
1-5	NS
1-15	<0.05
1-35	<0.05
5-15	<0.05
5-35	<0.05
15-35	NS

distances ( $X^2=25.05$ ,  $df=6$ ,  $P<0.001$ ). Figure 5 shows that the average number of days to first oviposition increases with distance from natural ponds. Pairwise comparisons of individual 'time-to-colonization' curves based on the Kruskal-Wallis test (Lee 1992) show that the time to colonization increases as distance from the natural breeding site increases but not in all instances (Table 3). More than 95% of all eggs were deposited within 15 m of the breeding ponds. No eggs were ever found in the pools at 100 m from the natural breeding ponds and eggs were found in a 60-m pond only during the final days of the study. Eggs were recorded on two occasions in a single 200-m treatment pool. We have included results from the 200-m pool in our analyses, however we question whether

the individuals that colonized that pool originated from the breeding pond under investigation.

## Discussion

Gray treefrogs breed over a period of several months during the summer in Missouri. The terrestrial habitat adjacent to the breeding site provides food and shelter throughout the prolonged breeding season. Other studies have shown that treefrogs move to and from a single breeding pond within a breeding season (e.g., Harris 1975; Murphy 1994). Amphibian movements around the breeding habitat can be part of normal foraging behavior within an individual's home range (Gibbons and Bennett 1974), or repeated movements to the pond to deposit additional clutches of eggs (Wells 1976; Perrill and Daniels 1983). Female gray treefrogs are only present at the breeding pond on nights in which they mate but may return on multiple nights during a breeding season (Godwin and Roble 1983; Sullivan and Hinshaw 1992). Male gray treefrogs spend a larger proportion of time at the breeding pond, but all males are not found at the breeding pond on every night of the breeding season that males are calling (Fellers 1979; Ritke and Semlitsch 1991).

However, it is unclear where adult gray treefrogs go when not attending the chorus at breeding ponds. In our study, adult gray treefrogs deposited eggs up to 200 m into the terrestrial habitat, but most breeding activity was within 15 m from the natural breeding pond. Whether treefrogs purposefully moved to the artificial pools from the natural breeding pond or encountered the pools during other activities away from the breeding pond remains undetermined. Males that moved away from the natural breeding pond to forage may have encountered a wading pool and attracted females that were returning to the natural breeding pond to deposit additional clutches. Alternatively, amplexant pairs may have encountered the artificial pools after leaving the male's perch site at the natural breeding pond. Sullivan and Hinshaw (1992) found that amplexant pairs of gray treefrogs move along the margin of the pond before oviposition. Regardless of the mechanism of colonization, each female that visited the artificial pools moved some distance through the terrestrial habitat surrounding the natural ponds.

For the 2001 breeding season, we observed 58 separate gray treefrog oviposition events at our artificial pools, and counted 52,102 eggs and tadpoles. The extent of artificial pool use in this study indicates that gray treefrogs do not exhibit strict breeding pond fidelity and readily breed in novel locations within a breeding season. Thus, the 'ponds as patches' metapopulation model is not strictly applicable, and gray treefrog subpopulations can consist of clusters of nearby ponds that exchange individuals within each breeding season. Sinsch (1992) conducted a *Bufo calamita* metapopulation study in which adjacent breeding sites were grouped into distinct breeding areas. Sinsch (1992) determined that most adult males stayed

within a single breeding area throughout the breeding season, but also recorded exchange of individuals between breeding areas over the period of several breeding seasons. Our data suggest that short distance movements between breeding sites by adults may be more common than generally perceived, and investigations of amphibian metapopulations should not assume a priori that each pond is a discrete breeding unit during a breeding season.

We found that the number of days until first colonization of artificial pools was positively related to distance from the natural breeding site. Thus, the probability of colonization of new ponds within a breeding season decreases as distance from the main breeding pond increases. This result suggests that the amount of terrestrial habitat used within a breeding season is confined to a quantifiable area surrounding breeding sites. Freda and Gonzalez (1986) determined that daily movements of *H. andersoni* were contained within 20 m of breeding ponds, and that most individuals remained within 70 m of the breeding pond throughout the breeding season. Kramer (1973) recorded movements up to 58 m into the terrestrial habitat surrounding breeding ponds, and movements up to 195 m between adjacent breeding sites for *Pseudacris triseriata* within a breeding season. Other studies of treefrog movements have also found that terrestrial movements during the breeding season occur at a relatively small scale (Jameson 1957; Ritke et al. 1991). Our findings correspond with previous studies and indicate that patches of aquatic habitat and adjacent forest can explicitly define local populations of the gray treefrog. The results of our study show that efforts to protect and maintain populations of amphibians should not be limited to the aquatic breeding habitat, and that use of terrestrial habitat surrounding breeding sites by amphibians should also be considered important.

For the gray treefrog in Missouri, we suggest that protection of terrestrial habitat within a 60-m radius from aquatic breeding habitat will provide terrestrial habitat for the majority of within-breeding-season activities. However, we present these data knowing that our approach to monitoring the distribution of adult treefrogs in the terrestrial habitat surrounding breeding ponds may have led to a biased interpretation of actual habitat use. By creating new breeding sites near the existing pond, we may have eliminated the need for longer-distance movements to locate suitable alternative breeding habitat and therefore underestimated the amount of terrestrial habitat needed to encompass a single population. Alternatively, the creation of new breeding sites may have drawn individuals further than usual from the natural breeding site, leading to an overestimation of the terrestrial habitat typically used by adult treefrogs during the breeding season. Nevertheless, our study has demonstrated that terrestrial habitat surrounding breeding sites is utilized by adult gray treefrogs within a single breeding season and may be important for population persistence.

As with any study regarding habitat use, our results are dependent upon the quality of habitat in which the study

was conducted. Our study sites were enclosed in closed-canopy, oak/hickory forest approximately 100 years old. Mature forest is good-quality habitat for gray treefrogs because it provides refugia during the breeding season while individuals are not foraging or breeding, and overwintering sites during the non-breeding season. The availability of refugia in the terrestrial landscape almost certainly influenced the movement distances of adult treefrogs in our study. In a landscape containing more widely separated refugia, we may have observed reproductive events at greater distances from the natural breeding site, due to a greater frequency of individuals making long-distance movements to reach appropriate terrestrial habitat. Our suggestion of a 60-m radius of core breeding habitat protection may not be broadly applicable to degraded environments, but can be used as a starting point for further investigations regarding species or area-specific conservation management.

While our study provides information on the extent of within-breeding-season adult movements, the extent of terrestrial habitat use between consecutive breeding seasons remains unresolved, and would be better studied using direct methods for following individuals in the landscape (i.e., radiotelemetry, mark-recapture). Non-breeding season terrestrial habitat use (e.g., overwintering sites) certainly could extend further from the breeding pond than the distances we recorded within a single breeding season, and has been investigated for pond-breeding salamanders (Semlitsch 1998; Trenham 1998). Semlitsch and Bodie (2003) summarize results from the literature regarding terrestrial habitat use by local populations of amphibians, and report a mean minimum (159 m) and maximum (290 m) distance of migration that exceeds our observed movements within a single breeding season. Furthermore, there is evidence that juveniles accomplish the majority of dispersal between breeding sites (Gill 1978, Breden 1987, Berven and Grudzien 1990), and that the distances moved by juveniles between populations may be even greater than those traveled by adults within local populations (Breden 1987). Our data show that suitable terrestrial habitat surrounding breeding sites can lead to colonization of new breeding sites and may help to buffer local populations of treefrogs from extinction. A better understanding of terrestrial habitat requirements at each life-history stage is critical for effective amphibian conservation planning.

**Acknowledgements** We would like to thank J. Crawford, G. Woloszyn, D. Johnson and T. Green for assistance in monitoring ponds and counting eggs. We also thank G. Woloszyn for assistance in filling wading pools, and C. Dillman for helping to transport and arrange the wading pools into transects. We thank J. Millsbaugh for permission to access the field sites at the Baskett Wildlife Research Area. We also thank B. Rothermel, T. Green, J. Crawford and two anonymous reviewers for comments on early drafts of this manuscript. Funding for this research was provided by a grant from the U.S. Geological Survey (01CRAG0007) to R.D.S.

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