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Terrestrial Habitat Use and Winter Densities of the Wood Frog (*Rana sylvatica*)

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ABSTRACT.—Few studies have systematically investigated the overwintering ecology of anurans. We used large-scale field enclosures to measure the winter densities of Wood Frogs (*Rana sylvatica*) in an upland deciduous forest adjacent to two breeding pools in eastern Massachusetts. Pitfall traps associated with one of our enclosure arrays were operated continuously from March to December 2000. Wood Frog densities ranged from 0–6.3 Wood Frogs/100 m² ($\bar{x}$ = 1.4, SD = 1.6, *N* = 17 enclosures) and declined as distance to the nearest breeding pond increased. The sex ratio of Wood Frogs wintering close (< 65 m) to the pond was more highly skewed toward males than the sex ratio of Wood Frogs wintering further from the pond (8:1 vs. 1.6:1). Adult Wood Frogs apparently only occupied this upland forest habitat during late fall and winter and did not use it during the summer active period. These results suggest that few wintering females may be protected within narrow regulatory buffers adjacent to breeding ponds and that the effects of habitat destruction on Wood Frog mortality may vary dramatically by season.

Many pool-breeding amphibians spend the majority of their lives as adults and juveniles in terrestrial habitats surrounding breeding ponds. Human land uses such as forestry, agriculture, and roads affect the movement patterns and breeding distributions of some amphibian species (e.g., DeMaynadier and Hunter, 1998, 1999; Gibbs 1998a,b; Findlay and Bourdages, 2000). In many areas, terrestrial habitats around breeding pools are coming under increasing development pressure, so increased attention has been focused on the conservation implications of such development (Burke and Gibbons, 1995; Semlitsch, 1998). However, research on the terrestrial ecology of pool-breeding amphibians has lagged far behind research on breeding and larval ecology. An improved understanding of the terrestrial ecology of aquatic-breeding amphibians is not only important from a conservation perspective, but it may be vital to our understanding of the evolutionary ecology and population dynamics of these species. Selection pressures in the terrestrial environment may play a significant role in shaping life history evolution as well as a variety of other traits (Wilbur, 1980; Berven, 1995). In addition, the potential role of terrestrial resources in limiting or regulating population size in general has not been investigated (Walls, 1990; Van Buskirk and Smith, 1991).

The Wood Frog (*Rana sylvatica*) is widely distributed throughout northern and eastern North America, generally inhabits moist, lowland deciduous forests, and breeds in pools lacking fish (Klemens, 1993; Degraaf and Yamasaki, 2001; Hulse et al., 2001). Wood Frogs are freeze tolerant and winter under leaf litter and duff, or in shallow burrows (Schmid, 1982; Hulse et al., 2001; JVR, pers. obs.). Although some researchers have described Wood Frog summer habitat use (Heatwole, 1961; Bellis, 1965), little is known about the movement patterns of this species (but see Berven and Grudzien, 1990) or about differences in summer and winter habitat use. However, Licht (1991) found that Wood Frogs exposed to cold temperatures in the laboratory sought out moist soils rather than more saturated mud. Zweifel (1989) hypothesized that it might be advantageous to males to hibernate close to the breeding pond, as this would enable them to arrive at the breeding pond earlier during a period of explosive spring breeding. In this study, we provide what we believe are the first reported measurements of Wood Frog winter population densities. In addition, we investigate relationships between density, sex ratio, and distance to the breeding ponds, as well as the phenology of Wood Frog movement through terrestrial habitats, and discuss the conservation implications of our results.

MATERIALS AND METHODS

During winter 1999–2000, two arrays of field enclosures were constructed in oak-dominated (*Quercus* spp.) upland deciduous forest adjacent to two Wood Frog breeding ponds in Sudbury, Massachusetts (42°21′N, 71°26′W; Fig. 1). Enclosures were placed within blocks of well-drained upland forest habitat qualitatively similar to upland habitat located at other orientations to the breeding ponds, free of foot trails, and as close to the breeding ponds as possible while avoiding poorly drained soils. The seventeen 16 × 17 m (272 m²) enclosures were constructed of 0.9 m silt fencing partially buried in a 25 cm deep trench. Pitfall traps (19 liters) were placed in the corners of each enclosure and along the external walls of the enclosure arrays at the junction of each enclosure. Construction of the enclosures was initiated during the last week in November and completed on 8 December. By late November, Wood Frogs in our region have generally arrived at wintering sites and are inactive (Hulse et al., 2001; JVR, unpubl. data). Thus, wintering Wood Frogs, if present, were fenced in by the enclosures. The distance from the center of each enclosure to the nearest pond edge was recorded. Pitfall traps were kept closed until 1 March, prior to the spring prebreeding migration that began on 9 March (Fig. 2).

During the spring prebreeding migration, Wood Frogs were captured within the enclosures (*N* = 73) and at the outer walls of the enclosures moving to-

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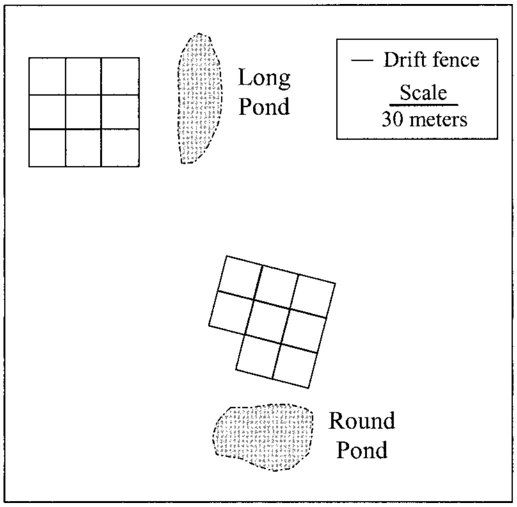

FIG. 1. Map of study site in Sudbury, Massachusetts. Seventeen 272-m^2 field enclosures were constructed adjacent to two woodland pools used for breeding by Wood Frogs. Pitfall traps were located at the four corners of each enclosure, as well as along the external walls of the enclosure arrays at the corners (two traps) and at the junction between enclosures.

ward ($N = 125$) or lateral to ($N = 102$) the nearest breeding pond. The sex of each captured individual measuring 38 mm or more (SVL) was determined by the presence or absence of male nuptial pads on the inner digits of the front limbs, whereas individuals < 38 mm in length were classified as juveniles (Bellis, 1965). After processing, individuals were released into the pond they were moving toward, based upon their location of capture. Wood Frogs captured moving laterally relative to the nearest breeding pond were released in their apparent direction of movement at the opposite side of the enclosure array. Wood Frogs emerging from enclosures during the prebreeding migration were released to the nearest breeding pond if captured in either of the two pitfall traps closest to the pond and were assumed to be moving laterally if captured in the other two traps within a given enclosure. As the enclosures were to be used for experimental manipulations involving Spotted Salamanders (*Ambystoma maculatum*), no Wood Frogs were released back into the enclosures. Rather, once the prebreeding migration was completed, Wood Frogs captured at the outer walls of an enclosure array were released at the opposite end of the array, as described above. External traps at the Round Pond array were shut down in late April, but traps at the Long Pond array were operated continuously through the following December (Fig. 1). During the spring, traps were checked the day after every nighttime rain, and at least once every 2–3 days, regardless of weather. Traps operated during the other seasons were checked after each nighttime rain and at least once every week, except when a solid snow pack was present. The bottom of each pitfall trap was lined with a 25 × 25 cm sponge, which was kept damp throughout the study to prevent desiccation of amphibians.

Wood Frogs emerging from enclosures in the early spring were known to have wintered <65 m from the nearest breeding pond, whereas Wood Frogs captured at the outer wall of each enclosure array located roughly parallel to the pond shore, were considered to have wintered > 65 m from their breeding pond. Although these individuals could have wintered closer to the breeding pond if they first moved directly away from the pond, and then abruptly reversed direction, our data from another site indicate that this is unlikely. At a site with concentric rings of drift fencing located 0, 60, 100, and 200 m from a breeding pond, it was extremely rare for Wood Frogs to be captured moving away from the breeding pond during the prebreeding migration (Regosin et al., unpubl. data). Thus, we obtained data on the winter densities of Wood Frogs within 17 enclosures adjacent to two breeding ponds. To test for a relationship between winter Wood Frog densities and distance to the nearest breeding pond, linear regression analysis was performed on square-root transformed counts (Sokal and Rohlf, 1981). Using contingency table analysis, we were also able to compare the sex ratio of animals wintering within the enclosures, less than 65 m from the breeding ponds, with animals wintering at greater distances to the breeding ponds.

RESULTS

The phenology of Wood Frog captures associated with traps at the Long Pond array operated continuously from 1 March to 31 December 2000 is shown in Figure 2. Although adults were captured emigrating from the breeding ponds during late March and early April, they were almost never captured from mid-April through early November, indicating that they were not using this upland deciduous forest habitat for feeding or shelter during their active period. In the fall, adults were captured during a very narrow period in early to mid-November (Fig. 2). At this time, 17 of 26 (65.4%) adult frogs were captured moving toward the nearest breeding pond, and only one individual was captured moving away from the breeding pond. The remaining 30.1% of individuals were captured in traps lateral to the nearest breeding pond. Metamorphosing juveniles began to emerge from the breeding ponds on June 27.

Winter densities of frogs within enclosures ranged from 0–6.3 frogs/100 m^2 ($\bar{x} = 1.4$, SD = 1.6, $N = 17$). Only two of 65 frogs (3.1%) apparently wintering in the enclosures were juveniles, whereas only seven (10.8%) were females. The sex ratio (males:females) was significantly more highly skewed toward males among animals wintering within the enclosures < 65 m from the nearest breeding pond (8:1), than among animals captured at the outer walls of the enclosures parallel to the pondshores and apparently overwintering >65 m from their breeding pond (1.6:1; $\chi^2 = 13.7$, df = 1, $P < 0.001$; Fig. 3). Males were estimated to be 4.9 times more likely than females to overwinter < 65 m from their breeding pond (95% CI for odds ratio, 1.9–14.2)

To examine whether gender differences in habitat use might be explained by gender differences in orientation (e.g., females were just as close to the pond but at different compass directions), we analyzed available migratory orientation data from the 1998

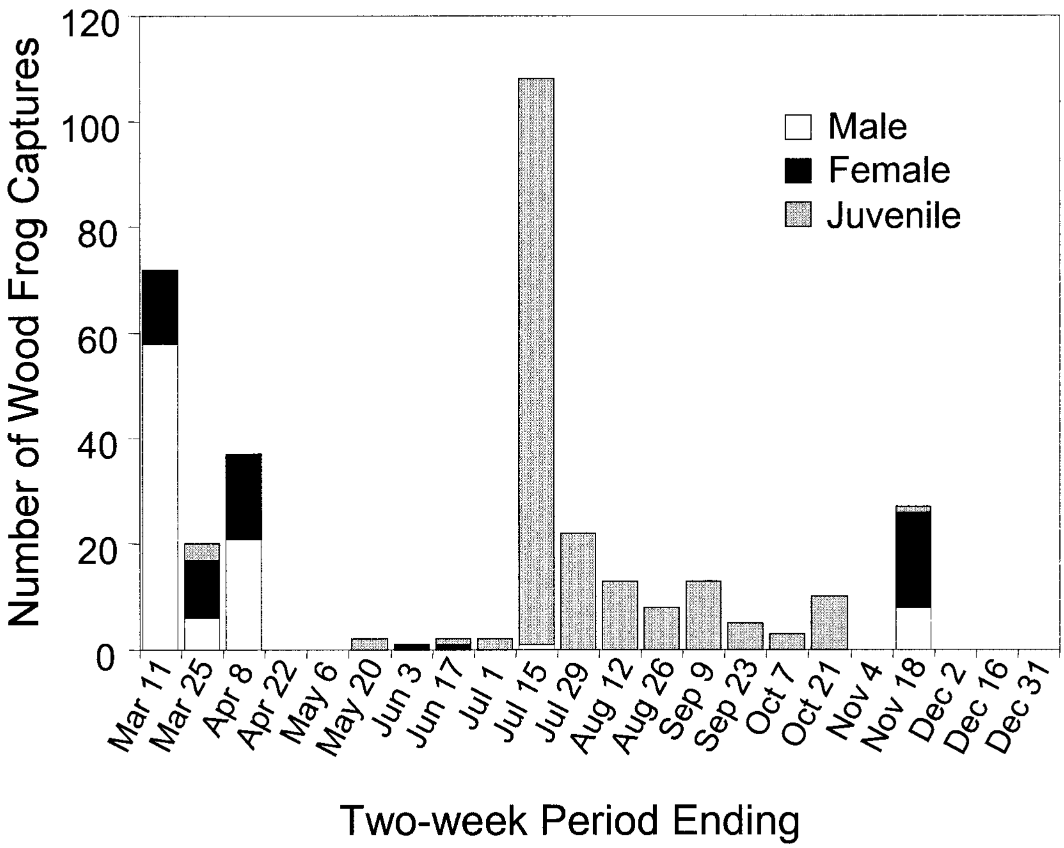

FIG. 2. Seasonal phenology of Wood Frog captures at the outer walls of the Long Pond enclosure array. Pitfall traps were operated continuously from 1 March to 31 December 2000. Wood Frogs were first captured emerging from hibernation on 9 March. Juveniles captured prior to June 28 are presumed to be yearlings that metamorphosed in 1999.

breeding season. During March 1998, both breeding ponds were fully encircled by drift fences located approximately 30 m from each pondshore (pairs of 19-liter pitfall traps spaced at 15-m intervals). These fences were constructed while the prebreeding migration had already begun, but construction was completed prior to the postbreeding migration. During the 1998 postbreeding migration, the distributions of male and female frogs among pitfall traps did not differ at either pond (Kolmogorov-Smirnov two sample test, Oblong Pond: D = 0.04, $N = 607$, $P > 0.9$; Round Pond: D = 0.05, $N = 1437$, $P > 0.3$). Similar results were obtained for that portion of the prebreeding migration for which data were available (Kolmogorov-Smirnov two sample test, Oblong Pond: D = 0.10, $N = 132$, $P > 0.9$; Round Pond: D = 0.07, $N = 232$, $P > 0.9$). The density of frogs wintering in the enclosures increased as distance to the nearest breeding pond decreased ($r^2 = 0.38$, $F_{1,15} = 9.39$, $P = 0.008$; with outlier deleted, $r^2 = 0.46$, $F_{1,15} = 12.21$, $P = 0.004$; Fig. 4).

DISCUSSION

Few studies have examined the ecology and habitat use of wintering amphibians (e.g., Lamoureux and Madison, 1999), and to our knowledge ours is the first study to directly measure winter densities of a ranid. Wood Frog winter densities reported here ($\bar{x} = 1.4/100\ m^2$) were considerably lower than the 0.13–0.75 frogs/m^2 reported for three 8-m^2 plots in a forested wetland in early October (Heatwole, 1961). However, Heatwole suggested that the Wood Frogs he observed might not yet have been hibernating. Although enclosures at our site were large, and the enclosed habitat was qualitatively similar to the upland habitat at other orientations to the ponds, enclosures were not randomly placed, and Wood Frog densities in upland habitats at other orientations may have differed from the densities we observed. The density of Wood Frogs varied considerably among enclosures (range: 0–6.3/100 m^2), and it is unknown to what extent Wood Frogs densities are influenced by microhabitat variation in factors such as soil moisture, aspect, or leaf litter depth. Although our results suggest that Wood Frog densities decline as distance to the breeding pond increases, this finding should be viewed with caution, as the enclosures we studied were contiguous and thus not spatially independent.

We believe that our estimates of winter density are reasonably accurate. However, there are two potential sources of error. First, depending upon weather con-

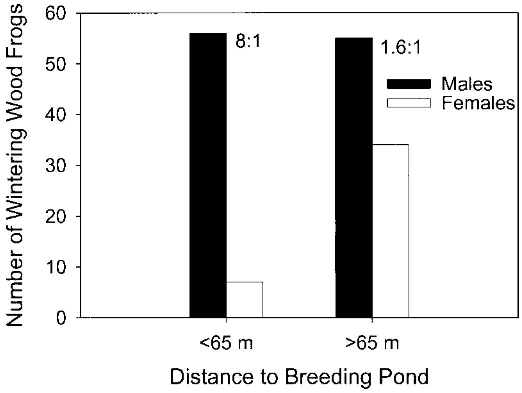

FIG. 3. Sex ratios of wintering Wood Frogs migrating to breeding ponds in spring 2000. The sex ratio (males:females) is significantly higher in the enclosures < 65 m from the breeding ponds, than at their outer walls furthest (> 65 m) from the breeding ponds ($P < 0.001$).

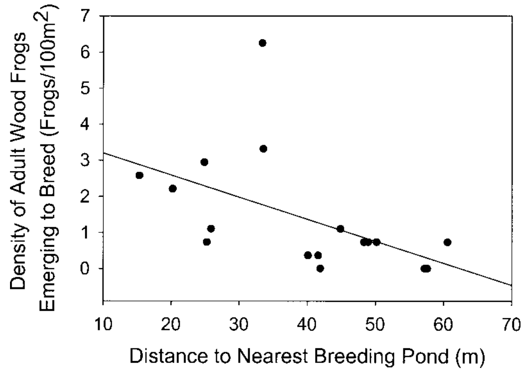

FIG. 4. Relationship between Wood Frog winter densities in 17 field enclosures and distance to the nearest breeding pond. Regression analysis performed on square-root transformed counts shows a significant negative relationship ($y = 2.2 - 0.03x$, $P = 0.008$).

ditions, we have captured small numbers of Wood Frogs in December in other years at this and other sites (JVR and BSW, unpubl. data). Frogs moving during December would not have been able to enter our enclosures, thereby resulting in an underestimate of winter densities. Second, although we are not aware of any published data on trespass (moving across drift fence without being captured) rates in Wood Frogs, small numbers of Wood Frogs may have trespassed across drift fences during the spring migration (Dodd and Scott, 1994). However, our observation that few Wood Frogs were captured in enclosures located furthest from the breeding ponds (Fig. 4), suggests that trespass was not a significant factor in explaining our results. If the trespass rate were high, large numbers of Wood Frogs would have been expected to be captured emerging from these enclosures, as large numbers of Wood Frogs ($N = 125$) were captured moving toward the ponds at the outer walls of these enclosures.

One of our most important findings is that the sex ratio of adults changed with distance from the breeding pool, with the number of males per female declining as distance to the breeding pond increased. This difference in sex ratios by distance suggests that females, on average, winter farther from the breeding pond than do males. The observation that the migratory orientations of males and females did not differ, suggests that differences in orientation are not likely to explain observed differences in upland habitat use among the sexes. Zweifel (1989) hypothesized that male Wood Frogs might gain a fitness advantage by hibernating close to the breeding pond, because they could arrive to breed earlier in the spring. Our finding of a highly male-biased sex ratio near the pond is consistent with this hypothesis. This contrasts with reported results for *Rana lessonae* and *Rana esculenta*, where hibernation distance from the breeding pond was not related to sex (Holenweg and Reyer, 2000).

Wood Frogs wintered in upland deciduous forest habitat within 65 m of the breeding ponds but did not use this habitat for foraging or shelter during the April to November active period. This result is consistent with reports that Wood Frogs are more frequently encountered in moist lowland forests outside of the winter months (Heatwole 1961; Bellis, 1965; Klemens, 1993; Degraaf and Yamasaki, 2001; Hulse et al., 2001). Although additional research is needed to determine the extent to which Wood Frogs may winter in suitable microhabitats within forested wetlands, there is some evidence that Wood Frogs avoid saturated soils during cold weather, perhaps because these soils are less suitable for wintering (Licht, 1991). Our observation of Wood Frogs moving into forested uplands near breeding pools in late fall is consistent with this finding. Such seasonal variation in habitat use, and associated wide-ranging movement patterns, may render amphibian populations more vulnerable to habitat loss and fragmentation (Lamoureux and Madison, 1999).

Our results suggest that the impacts of upland forest loss near Wood Frog breeding pools would differ by season. Habitat destruction near breeding ponds between November and March (in our region) might kill large numbers of wintering Wood Frogs, whereas similar activities at other times of year would not. To reduce construction-related Wood Frog mortality, regulators might prohibit construction during the winter hibernation period, or use silt fencing to exclude Wood Frogs from areas slated for winter construction. In the United Sates, many small isolated wetlands such as those used by Wood Frogs for breeding do not have legal protection (Snodgrass et al., 2000). Even where such wetlands are protected, state and federal wetland regulations generally protect little or no upland surrounding wetlands (Burke and Gibbons, 1995; Semlitsch, 1998). Our results suggest that relatively few wintering Wood Frogs would be protected by narrow (15–30 m) regulated terrestrial buffer zones surrounding breeding ponds and that the overwhelming majority (perhaps around 90%) of these animals would be male. Habitat loss that disproportionately impacts females would increase the risk of local extinction, particularly for small populations with high variability in recruitment between years, which is common for pool-breeding amphibians (Berven, 1995).

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