The effects of clearcuts and forest buffer size on post-breeding emigration of adult wood frogs (*Lithobates sylvaticus*)

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ABSTRACT

The establishment of terrestrial buffer zones around vernal pools has been recommended to provide upland habitat for pool-breeding amphibians in areas where forestry practices occur adjacent to breeding sites. However, few studies have empirically tested the effectiveness of buffers. We assessed post-breeding emigration behavior (net emigration distance, rate of movement, proportionate use of available habitats) of radio-tagged adult wood frogs (*Lithobates sylvaticus*) at nine vernal pools with experimental forest buffer treatments in central Maine, USA. Buffer treatments were either 30-m ($N = 3$) or 100-m ($N = 3$) forest buffers surrounded by a 100-m wide clearcut; pools surrounded by uncut forest served as reference sites ($N = 3$). We tracked 33 individuals in 2004 and 2005, for an average of 41 days, as they emigrated from breeding pools. Recently clearcut habitat was permeable to emigrating adult wood frogs, particularly females. A higher proportion of frogs at 30-m buffer sites than at 100-m buffer sites traveled through the clearcuts to reach intact forest beyond, suggesting that 30-m buffers may not provide sufficient upland habitat to support adult wood frog populations. There was high variability in emigration behavior among frogs, regardless of buffer treatment, and males and females tended to exhibit differential responses to different buffer sizes and to clearcut habitat. Although wood frogs in this study utilized both 30-m and 100-m forest buffers, variability between sexes and density-dependent effects could render small buffers (e.g., 30 m or less) inadequate to support these populations.

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1. Introduction

Vernal pools are common throughout northern New England forest ecosystems and constitute vital habitat for several amphibian species (Gibbs, 1993). Amphibians utilize pools for breeding and larval development, yet most species spend the majority of their adult lives in the terrestrial environment (Berven, 1990; Hunter et al., 1999). The spatial arrangement of breeding sites within a matrix of suitable upland habitat permeable to amphibian movement is of critical importance to their survival (Dunning et al., 1992; Pope et al., 2000; Semlitsch and Bodie, 2003; Hocking and Semlitsch, 2007), particularly in landscapes subject to disturbance (Semlitsch et al., 2009). Current federal wetland regulations, however, do not protect these isolated wetlands or the adjacent upland habitat from land-use practices such as timber harvesting (Gibbons, 2003; Burne and Griffin, 2005). Protection of suitable terrestrial

habitat through the use of forested buffer zones is integral to effective conservation of vernal pool-breeding amphibians (Calhoun and deMaynadier, 2004; Harper et al., 2008).

Intensive forest management can degrade terrestrial habitat by reducing amphibian microhabitat provided by leaf litter and coarse woody debris (McLeod and Gates, 1998; Semlitsch, 2000). Additionally, canopy removal by means of clearcutting eliminates shade, increases ground surface temperatures, and reduces soil moisture, thereby making such areas inhospitable or less suitable for many amphibian species (Semlitsch, 2000). Wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*) tend to be less abundant in clearcuts than in uncut forests (deMaynadier and Hunter, 1999) and clearcuts are associated with decreased juvenile survival for a number of amphibians (Patrick et al., 2006, 2008; Rothermel and Semlitsch, 2006; Todd and Rothermel, 2006).

The effects of clearcuts on amphibian movement are not well understood. The creation of open areas by timber harvesting can disrupt amphibian migration routes between breeding pools and upland habitat (deMaynadier and Hunter, 1995; Todd et al., 2009). Adult wood frogs have been found to travel hundreds of meters from breeding pools during post-breeding emigration, with maximum migration distances of approximately 395 m and

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340 m reported by Rittenhouse and Semlitsch (2007) and Baldwin et al. (2006), respectively. Because moving through open habitat increases the risk of desiccation and predation, forest clearcutting over a broad landscape area may significantly alter amphibian migration behavior (Rittenhouse and Semlitsch, 2009; Rittenhouse et al., 2009).

The short life span, high fecundity, and long migration distances of wood frogs make them especially sensitive to habitat loss and alteration (Harper et al., 2008). One method designed to protect important upland amphibian habitat surrounding vernal pools is the implementation of terrestrial buffer zones. Recommended buffer zone widths range from 30 to 290 m from the pool edge, and their efficacy has recently been tested through the use of simulation models. These models showed that regulations protecting 30 m or less of surrounding terrestrial habitat are inadequate to support viable populations of pool-breeding amphibians (Harper et al., 2008). To our knowledge, there has been no prior field experiment designed specifically to test whether wetland buffers provide sufficient protection for vernal pool-breeding amphibians, or to compare buffers of different widths. We conducted a large-scale field experiment with the following objectives: (1) to determine whether wood frogs will migrate through clearcuts; (2) to determine whether buffer size affects wood frog post-breeding emigration behavior (use of clearcuts, rate of movement, and emigration distance); and (3) to determine whether male and female wood frogs exhibit differential post-breeding emigration behavior.

2. Methods

2.1. Study site

This study was conducted on industrial forest land owned and managed by International Paper Company/Sustainable Forest Technologies, totaling 120,646 ha (289,552 acres) in Penobscot and Washington counties, Maine. Forests were mixed hemlock- (*Tsuga canadensis*) northern hardwood (*Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*), with a network of vernal pools and dirt access roads throughout.

2.2. Buffer width manipulations

To examine how post-breeding movement of wood frogs is influenced by forest buffer width surrounding vernal pools, we completely encircled nine vernal pools with drift fences. Study pools were selected based on several criteria. All vernal pools were: (1) initially surrounded by at least a 1000-m radius of relatively undisturbed forest (logging > 60 years ago); (2) similar in hydroperiod (holding water at least five months post ice-out the year prior to the study); and (3) between 0.1 and 0.3 ha (which is typical of vernal pools in the region) (Gibbs, 1993). Because of the complex landscape, we were not able to standardize the distance from our study pools to the nearest neighboring vernal pool or dirt road.

We randomly assigned pools to one of three treatments: reference (i.e., uncut treatment; N = 3), clearcut with 100-m buffer (N = 3), or clearcut with 30-m buffer (N = 3). Between September 2003 and March 2004, International Paper Company created experimental buffers by clearcutting forest (removed all merchantable trees ≥5 cm dbh) around specified vernal pools. Pools in the 30-m and 100-m buffer treatments had a 100-m wide concentric band of forest clearcut around the forest buffer zone (Fig. 1). Experimental buffer widths were based on the range provided by current recommendations (Semlitsch, 1998; Richter et al., 2001) and our 30-m buffer treatment is similar to more recent buffer recommendations for vernal pools (Calhoun and deMaynadier, 2004). We mapped vernal pool, buffer, and clearcut perimeters using a Trimble Pathfinder

Table 1
Number of adult female (F) and male (M) wood frogs radio-tracked at each buffer treatment (N = 33).

	2004		2005		Total
	F	M	F	M	F + M
Reference	2	2	5	1	10
100-m buffer	2	3	4	3	12
30-m buffer	3	2	6	0	11

Pro XR GPS unit (Trimble Navigation Limited, Sunnyvale, CA; accurate to 0.5 m). Red pine (*Pinus resinosa*) and spruce (*Picea* spp.) were planted in the experimental clearcuts post-harvest.

2.3. Post-breeding movement

In April 2004 and April 2005, we collected adult wood frogs at drift fences as they emigrated from the nine study pools (Tables 1 and 2). Radiotransmitters (model BD-2; Holohil Systems Ltd., Carp, Ontario, Canada) with expected battery life of five weeks were externally attached to the frogs' waists using belts made of Teflon tubing (Bartelt and Peterson, 2000). The belt was positioned on the waist of the frog by sliding it over the extended hind legs. The transmitter-belt package was approximately 8% of the average frog mass (7.2 ± 0.9 g). The cotton thread used to hold the tubing together was susceptible to moist conditions and deteriorated over time, allowing unrecovered radios to fall off the frogs (Waye, 2001). Transmitter belts were attached in the field and frogs were handled as little as possible. Once the belt was attached, the frog was released approximately 2–3 m from the drift fence on the opposite side of the fence from the point where it was captured.

Our target tracking period was from spring post-breeding through summer; however, depredation and battery failure events resulted in reduced tracking times for some frogs (Table 2). We located each animal every other day from capture until termination using an Advanced Telemetry Systems Challenger 2000 receiver and a hand-held three-element Yagi antenna. Animals still being tracked after four weeks were captured and reoutfitted with new transmitters (N = 13). Frogs were checked for skin abrasions each week, and if present, a topical antibiotic/antiseptic (e.g., Bactine®) was applied to the skin. If severe abrasions were present, the transmitter was removed and the animal was released in order to prevent unnecessary injury or fatality (N = 6). When an individual was located, we determined its position by direct overhead localization (Madison, 1997), marked the location with a labeled flag, recorded the location using a Trimble Pathfinder Pro XR GPS, and subsequently plotted the location on a Geographic Information System map of the site. We categorized the location of each frog into one of three habitat types: buffer, clearcut, or forest (wooded area beyond the clearcut).

2.4. Data analysis

For each frog, we calculated the final straight-line distance from the breeding pool edge at the end of the tracking period (from pool edge to final location) using ArcViewGIS 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA). This distance value (hereafter "net emigration distance") may not reflect the total distance traveled, including lateral movements and backtracking for example, but rather reflects the distance of the frog's final location from the breeding pond. We used the net distance value to calculate the mean rate of movement during the tracking period (meters per day). Because no individual frogs were tracked in both 2004 and 2005, and because preliminary analyses suggested no effect of year tracked (P = 0.437), for all subsequent analyses we combined data across years to increase error degrees of freedom.

Table 2

Summary of post-breeding emigration and demographic data for 33 adult wood frogs radiotracked at reference (REF) and treatment (30-m or 100-m buffer) pools in central Maine. The fate of each frog was assigned to one of the following categories: LB – lost belt (dropped off); RS – removed belt due to sores; M – mortality (dead frog was recovered); L – lost signal (could not relocate); R – removed belt at the end of the season. Buffer, clearcut, and forest columns provide the number of days an individual was tracked in the habitat and, in parentheses, the proportion of days tracked in that habitat.

Frog ID	Sex	SVL (mm)	Mass (g)	Trt	Site	Year	Tracking began	Tracking ended	Net dist. (m)	Total days tracked	Buffer days (Prop.)	Clearcut days (Prop.)	Forest days (Prop.)	Fate
30F104	F	48	14.3	REF	30	2004	5-May	7-Jun	0	34	N/A	N/A	33	LB
30F204	F	53	14.0	REF	30	2004	3-May	10-Jun	149	39	N/A	N/A	74	L
30F105	F	50	14.5	REF	30	2005	28-Apr	25-May	99	28	N/A	N/A	26	L
30F205	F	55	15.0	REF	30	2005	28-Apr	25-May	51	28	N/A	N/A	51	RS
30F305	F	57	15.3	REF	30	2005	28-Apr	28-May	185	31	N/A	N/A	29	L
124F105	F	58	14.0	REF	124	2005	3-May	28-May	95	26	N/A	N/A	23	L
141F105	F	48	15.0	REF	141	2005	27-Apr	21-May	81	25	N/A	N/A	23	L
39F104	F	50	14.0	100 m	39	2004	29-Apr	29-May	108	31	3.5 (0.11)	27.5 (0.89)	0	M
55F104	F	51	15.0	100 m	55	2004	3-May	5-Jun	298	34	12 (0.35)	1 (0.03)	21 (0.62)	LB
25F105	F	49	14.8	100 m	25	2005	25-Apr	11-May	226	17	3.5 (0.21)	2 (0.12)	11.5 (0.68)	L
39F105	F	55	16.0	100 m	39	2005	22-Apr	20-May	137	29	3.5 (0.12)	25.5 (0.88)	0	L
39F205	F	49	13.0	100 m	39	2005	2-May	29-May	11	28	28 (1.00)	0	0	L
55F105	F	53	11.5	100 m	55	2005	1-May	28-May	83	28	28 (1.00)	0	0	L
7F104	F	52	14.0	30 m	7	2004	2-May	18-Jul	350	78	14 (0.18)	1 (0.01)	63 (0.81)	RS
7F204	F	44	10.8	30 m	7	2004	2-May	12-Jun	325	42	5.5 (0.13)	9 (0.21)	27.5 (0.65)	L
[a]59F104	F	52	15.3	30 m	59	2004	3-May	23-Aug	166	113	102.5 (0.91)	9 (0.08)	1.5 (0.01)	R
7F105	F	57	15.5	30 m	7	2005	28-Apr	25-May	46	28	11.5 (0.41)	16.5 (0.59)	0	LB
7F205	F	42	12.5	30 m	7	2005	2-May	28-Jun	153	58	25.5 (0.44)	5 (0.09)	27.5 (0.47)	RS
7F305	F	53	13.8	30 m	7	2005	2-May	5-Jul	244	65	22.5 (0.35)	14 (0.22)	28.5 (0.44)	L
20F105	F	52	11.5	30 m	20	2005	2-May	28-May	35	27	1.5 (0.06)	25.5 (0.94)	0	RS
59F105	F	54	13.5	30 m	59	2005	25-Apr	28-May	273	34	7 (0.21)	1 (0.03)	26 (0.76)	L
59F205	F	56	13.5	30 m	59	2005	1-May	21-May	211	21	1 (0.05)	1 (0.05)	19 (0.90)	L
30M104	M	50	13.5	REF	30	2004	16-May	29-Jun	0	45	N/A	N/A	42	RS
30M204	M	49	10.3	REF	30	2004	21-Jun	23-Aug	127	64	N/A	N/A	63	R
141M105	M	49	12.0	REF	141	2005	29-Apr	21-May	88	23	N/A	N/A	20	L
39M104	M	47	12.5	100 m	39	2004	2-May	23-Aug	215	114	92.5 (0.81)	2 (0.02)	19.5 (0.17)	R
39M204	M	48	12.0	100 m	39	2004	2-May	12-Jun	20	42	42 (1.00)	0	0	L
55M104	M	47	12.5	100 m	55	2004	3-May	5-Jun	47	34	34 (1.00)	0	0	LB
39M105	M	47	11.5	100 m	39	2005	2-May	29-May	24	28	28 (1.00)	0	0	L
39M205	M	55	11.5	100 m	39	2005	2-May	29-May	6	28	28 (1.00)	0	0	L
55M105	M	47	11.5	100 m	55	2005	1-May	1-Jul	125	62	58.5 (0.94)	3.5 (0.06)	0	LB
7M104	M	54	13.8	30 m	7	2004	2-May	10-Jun	0	40	40 (1.00)	0	0	M
59M104	M	48	11.0	30 m	59	2004	26-May	30-Jun	0	36	36 (1.00)	0	0	RS

[a] Only individual that traveled through the clearcut into the forest, but then returned to the clearcut for its final recorded location.
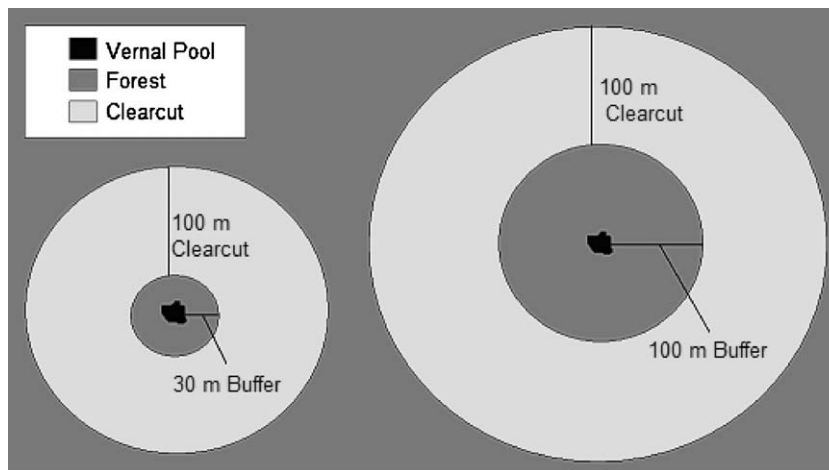
Fig. 1. Schematic of experimental design of 30-m and 100-m vernal pool buffer treatments; reference pools (not shown) were surrounded by >1000 m uncut forest.

We tested for effects of buffer treatment and sex on both net emigration distance and mean rate of movement using Linear Mixed Effect (LME) models (Table 3). As elaborated on below, we ran two models for each response variable: one with both sexes and one with females only. We included the number of days tracked as a fixed effect in net emigration distance models, and we used pool site as a random effect in all models to account for variability associated with different sites. Although body size might be expected to influence emigration rate and distance, preliminary analyses determined that neither snout-vent length ($0.441 > P < 0.819$) nor mass ($0.587 > P < 0.668$) significantly affected either response variable, thus body size variables were not included in final models. Prior to analysis with LME models, we examined whether migration data met assumptions of normality and homogeneity of variances. We log transformed net emigration distance data accordingly; however, rate of movement data did not require transformation.

Male wood frogs are generally smaller than females, and due to body mass restrictions for attaching transmitters, there was an unequal sample size of radio-tagged male ($N = 11$) and female ($N = 22$) frogs. Despite the low sample size of males, we retained these data because sex differences in habitat use have previously been documented for adult wood frogs (Regosin et al., 2003). However, we included a second set of models using only female frog data to explore how the inclusion of male frog data may have biased the initial models.

The nature of radiotracking data (e.g., low sample sizes, high variability) can limit the power to detect treatment differences using formal, inferential statistics. Consequently, we employed descriptive statistics and qualitative summarization of the data to complement formal tests with LME models. We calculated mean ± SE and median net emigration distances and rates of movement for males and females in each treatment group. For frogs tracked at buffer treatment sites ($N = 22$), we calculated the number

Table 3
Results of Linear Mixed Effect Models testing for effects of 30- and 100-m buffers (trt30, trt100) relative to reference sites, males relative to females, number of days tracked (days), and the interaction of buffer treatment and sex on net emigration distance from the breeding pool (net distance) and mean distance (m) emigrated per day (rate of movement) by adult wood frogs ($N = 22$ females, 11 males). Pool site was included as a random effect in all models.

|	Value	SE	DF	t-Value	P-value
Net distance: both-sexes model					
Intercept	3.4625	0.6322	20	5.4765	0.000
trt30	0.7507	0.7429	6	1.0105	0.351
trt100	0.6823	0.7710	6	0.8849	0.410
sexM	−1.0843	0.9696	20	−1.1184	0.277
Days	0.0167	0.0118	20	1.4212	0.171
trt30:sexM	−3.7640	1.4803	20	−2.5426	0.019
trt100:sexM	−0.2031	1.2513	20	−0.1623	0.873
Net distance: females-only model					
Intercept	3.7388	0.6727	12	5.5582	0.000
trt30	0.9490	0.7364	6	1.2888	0.245
trt100	0.6611	0.7292	6	0.9066	0.400
Days	0.0075	0.0151	12	0.4993	0.627
Rate of movement: both-sexes model					
Intercept	1.2100	0.4343	21	2.7864	0.011
trt30	1.3567	0.5790	6	2.3431	0.058
trt100	0.6333	0.6392	6	0.9908	0.360
sexM	−0.2933	0.7928	21	−0.3700	0.715
trt30:sexM	−2.2733	1.1980	21	−1.8976	0.072
trt100:sexM	−0.6183	1.0337	21	−0.5982	0.556
Rate of movement: females-only model					
Intercept	1.2100	0.4651	13	2.6017	0.022
trt30	1.3567	0.6201	6	2.1878	0.071
trt100	0.6333	0.6846	6	0.9252	0.391
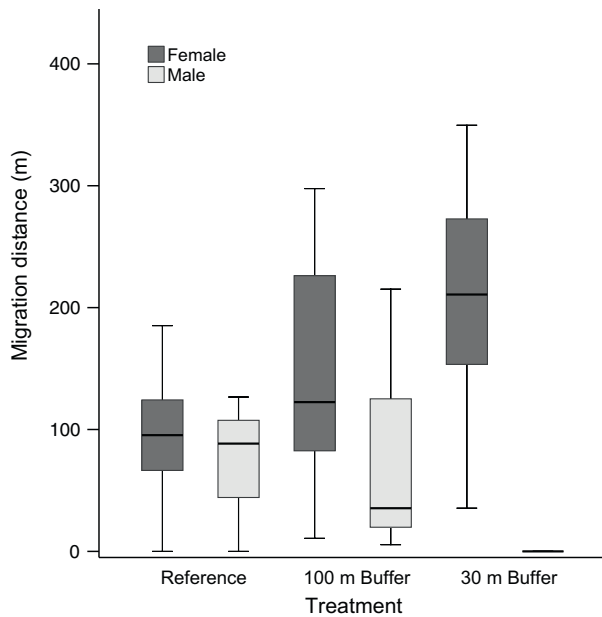
Fig. 2. Net emigration distance (m) from the breeding pool for adult wood frogs at three buffer width treatments in Maine. The two males radio-tracked at the 30-m buffer sites remained at the wetland for the duration of the tracking period, resulting in a net emigration distance of 0 m. Plots represent the minimum, first quartile, median, third quartile, and maximum.

of days and proportion of time spent in each habitat type during the tracking period. All analyses were conducted using R 2.10.1.

3. Results

Fourteen wood frogs were radio-tracked in 2004 (between 30 April and 25 August) and 19 in 2005 (between 25 April and 11 July), for a total of 33 frogs and 422 locations. Between 2004 and 2005, we tracked a total of ten adult wood frogs from reference sites, 12 from 100-m buffer sites, and 11 from 30-m buffer sites (Table 1). Individual frogs were tracked between 17 and 114 days (Table 2). The mean ($\pm$SE) number of days tracked was 41 ± 3 days, with males (47 ± 5 days) monitored slightly longer on average than females (38 ± 3 days).

There was no significant difference in net emigration distance among buffer treatments or between sexes, and there was no significant effect of number of days tracked (Table 3). There was a significant difference in net emigration distance for males in the 30-m treatment group ($P = 0.019$; Table 3; Fig. 2); however, this difference can be explained by the fact that both of the two male frogs tracked in the 30-m buffer group remained at the pond edge during the entire tracking period (net distance = 0 m; Fig. 2; Tables 2 and 4).

Table 4
Descriptive statistics (mean $\pm$ SE, medians) for net emigration distance (m) and mean rate of movement (m/day) by female and male adult wood frogs at reference, 30-m buffer, and 100-m buffer pools in Maine.

Treatment group	Net emigration distance (m)		Mean rate of movement (m/day)	
	Mean $\pm$ SE	Median	Mean $\pm$ SE	Median
Females, Ref.	94.58 ± 16.29	95.37	1.21 ± 0.21	1.22
Females, 100 m	143.67 ± 32.19	122.47	1.84 ± 0.41	1.57
Females, 30 m	200.34 ± 29.66	210.75	2.57 ± 0.38	2.70
Males, Ref.	71.69 ± 27.59	88.43	0.92 ± 0.35	1.13
Males, 100 m	72.75 ± 26.51	35.42	0.93 ± 0.34	0.45
Males, 30 m	0.00	0.00	0.00	0.00

The results of the females-only model for net emigration distance were concordant with the both-sexes model; there were no significant effects of buffer treatment or number of days tracked for female frogs (Table 3).

We detected several marginally significant trends from the rate of movement models (Table 3). Similar to the distance results, males from the 30-m buffer group were set apart due to their lack of movement away from the breeding pool ($P = 0.072$; Tables 2 and 3). There was also a non-significant trend ($P = 0.058$) of frogs at 30-m sites moving at a faster rate than those at reference sites (Table 3). Because, in our study, males at 30-m sites did not emigrate away from the pond, this trend was driven by fast-moving females at 30-m sites (Table 4). The females-only model for rate of movement corroborated the non-significant trend of faster female frogs at 30-m sites ($P = 0.071$; Tables 3 and 4). Rate of movement of frogs at 100-m sites did not differ significantly from those at reference sites (Table 3).

Ten of the 23 frogs (43%) tracked at buffer treatment sites migrated through clearcuts into the surrounding forest (three from the 100-m buffer sites and seven from the 30-m buffer sites) and these frogs showed no synchronicity in their entrance into or exit from the clearcuts (Table 2). Only one of the ten to migrate into the outer forest was a male. The majority (58%) of frogs tracked at the 100-m buffer sites remained within the buffer, whereas only 36% of those at the 30-m buffer sites remained within the buffer (Table 2). Females moved, on average, the shortest distance at reference sites and farthest at 30-m buffer sites (Table 3). Males moved, on average similar distances at reference and 100-m sites, and the two males tracked at 30-m sites moved 0 m (Table 3). On average, females moved farther and faster than males in all three treatment groups (Table 4).

All of the 9 females tracked at 30-m sites entered the clearcut during the tracking period, and 7 of the 9 moved into the forest beyond the clearcut (Table 2). The 30-m females that passed through the clearcut did so in 1–14 days (1, 1, 1, 5, 9, 9, 14), whereas the two females that did not enter the forest were tracked in the clearcut for 16.5 and 25.5 days, respectively (Table 2). One 30-m female (Table 2; ID:59F104) that reached the clearcut in 9 days was last located back in the clearcut after being tracked for 113 days; she was the only individual tracked in this study that returned to the clearcut after successfully reaching the forest beyond. Neither of the two 30-m males exited the buffer during the tracking period (Tables 2 and 4).

Two of the six 100-m females remained in the buffer. Of the four that moved into the clearcut, two continued into the forest (in a maximum of 2 days) and two were located within the clearcut for the remainder of the tracking period (25.5 and 27.5 days, respectively) (Table 2). Four of the six 100-m males remained in the buffer during tracking. Of the two that left the buffer, one passed through the clearcut in 2 days and moved into the forest for the remainder of the tracking period; the other was tracked within the clearcut for 3.5 days before its belt dropped off and was recovered (Table 2).

4. Discussion

Our first objective in this study was to determine whether wood frogs will migrate through clearcut zones in the upland areas adjacent to breeding pools. We found that recent clearcuts were highly permeable to adult wood frogs during post-breeding emigration. A major concern with clearcutting adjacent to vernal pools is that the practice can greatly reduce soil moisture content and increase ambient temperature and wind (Dupuis et al., 1995; Chen et al., 1999), both of which increase desiccation risk and can reduce amphibian survival (Rothermel and Luhring, 2005; Todd and

Rothermel, 2006; Rittenhouse et al., 2008). Surface temperatures within our experimental clearcuts (36 °C) were, in fact, significantly higher than temperatures within both the forest buffers (20 °C) and the forested reference sites (17 °C). We demonstrated that adult wood frogs, primarily females, were able to migrate through clearcuts despite the harsh conditions associated with this habitat.

Although previous studies have shown an avoidance of clearcut habitat by pool-breeding amphibians (e.g., Rothermel and Semlitsch, 2002; Rittenhouse and Semlitsch, 2006), recent findings suggest clearcuts may not be as significant a barrier to movement as previously thought (Chan-McLeod, 2003; Semlitsch et al., 2008; Patrick et al., 2006; Rittenhouse and Semlitsch, 2009). Rather than avoiding clearcuts altogether, amphibians may be able to utilize refugia within these habitats in order to reduce desiccation rates. The availability of refugia, however, varies in different landscapes and may influence frogs' ability and willingness to use clearcuts. Our study sites were located in a landscape with abundant standing water and moist refugia, whereas the oak-hickory forests where some previous studies (e.g., Rothermel and Semlitsch, 2002) were conducted were absent of standing water, which may explain differential use and avoidance of clearcuts by frogs in different studies.

In this study, adult wood frogs varied in their timing of migration through the available upland habitats, yet tended to move through experimental clearcuts quickly (in less than six days, on average). When located within the clearcuts, the frogs in our study were typically observed in moist areas (e.g., pools, puddles, water-filled tip-up mounds) and under coarse woody debris (pers. obs., Freidenfelds), an association that has previously been shown to increase survival rates of juvenile American toads (*Bufo americanus*), green frogs (*Lithobates clamitans*), and wood frogs in experimental enclosures (Rittenhouse et al., 2008). Moreover, in clearcut areas, forest regeneration begins shortly after timber harvesting and can add significant new plant growth within a few growing seasons (Boring et al., 1981; White, 1991; Ward et al., 2006). New growth may provide shade and refugia to facilitate movement of amphibians through even very recently clearcut areas.

Another objective was to determine the impacts of buffer size on post-breeding emigration of adult wood frogs. Frogs in this study migrated into and through clearcut areas, yet this behavior was exhibited by a greater proportion of frogs at small (30-m) buffer sites than at large (100-m) buffer sites. The number of adult wood frogs emigrating from our study sites was similar (unpublished data, Babbitt), which suggests that there may be similar numbers of adult frogs entering the upland areas adjacent to the vernal pools. If these data reflect the total population size and if frogs remain within the buffer, then frogs in small buffers would experience higher densities of neighbors than would frogs in larger buffers, and thus may have more incentive to travel through the clearcuts in search of suitable upland habitat that is less densely populated. This may partially explain why, at least for females in our study, frogs at reference sites moved shorter distances than those at buffer sites. Based on the reference data, one might assume that a 100-m buffer provides adequate terrestrial habitat. However, data from our buffer treatment sites suggest that both 30-m and 100-m buffers may be insufficient, as a relatively high percentage of the study population (82% of 30-m frogs; 50% of 100-m frogs) left the forest buffers.

Recent research with wood frogs has demonstrated that density-dependent effects can result in increased mortality of juveniles, decreased growth rates, and reduced rates of reproductive development (Harper and Semlitsch, 2007; Patrick et al., 2008), and that as the number of juveniles produced increased, the number of surviving adults plateaued (Berven, 2009). If buffer size is, in fact, negatively related to wood frog density, frogs in small buffers may incur greater fitness costs than those in large buffers. As individual frogs move greater distances from a breeding pool, they may experience fewer negative density-related effects and they may benefit from the higher-quality habitat available to them. However, there is a potentially important tradeoff associated with migrating beyond the buffer zone. Frogs that migrate longer distances, and through harsh clearcut habitat, to avoid living at high densities within the buffer zone may experience greater energy expenditure and risk of predation and desiccation than those that stay close to the breeding pool (Rittenhouse et al., 2009).

We observed high variability in emigration behavior among frogs, regardless of buffer treatment. Several frogs remained at or very close to the breeding pool during the entire tracking period. Some frogs sought out aquatic sites such as streams, seeps, and neighboring vernal pools, whereas others inhabited leaf litter and coarse woody debris in the surrounding upland (pers. obs., Freidenfelds). For those that migrated away from the pool, movement paths were typically straight lines outward from the pool; with only one exception, frogs did not migrate away from and then return closer to the pool. There are other microhabitat and landscape features that may be equally, if not more, important than forest buffers for influencing movement paths and other aspects of adult wood frog emigration behavior. However, we did not quantify those features, as buffer-zone impacts were the main focus of our study.

The mean and median net emigration distances for both sexes at reference sites (undisturbed forest) were approximately 90 m from the breeding pool. These values are comparable to, yet slightly lower than, those reported for wood frogs in other studies (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2007). Based on data from Rittenhouse and Semlitsch (2007), Harper et al. (2008) calculated that only approximately 28% and 7% of a wood frog population uses terrestrial habitat within 100 and 30 m of the breeding wetland, respectively. Similarly, a meta-analysis of data from 19 species of frogs estimated that core terrestrial habitat extends on average 205–370 m from the aquatic breeding site (Semlitsch and Bodie, 2003). To our knowledge, ours is the first large-scale experimental field study to support these models and demonstrate that while 100 m of intact forest around a vernal pool may protect some of adult wood frogs in a breeding population, a 30-m forest buffer is likely inadequate to provide sufficient upland habitat. Our data indicate that adult female wood frogs consistently migrate out of buffer zones, through clearcuts, and into the forest beyond the clearcut zone.

Our final objective was to determine whether male and female wood frogs exhibit differential responses to 30- and 100-m buffers and exhibit generally different emigration behavior. In this study, female wood frogs in 30-m buffer groups migrated farther, and moved at a faster rate, than females in 100-m buffer and reference groups. Males in this study moved similar distances at reference and 100-m buffer sites, but the two males we tracked at 30-m sites never left the pond edge. In all three treatments, females moved farther from the breeding pool and faster, on average, than males, suggesting that female wood frogs utilize different habitat than males during the non-breeding season. The costs and benefits of migrating, particularly through clearcut habitat, may differ between the sexes. Producing a clutch of eggs is energetically expensive (Duellman and Trueb, 1986) and females may require higher quality habitat and lower conspecific densities to obtain sufficient resources for egg production. Males, on the other hand, may maximize their reproductive success by overwintering closer to the breeding pool, ensuring that they arrive at the breeding chorus as early as possible in the spring (Regosin et al., 2003, 2005). This sex-biased difference in habitat use may have critical implications for forest management. Habitat disturbance (e.g., via clearcutting) that disproportionately impacts females can exacerbate natural population fluctuations that occur as a result of environmental stochasticity (Berven, 1990, 2009; Regosin et al.,

2003; Harper et al., 2008), and may increase the risk of local extirpations.

5. Conclusions

Connectivity between breeding sites and terrestrial habitat is essential for vernal pool-breeding amphibians. Because open areas such as clearcuts are typically harsh environments, they are often considered barriers to amphibian movement. However, we found that adult wood frogs readily migrated through recent clearcuts to reach the intact forest beyond. The presence of coarse woody debris, moist landscape features (e.g., pools, puddles, tip-ups), and new growth most likely facilitates movement through clearcuts by providing refugia for amphibians; therefore, these features should be retained in regenerating clearcut areas to increase habitat permeability. Many of their life history traits, including their migration behavior, make wood frogs particularly sensitive to habitat loss. Our findings support the importance for population viability of maintaining large areas of forest habitat immediately adjacent to vernal pools (Calhoun and deMaynadier, 2004) because although wood frogs utilized forest buffers of both sizes, variability between sexes and density-dependent effects could render small buffers (e.g., 30 m or less) inadequate terrestrial habitat for these populations (Guerry and Hunter, 2002; Mattfeldt, 2004; Herrmann et al., 2005). Although we need a greater understanding of the population-level impacts of clearcuts adjacent to breeding pools, and of different sizes and types of buffers, based on these data we encourage the use of larger forest buffers ($\geq$100 m) in addition to the preservation of intact forest beyond the disturbed area (e.g., clearcut) as key parts of a management plan.

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