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Survival costs associated with wood frog breeding migrations: effects of timber harvest and drought

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Abstract. Migration presents a trade-off for individuals between the potential fitness benefits of reaching high-quality habitat vs. the potential costs of migration. Within an information-theoretic framework, we examined the costs of migration for adult wood frogs (*Rana sylvatica*) in response to timber harvest and annual weather conditions using Cox proportional-hazard estimates of survival. In 2004 prior to timber harvest, survival did not differ between the inside (0.75, SE = 0.078) and outside (0.73, SE = 0.235) of the circular timber harvest arrays (each 164 m radius). Following timber harvest, survival inside arrays in both 2005 and 2006 (0.22, SE = 0.065; 0.42, SE = 0.139) was lower than survival outside of the arrays and prior to harvest. Sources of mortality included predation in all years and desiccation in the drought year of 2005. The most-supported models for explaining both predation and desiccation risks reflected behaviors as opposed to timber harvest or weather conditions. Both predation and desiccation risks increased when frogs made frequent movements or were located near breeding ponds. Optimal behaviors for reducing predation and desiccation risks were the same before and after timber harvest; however, the survival consequences for not adopting these behaviors were more severe following harvest. Our results provide empirical evidence for (1) the ecological pressures that influence migratory behavior and (2) differential survival in relation to migratory behavior which reveals why frogs move relatively long distances away from breeding sites.

Key words: *anuran; desiccation; drought; predation; radiotelemetry;* Rana sylvatica; *timber harvest; wood frogs.*

Introduction

Migration presents a trade-off for individuals between the potential fitness benefits of reaching high-quality breeding and nonbreeding habitat vs. the potential costs of migration. The response of individuals to this trade-off can be observed through alterations in migratory behavior, such as the route traveled, timing, duration, and distances migrated. Migratory behavior is central to individual-based definitions of migration and provides insight into mechanisms of the migration process (Dingle and Drake 2007). Further, natural selection acts on migration through changes in migratory behavior of individuals in response to current conditions and differential survival or reproduction (Gauthreaux 1980). However, the full scope of species migration includes not only the migratory behavior of individuals but also the ecology of populations (Dingle and Drake 2007).

The function of migration is to maintain population persistence by escaping or colonizing high-quality habitats that are spatially or temporally separated (Dingle and Drake 2007). Migration arises in populations where replacement rates (R_0), a function of survivorship (l_x) and birth rate (m_x), are greater for migrants than for nonmigrants (Gauthreaux 1980). Reproductive success often is the ultimate benefit of migrations. For example, young of neotropical migrating birds are born into habitat with seasonally abundant food resources and adults overwinter where foraging habitat allows them to acquire adequate energy for reproduction the following year (Gauthreaux 1980, Sillett and Holmes 2002). In comparison, costs of migration are most extreme when survival is reduced because mortality excludes future reproductive success. Robust estimates of reproductive success and adult survival in natural populations under varying environmental conditions enhance our understanding of migration.

Amphibians that retain aquatic egg and larval life stages benefit from the abundant food resources and minimal predators found in ephemeral wetlands used as breeding habitat. Costs of migration are likely not trivial for pond-breeding amphibians because many species are known to forego breeding migrations in a given year to increase reproductive success in subsequent years (Church et al. 2007). First, migration includes an expenditure of energy. Amphibians that are early-spring breeders rely on fat reserves obtained during the previous fall for overwintering, movements to the breeding site,

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and breeding activities (i.e., calling and mating). For example, the short breeding season of wood frogs may be limited by energy reserves, because male frogs begin the breeding season with only enough stored energy in the form of glycogen to call for five hours per night for five nights (Wells and Bevier 1997). Movements away from the breeding site then require energy for locomotion and thus emigration distances traveled by frogs may also be limited by energy reserves. Second, movement activity may attract predators (Skelly 1994, Yoder et al. 2004). Longer migration distances may increase exposure to predators, resulting in increased predation risks. In addition to energy expenditure and predation risk, water balance is a critical process for amphibians in terrestrial habitats (Jorgensen 1997, Seebacher and Alford 2002). Leaving nonbreeding habitat that contains adequate moisture levels and migrating on the surface of the leaf litter may expose frogs to desiccation risks. Local weather conditions may modify desiccation risks on both daily (e.g., weather fronts that bring rainfall) and yearly (e.g., drought vs. wet years) timescales.

Terrestrial adult pond-breeding amphibians undergo round-trip breeding migrations that include movements to aquatic breeding habitats and return movements to nonbreeding habitat (Semlitsch et al. 2008). For example, adult wood frog (*Rana sylvatica*) use of nonbreeding habitat declines as the distance between breeding sites and nonbreeding habitat increases (Rittenhouse and Semlitsch 2007*b*). This result suggests that adults returning to nonbreeding habitat may balance the potential fitness benefits of reaching high-quality nonbreeding habitat with the costs of migration. We suggest that land use in the habitat surrounding wetlands may alter this trade-off, and thus influence the distances amphibians migrate from breeding sites. The habitat requirements of local amphibian populations have been defined based on migration distances (Semlitsch and Bodie 2003, Rittenhouse and Semlitsch 2007*a*). Therefore, quantifying the costs of migration will enhance our understanding of the habitat requirements of local amphibian populations.

We examined the cost of migration for adult wood frogs during movements from breeding ponds to nonbreeding habitat. Our first objective was to identify sources of mortality and to estimate survival for the post-breeding migration period. Our second objective was to evaluate support for survival hypotheses pertaining to experimental timber harvest and annual weather conditions and to the two dominant sources of mortality, predation and desiccation. We used known fate telemetry data to identify sources of mortality and Cox proportional-hazard models that assess the effects of covariates at the time of each mortality event.

Methods

Study site

We conducted our study at the Daniel Boone Conservation Area (DBCA; 1424 ha) in Warren County, Missouri, USA. The area contains mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with sugar maple (*Acer saccharum*) beginning to establish in the understory (i.e., Outer Ozark Border Subsection as described by Nigh and Schroeder [2002]). Local relief (i.e., elevation change within 2.59 km^2) ranges from 46 to 76 m. Small, intermittent streams (referred to as drainages) begin in DBCA and flow south towards the Missouri River, cutting through loess ridgetops and exposing limestone rock. Amphibian breeding sites are ponds that were constructed 27–47 years ago on ridge tops as wildlife watering holes and were naturally colonized by a variety of amphibian species (Hocking et al. 2008).

For the purpose of summarizing weather conditions, we defined spring as 1 February through 30 June. Spring weather conditions in 2004 were typical to slightly cool and moist. The average daily spring temperature was 20.02° ± 9.27°C and total rainfall was 49.91 cm. Central Missouri experienced a severe spring drought in 2005 which ranked as the third driest spring on record (NOAA weather station in St. Louis) and spring rainfall in 2006 was also below average. Average daily spring temperature was 21.45° ± 9.32°C in 2005 and 21.82° ± 10.08°C in 2006 and total spring rainfall was 34.87 cm in 2005 and 38.56 cm in 2006.

Experimental timber harvest

Timber harvest treatments were applied to replicate amphibian breeding sites in summer and fall of 2004 as part of a collaborative project referred to as Land-use Effects on Amphibian Populations (LEAP). Each timber harvest array consisted of four forestry treatments: clearcut with high levels of coarse woody debris (high-CWD), clearcut with less CWD (low-CWD), partial canopy removal, and control forest (Semlitsch et al. 2008). Each array was circular with a 164 m radius, centered on a pond (i.e., Ponds 2 and 5), divided into four equal quadrants (~2.11 ha each), and a forestry treatment was randomly applied to each quadrant with the condition that the control and partial treatments were opposite of each other. In both clearcut treatments, all marketable timber greater than 25 cm in diameter at breast height was removed for sale. High-CWD treatments had the remaining trees (<25 cm dbh) felled and left on the ground. Low-CWD treatments had the remaining trees girdled and left standing to reduce the CWD on the ground. Partial harvest treatments were thinned to a basal area of 5.6 m^2/ha or approximately 60% stocking level by girdling or felling poor-quality trees and undesirable species (primarily *Acer saccharum*). Control treatments were not experimentally manipulated.

Radiotelemetry

We radio-tracked adult frogs at three ponds in 2004 (Pond 2, Pond 5, and Pond 27 [also known as Teacup Pond]) and at two ponds in both 2005 and 2006 (Pond 2

and Pond 5). The data collected in the spring of 2004 occurred prior to timber harvest. We captured frogs at the ponds by hand and using minnow traps in 2004 and drift fences with pitfall traps in 2005 and 2006. We attached transmitters (model BD-2 with whip antennae and 1 mm diameter tube; Holohil Systems, Inc., Carp, Ontario, Canada) weighing 1.0 g or approximately 7% of average frog body mass by using a belt constructed from 1 mm stretch bead cord (Mainstays Crafts, Sulyn Industries Inc., Coral Springs, Florida, USA; as in Baldwin et al. 2006 and Rittenhouse and Semlitsch 2007*b*). Within a given year, most frogs were fitted with transmitters within a 3–4-d period. If transmitters could not be immediately attached upon capture, we placed frogs in enclosures ($1 \times 2 \times 1$ m) at the pond edge for less than 2 days. We released frogs in leaf litter within 5 m of the pond edge in 2004 and 2005. To determine the behavioral response to timber harvest and to increase the number of observations within each timber harvest treatment, we released frogs approximately 80 m from the pond edge within the center of the timber harvest treatments in 2006. The direction the frog left the pond was the direction in which frogs were released. The displacement did not alter the direction traveled, the drainages used as summer habitat or the net distance from the pond traveled during the study period (see Rittenhouse [2007] for further details). The study periods were 6 March–27 April 2004, 23 March–10 May 2005, and 10 March–5 May 2006, with start dates varying based on when breeding occurred. We assumed that transmitters do not increase predation risk, because radio transmitters have limited effects on wood frog antipredator behavior (Blomquist and Hunter 2007).

We relocated frogs during daylight hours for 50 consecutive days using a R2000 ATS receiver and yagi antenna (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). Upon homing to the frog, we obtained a visual sighting, carefully pulled out the whip antenna from beneath leaf litter, and placed a wire flag next to the frog. If the antenna was visible next to the flag upon subsequent relocations, we did not disturb the frog by obtaining a visual sighting. All movements greater than 10 cm were marked with a flag. Flags were later mapped with a compass and tape measure or GPS unit with submeter accuracy (Trimble Pathfinder Pro XL or Trimble Geo XT; Trimble, Sunnyvale, California, USA) and imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California, USA).

We recorded the fate of all individuals and categorized mortality as predation, desiccation, or unknown. Predation was assigned when the transmitter was recovered with tooth marks and/or body parts from the frog. Desiccation was defined as events where frogs were found at the same location as the previous day, depleted of body water with no signs of predation. Unknown was assigned to events where frogs were found with no signs of predation or desiccation.

Analysis

We used an information-theoretic approach to investigate support for three sets of models that represented hypotheses regarding (1) survival, (2) predation, and (3) desiccation. Each candidate model was expressed as a Cox proportional-hazard regression model (Cox 1972). First, we assessed competing models that represent the effects of timber harvest and yearly weather conditions on wood frog survival (response = alive or dead) while migrating away from breeding ponds. The most-supported model for explaining the effects of timber harvest and drought was used as a candidate model in the other two investigations. We then assessed models that represent alternative hypotheses for wood frog predation risk (response variable = depredated or not depredated) and desiccation risk (response variable = desiccated or not desiccated).

We identified both time-independent and -dependant covariates hypothesized to affect predation or desiccation risks (Table 1). These covariates were based on individual characteristics (e.g., sex, body condition, movement frequency), location within the landscape (e.g., net distance from pond), and daily weather conditions (e.g., high daily temperature, total rainfall, number of days since a rainfall greater than 10 mm) obtained from a weather station in Hermann, Missouri, about 8 km from DBCA. We observed multicollinearity among some weather variables as indicated by the variance inflation factor (P. D. Allison, *unpublished manuscript*). Therefore, we limited the number of weather variables in a candidate model, often only including the number of days since a large rainfall. Large rainfall was defined as 10 mm of rain or the amount of rain needed to recharge the moisture within the leaf litter layer (O'Connor et al. 2006).

Cox proportional-hazard models use a partial likelihood function to estimate a hazard function based on a "risk set" of all the individuals alive on a given day, and thus the hazard for an individual is a proportion of the hazard for any other individual (Allison 1995). The hazard models used are expressed as

$$S(t) = S_0(t)\exp(\beta_1[x] + \beta_2[x] + \cdots + \delta_1[x] + \delta_2[x] + \cdots)$$

where $S(t)$ is the survival probability at time t (Julian date, where Julian day 1 = 1 January) for a frog with covariate values x. $S_0(t)$ is the baseline survivor function, which is estimated by setting all covariates equal to zero and is not specified by the researcher (Allison 1995). The regression coefficients for time-independent (β) and time-dependent (δ) variables measure the degree to which each covariate in the model affects survival. A valuable characteristic of this model is its ability to handle both time-independent and time-dependent covariates (Yoder et al. 2004). The model only includes a single coefficient for each time-dependent covariate even though the value changes over time and thus inferences are drawn for specific time points. To fulfill

TABLE 1. Description of covariates used in Cox proportional-hazard models for the wood frog (*Rana sylvatica*).

Variable name	Covariate type	Description
Year	I	year of study (2004, 2005, or 2006)
Treatment	D	frog location classified as control, partial, clearcut high CWD, clearcut low CWD, or outside the timber harvest array
Arrays	D	frog location classified as inside or outside of circular timber harvest arrays
Sex	I	male or female
Body condition	I	snout–vent length divided by body mass
Movfreq	I	number of movements (>10 cm) divided by the number of daily relocations
Netdispond	D	net distance from pond to frog location (m)
Tenmm	D	number of days since rainfall of >10 mm
Precip	D	total daily rainfall (mm)
Temphigh	D	daily high air temperature
Templow	D	daily low air temperature
Humdlow	D	daily low air humidity
Dewavg	D	daily average dew point
Wind	D	daily high sustained wind speed

Notes: Covariate type differs based on whether the covariate does not change with time (time independent; I) or changes daily (time dependent; D). CWD is coarse woody debris.

data requirements of the model, we conducted daily measurements of time-dependent covariates (e.g., net distance from pond, the timber harvest treatment the frog was located within, and daily weather conditions) throughout the 64-day study period from Julian day 66 to 130 (i.e., 6 March–9 May). Although survival can be estimated for any day in this period, all inferences reported were drawn for Julian day 130. We used the counting process syntax in SAS to incorporate time-dependent covariates with time measured as Julian date (PROC PHREG, SAS Institute 2005; P. D. Allison, *unpublished manuscript*).

We ranked the candidate models within each of the three model sets and selected the best approximating model using the change in Akaike Information Criterion (ΔAIC) and Akaike weights (ω). We model-averaged the top ranking models that were within 2 AIC units of each other for both the predation and desiccation analyses and inferences are drawn from the model-averaged coefficients. We calculated hazard ratios and 95% confidence limits for parameters in the final model to facilitate interpretation (Keating and Cherry 2004). The hazard ratio describes the relative risk between values of an individual covariate, by representing the magnitude of change resulting from an incremental change in covariate. Hazard ratios > 1 indicate that risk to survival increases (i.e., mortality more likely) and ratios < 1 indicate that risk to survival decreases (i.e., mortality less likely).

Hypotheses for survival models

To fully encapsulate data collected before and after the experimental timber harvest, we included a priori models that represent year and the effects of timber harvest treatment interacting with year. Timber harvest treatment was expressed in two ways, by classifying frog locations as within control, partial, high CWD, low CWD, or outside of the timber harvest array (covariate referred to as "treatment") or by classifying frog locations as inside or outside of the 164-m circular timber harvest array (covariate referred to as "array").

Hypotheses for predation models

We developed a set of 13 a priori candidate models based on hypotheses that predation risk would increase when close to breeding ponds due to the high density of frogs attracting predators and if frogs made frequent daily movements that may attract predators. We hypothesized that predation risk would increase after many days without rain due to scent accumulating at a location, or on windy days due to disturbance of the boundary layer of air near the ground that may disperse scent. The most-supported model from the survival analysis was included as a candidate model to explore the effects of timber harvest and drought on predation. We hypothesized additive effects when these conditions occurred in combination. We hypothesized that movement frequency and days since rainfall greater than 10 mm would interact, because remaining in the same location may limit exposure to predators but scent of frogs may accumulate at that location after several days without rain. We hypothesized that movement frequency and net distance from pond would interact. When near the pond, frogs that move frequently may be depredated more than frogs that remain still due to predators searching areas with high density of frogs. Frogs may have similar predation risks regardless of movement frequency when far from ponds because predators may not search for frogs when frog densities are low.

Hypotheses for desiccation models

We developed a set of 15 a priori candidate models based on hypotheses that desiccation risk would increase when close to breeding ponds because of their location on ridge tops, or if a frog made frequent daily

TABLE 2. Summary of number of wood frogs tracked and the causes of mortality.

Year	No. with transmitters (males, females)	No. deaths	Cause of mortality		
			Predation	Desiccation	Unknown
2004	42 (36, 6)	9	9	0	0
2005	49 (29, 20)	31	13	13	5†
2006	26 (17, 9)	10	7	0	3‡

† Two suspected old-age deaths, three suspected handling-stress deaths.
‡ Two suspected old-age deaths, one suspected exposure death.

movements, suggesting that the microhabitat at the location is poor quality. We also hypothesized additive effects when these conditions occurred in combination. We hypothesized that movement frequency and net distance from pond would interact, because when close to ponds frogs that moved frequently may be exposed to desiccation risks more than frogs that did not move. When far from ponds moisture in drainages is more readily available and thus frogs may have similar desiccation risks regardless of movement frequency. The most-supported model from the survival analysis was included as a candidate model to explore the effects of timber harvest and drought on predation. We also hypothesized that daily weather conditions would greatly influence desiccation risk. Desiccation risk was hypothesized to increase with increased daily maximum and minimum air temperatures, low daily relative humidity, decreased average daily dew point, and sustained wind, and with decreased daily rainfall and number of days since 10 mm of rain. We restricted the number of covariates in each candidate model due to limited number of desiccation events and multicollinearity between weather variables. Therefore, most candidate models contain only one weather covariate or combinations with the least amount of multicollinearity.

RESULTS

We tracked a total of 117 adult wood frogs for 50 days or until mortality, resulting in a mean of number of days tracked of 42 days in 2004, 22 days in 2005, and 24 days in 2006 (Table 2). One frog was not included because the transmitter was shed during the first movement. Several classifications of mortality events warrant explanation. First, six mortality events were assigned as predation based on transmitters recovered 5–20 m from the previous relocation with the belt still tied and without teeth marks. We do not believe transmitters were shed because frogs had previously made large movements without shedding the belt, and in four of these six events, the PIT tag inserted between the skin and muscle of the frog for identification was found within 1 m of the transmitter. Second, one transmitter-tagged frog was lost in 2005 on the 52nd day of tracking. We believe the battery failed (40-d manufacturer's warrantee) and censored this frog at last visual location. Third, on the 39th day of tracking in 2006 following a rain event, we found seven transmitters with broken belts and antennas through the litter in exactly the same location as the previous day. We attributed this event to belts becoming brittle and breaking as opposed to predation, because on the previous day we found one frog sitting within a broken belt and had replaced the belt. Further, transmitters in all suspected predation events were found >1 m from the previous location. Two transmitters were also found in a similar manner near the completion of the study in 2005. These nine events were censored and not included as mortality events.

Causes of mortality

We classified 29 mortality events as predation, 13 as desiccation, and eight as unknown (Table 2). We confirmed predation by eastern garter snakes (*Thamnophis sirtalis*; $n = 6$) using forced regurgitation to retrieve the frog and transmitter from the stomach of the snakes. We suspect a wide range of other predators: raccoon or other medium-sized mammal based on frogs found missing large body parts (e.g., leg or head; $n = 8$) and when a PIT tag was found with no body parts ($n = 6$); raptors or owls ($n = 5$) based on transmitters found in avian scat or >300 m from the location the previous day; turkey ($n = 1$) based on scratches in the leaf litter; small mammal ($n = 3$) based on frogs lying on their back with small bites on the stomach or hind legs or a transmitter found in a burrow. Mortality events classified as unknown are suspected to result from handling stress ($n = 3$), exposure to below-freezing air temperatures when the frog was in a clearcut at a location with minimal litter ($n = 1$), and old age ($n = 4$). We suspect old-age based on individuals located at the edge of standing water with no sign of physical injury. In no other instances were frogs located in standing water.

Survival models

We found strong support ($\omega = 0.89$; Table 3) for the model that contained the interaction between year and frog locations classified as inside or outside the 164-m timber harvest array (Table 4), and thus we based inferences on this model. Prior to timber harvest (2004), survival inside the array (0.75, SE = 0.078) did not differ from outside the array (0.73, SE = 0.235), and these values are comparable to survival outside the array in 2005 (1.00, SE = 0.0003) and 2006 (0.73, SE = 0.164). However, survival inside the array following timber harvest was low in both 2005 (0.22, SE = 0.065) and 2006 (0.42, SE = 0.139) and lowest during the drought year of

TABLE 3. Cox proportional-hazard models ranked by the change in AIC_c for wood frog survival, survival from predation, and survival from desiccation in a Missouri, USA, oak–hickory forest, 2004–2006.

Model	Log-likelihood	k	AIC_c	ΔAIC_c	ω
Survival					
Arrays × year	−201.992	5	414.003	0	0.899
Year	−207.222	2	418.447	4.444	0.097
Treatment × year	−198.571	14	425.268	11.266	0.003
Null	−215.926	0	431.851	17.849	0
Predation					
Netdispond movfreq tenmm windhigh	−112.115	4	232.243	0	0.551
Netdispond movfreq	−114.815	2	233.633	1.39	0.275
Main effects model	−111.096	7	236.226	3.983	0.075
Arrays × year netdispond movfreq tenmm windhigh	−109.791	9	237.637	5.394	0.037
Arrays × year netdispond movfreq	−111.931	7	237.896	5.653	0.033
Netdispond	−118.609	1	239.22	6.977	0.017
Movfreq tenmm mov × tenmm	−117.988	3	241.984	9.741	0.004
Movfreq	−120.059	1	242.118	9.875	0.004
Movfreq × netdispond	−121.046	1	244.094	11.851	0.001
Arrays × year mov × net tenmm windhigh	−114.529	8	245.101	12.858	0.001
Null	−123.202	0	246.403	14.16	0
Arrays × year mov × net	−117.253	6	246.531	14.289	0
Arrays × year	−118.711	5	247.44	15.198	0
Desiccation					
Netdispond	−44.613	1	91.228	0	0.64
Netdispond movfreq	−44.217	2	92.438	1.211	0.349
Arrays × year	−45.123	5	100.264	9.036	0.007
Movfreq × netdispond	−50.14	1	102.282	11.054	0.003
Tenmm dewavg windhigh	−49.006	3	104.018	12.791	0.001
Main effects model	−42.06	12	108.213	16.986	0
Dewavg	−53.347	1	108.695	17.467	0
Tenmm	−54.627	1	111.254	20.027	0
Humdlow	−54.679	1	111.359	20.131	0
Templow	−55.213	1	112.428	21.2	0
Movfreq	−56.034	1	114.068	22.841	0
Precip	−56.24	1	114.481	23.253	0
Null	−57.572	0	115.145	23.917	0
Temphigh	−57.48	1	116.962	25.734	0
Windhigh	−57.541	1	117.083	25.855	0

Note: Key to variables: ω, Aikake weight; k, number of parameters in the model.

2005 (Fig. 1). The candidate models with harvest treatment were not well supported when ranked against models with timber harvest expressed as inside or outside the array. A limited number of mortality events occurred in each of the four timber harvest treatments and the estimated coefficients within the models were not significant (all $P > 0.07$ for Wald χ^2). However, survival decreased in the expected order (i.e., control > partial > CWD retained > CWD removed) for models that contained the four timber harvest treatments.

Predation models

Survival from predation while frogs migrated from breeding ponds to nonbreeding habitat for a 90 day period was 0.67 (SE = 0.089; Fig. 2). Predation risk was best described by two competing models that both contained the variables net distance from pond and movement frequency (Table 3); therefore, we model-averaged estimates from these two models. Survival from predation increased when frogs were located at greater distances from the pond and decreased for frogs

TABLE 4. Parameter estimates, standard errors, Wald statistic, and hazard ratio from the most-supported model for wood frog survival; β is the regression coefficient.

Covariate	df	β	SE	Wald χ^2	P	Hazard ratio
Survival						
Inside arrays × preharvest	1	0.36512	0.79723	0.2098	0.647	1.441
Outside arrays × preharvest	1	0.43089	1.23171	0.1224	0.7265	1.539
Inside arrays × postharvest	1	1.8593	0.73756	6.3549	0.0117	6.419
Outside arrays × postharvest	0					

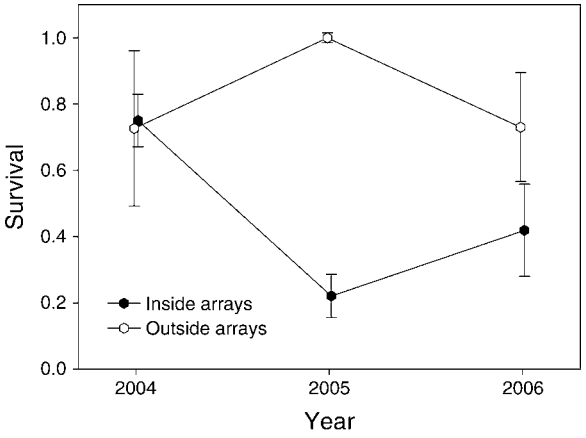

FIG. 1. Cox proportional-hazard survival estimates with 95% confidence intervals from the most-supported survival model for wood frogs (*Rana sylvatica*). Survival outside of the circular timber harvest arrays (open circles) was greater than 70% in all three years, whereas survival inside of the arrays (solid circles) was reduced following timber harvest. Survival was lowest inside the arrays during the drought year of 2005.

that made daily movements (Table 5). For example, cumulative survival for frogs located within 250 m of the breeding pond was less than 0.90, indicating that predation risks are greatest near the pond (Fig. 3). Wood frogs often remained in the exact same location for multiple days as indicated by a mean movement frequency of 0.33 ± 0.172 movements per total days tracked. Survival from predation was highest for frogs that remained in exactly the same location for multiple days and lowest for frogs that shifted within the leaf litter on a daily basis (Fig. 3). We found no evidence that predation risks were high on rainy nights when frogs made large migratory movements.

Desiccation models

Survival from desiccation while frogs migrated from breeding ponds to nonbreeding habitat for a 90-d period was 0.997 (SE = 0.00452; Fig. 2). All 13 desiccation events occurred between 30 March and 11 April 2005, with eight of these mortality events between 5 April and 8 April 2005. In contrast to our a priori expectation, candidate models describing dry, hot weather conditions were not the most-supported models (Table 3). Desiccation risk was best described based on two competing models that both contained the variable net distance from pond; therefore we model-averaged parameter estimates from these models. Survival from desiccation increases when frogs were located farther from ponds (Table 5), with cumulative survival less than 0.90 for frogs within 50 m of the pond (Fig. 4). Although single factor weather models were not well supported, the confidence intervals for the estimated coefficients suggest that desiccation was related to several weather variables, including number of days since rainfall greater than 10 mm ($\beta = 0.1656$, CI = 0.1262–0.3246), daily low humidity ($\beta = 0.0499$, CI = 0.0034–0.0966), and daily average dew point ($\beta = 0.1246$, CI = 0.0139–0.2352).

DISCUSSION

Migrations between breeding and nonbreeding habitat entail costs such as reduced survival or reduced reproduction (i.e., time or energy allocated to movement prevents foraging to acquire additional energy for future reproduction). Our results indicate that reduced survival is a cost of migration for adult wood frogs migrating

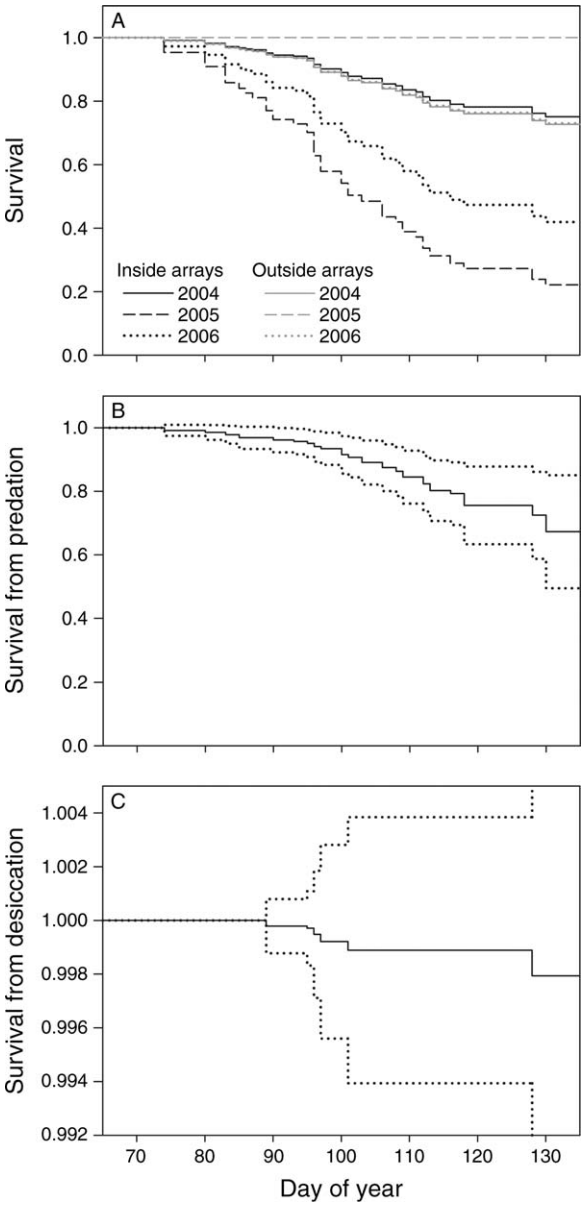

FIG. 2. Baseline survival functions for (A) the survival analysis, (B) the predation analysis, and (C) the desiccation analysis for wood frogs. (A) Survival is contrasted for frogs inside and outside the timber harvest arrays for years 2004–2006. In panels B and C, the dotted lines represent 95% confidence intervals.

TABLE 5. Parameter estimates, standard errors, 95% confidence intervals, and hazard ratio based on model-averaged estimates for predation and desiccation analyses.

Covariate	df	β	SE	95% CI		Hazard ratio
				Lower	Upper	
Predation						
Netdispond	1	−0.0097	0.00377	−0.01724	−0.00217	0.9903
Movfreq	1	3.63368	1.29086	1.05196	6.21541	37.8519
Tenmm	1	0.00558	0.03097	−0.05635	0.06751	1.0056
Windhigh	1	0.06479	0.05909	−0.05339	0.18297	1.0669
Desiccation						
Netdispond	1	−0.06752	0.02649	−0.12051	−0.01454	0.9347
Movfreq	1	0.49405	0.93567	−1.37729	2.36539	1.6389

from breeding ponds to nonbreeding habitat. To the best of our knowledge, these results are the first known-fate survival estimates produced for an amphibian. Mortality resulted from two sources: predation by a variety of predators and desiccation. In addition, survival declined in response to timber harvest and a severe drought year; however, these environmental conditions were not the best factors for explaining predation risk and desiccation risk. Notably, two covariates that reflect behavioral choices made by individuals explained both predation and desiccation risk: the location of a frog in the landscape relative to the breeding site and the movement frequency of that frog. Therefore, our results provide empirical evidence for (1) the ecological pressures that influence migratory behavior and (2) differential survival in relation to migratory behavior which reveals why frogs move relatively long distances away from breeding sites.

The location of a frog in the landscape affected desiccation risk, with the highest risk near breeding ponds and decreasing risk as frogs traveled away from breeding habitat. At our study site, the breeding sites are primarily located on ridge tops, whereas the nonbreeding habitat is moist drainages with intermittent flow following rain events (Rittenhouse and Semlitsch 2007*b*), and thus frogs at greater distances from ponds were located within moist and cool drainages where we never observed desiccation events. In a related experi-

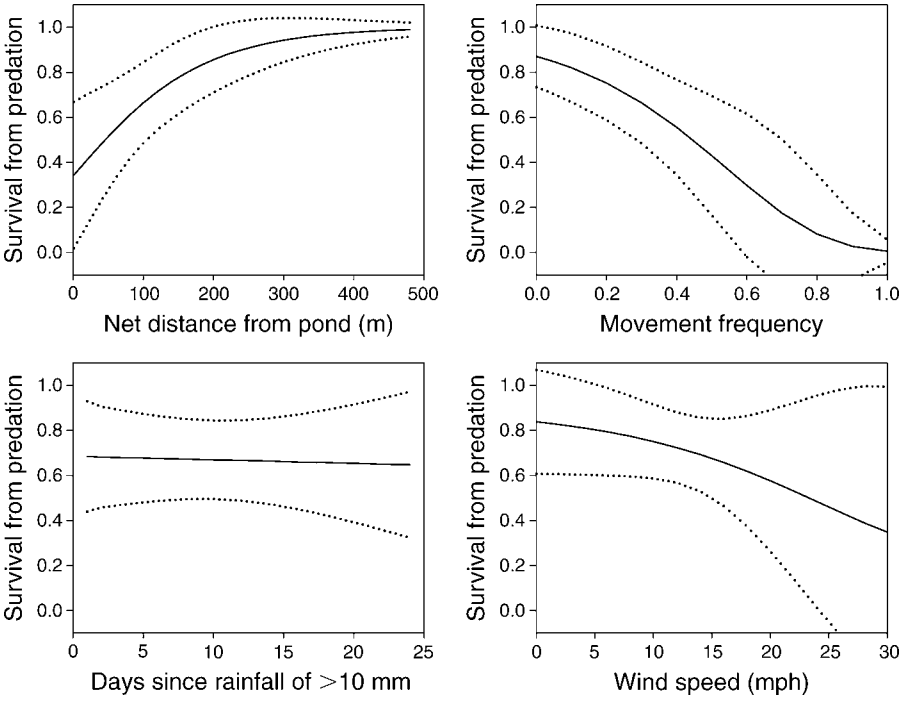

FIG. 3. Wood frog survival estimates (solid line) with 95% confidence intervals (dotted lines) inferred following model averaging of the most-supported predation models. We estimated survival for the range of values for each variable while holding the other variables at their mean value. Interpretation of these estimates assumes that frogs experienced the covariate of interest for the entire study period. For example, estimated survival from predation for a frog located at 200 m for the duration of the study is approximately 85%. For wind speed, 1 mile per hour (mph) = 1.6 km/h.

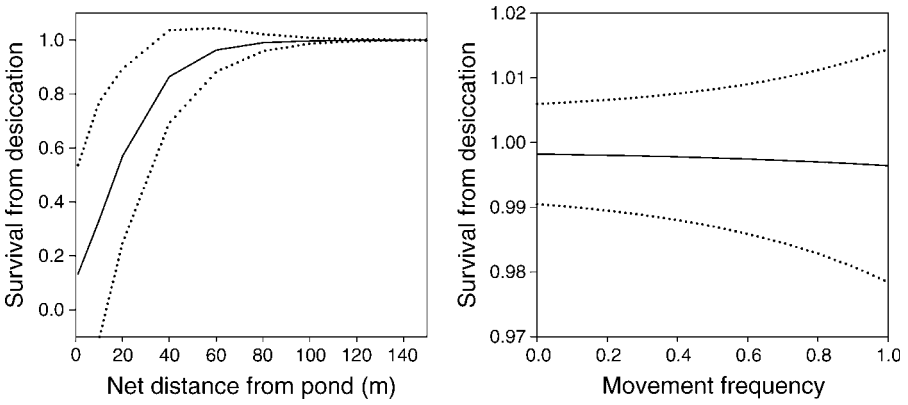

FIG. 4. Wood frog survival estimates (solid line) with 95% confidence intervals (dotted lines) inferred following model averaging of the most-supported desiccation models. We estimated survival for the range of values for each variable while holding the other variables at their mean value. Interpretation of these estimates assumes that frogs experienced the covariate of interest for the entire study period. For example, estimated survival from desiccation for a frog located >90 m from the pond for duration of the study approached 1.0 (100%).

ment in which we removed predation risks and constrained frogs to specific microhabitats to remove the behavioral choice component of habitat selection, survival within drainages was 2.3 times higher than on ridge tops (Rittenhouse et al. 2008). Although this pattern of desiccation risk varying with distance from breeding site is likely not universal among species, landscapes, or regions, our results demonstrate that variation in terrestrial habitat quality may provide the ecological pressures leading to amphibian migration away from breeding habitat.

Predation risks were also highest for wood frogs located near breeding ponds and we suggest that high predation risks near breeding sites may also influence migration in other species of pond-breeding amphibians. For example, high predation risks have been noted near amphibian breeding sites (Wassersug and Sperry 1977, Toledo 2005) and recent work indicates that the density of adults immediately adjacent to wetlands (i.e., within 30 m) is low outside of the breeding season (Gamble et al. 2006, Patrick et al. 2006, Rittenhouse and Semlitsch 2007*a*). Congregation reduces the effectiveness of being a cryptic prey item, because predators decrease movement rates to increase searching activities when cryptic prey are clumped or at high densities (Gendron and Staddon 1983). In addition, a recent mark–recapture study found that survival for male tiger salamanders can be up to 54% lower during the breeding season than for males that skipped breeding and remained in nonbreeding habitat (Church et al. 2007). Although the authors showed how energy demands may explain mortality of tiger salamanders during the breeding season, increased predation in or near breeding habitat is an additional source of mortality contributing to reduced survival near breeding sites. Amphibians with annual migrations make tradeoffs between the benefit of converging on areas with abundant resources for their young and their own survival cost of using habitat with high predation risks.

Predation risks can be a strong selective force for behavior (Lima and Dill 1989). The diversity of predators we documented expands the known list of wood frog predators (Baldwin et al. 2007) and indicates that wood frog behavior is constrained by the need to simultaneously avoid predators that use olfactory, auditory, and visual cues to locate prey. Avoiding visual predators is clearly important because wood frog coloration closely matches the oak-hickory leaf litter used as microhabitat in Missouri (Rittenhouse and Semlitsch 2007*b*). For prey species above the litter layer, breezy days create a linear odor plume that predators may use as a scent trail and windy days prevent the formation of scent trails because the wind disperses the odorant to concentrations level too low to detect within short distances. For example, breezy days (3–10 km/h) provide the optimal wind speeds for bird dogs use of odor trails (Conover 2007). Our result that predation risks for wood frogs increased during windy conditions indicates that frogs sitting within the leaf litter layer may hinder olfactory predators. On still or breezy days, the structure of leaf litter may prevent the spread of odorants by maintaining wind velocities within the litter near zero (Geiger 1965), but strong wind may break into the leaf litter layer and disperse odorants.

We found no evidence of predation while frogs were making single, long-distance, migratory movements at night during rain. This result conflicts with research on birds and mammals that indicates that predation risks increase with longer movement distances (Johnson and Gaines 1990, Alerstam et al. 2003, Yoder et al. 2004). In contrast, we found predation risks increased as movement frequency increased, indicating that multiple, short-distance, daily movements within leaf litter may attract visual and potentially auditory predators. Although availability of water has been used to explain why amphibians migrate during rainy nights (Madison 1997, Timm et al. 2007), migrating at night may also

limit visual predators and wet leaf litter may mask the noise created by saltatory movements.

Drought conditions in 2005 resulted in 13 desiccation events and this source of mortality was not observed in the other two years. Water balance has been hypothesized as a driving process for amphibians in terrestrial habitats (Thorson 1955, Jorgensen 1997) and mark–recapture studies have found reduced adult survival in years with low rainfall (Berven 1990), but the direct observation of desiccation events on free-ranging animals was only possible through the use of radiotelemetry. Notably, wood frogs were not willing to attempt migratory movements without rain, even when low soil moisture at their present location was causing them to desiccate. In addition, movements can be a reflection of the severity of the habitat. For example, wood frogs in New Brunswick restricted movement to rainfall events when in forest fragments more than pristine bogs (Mazerolle 2001). We showed that desiccation risk increased for frogs that made daily movements within the leaf litter. These small movements could be the response of frogs to the poor quality of the microhabitat, thus indicating that frogs were attempting to find a location with moister substrate. Alternatively, frogs that remained perfectly still in water conserving postures may have maintained body water better than frogs that moved within the leaf litter. In combination, the low movement frequency and the unwillingness to move without rain indicate that oak–hickory forest may be a harsh environment for wood frog migration. Therefore, we conclude that the availability of water may be a limiting factor for wood frog populations along the southwestern edge of the species range. Drought conditions, such as an increase in the number of days between rain events or a decrease in soil moisture levels, could prevent long term population persistence.

We found that survival was 3.4 times lower in 2005 and 1.8 times lower in 2006 than during the preharvest year. The reduced survival of frogs that were allowed to move freely throughout the timber harvest arrays supports previous research in which behavioral selection of habitat was restricted to microhabitats within an enclosure. For example, survival and growth was lower for southern toads (*Bufo terrestris*) constrained within clearcuts than in forested stands (Todd and Rothermel 2006). In our study, timber harvest reduced survival, but the model that reflected timber harvest was not the best predictor of either predation or desiccation risks when ranked against other a priori hypotheses. Models that reflected behavioral choices made by individual frogs (i.e., low movement frequency and moving away from the breeding site) were the best predictors of risk. These behaviors that produced the optimal survival strategies for avoiding risk were the same both before and after timber harvest. The notable difference following harvest was that the survival consequences for not adopting these behaviors were more severe.

In some situations, variation in adaptive behaviors in response to high mortality risks may regulate population dynamics in response to habitat change faster than demographic processes. For example, tadpoles generally maximize time and size at metamorphosis by increasing foraging in habitats with abundant food resources. However, when predation risk is high, tadpoles reduce activity in habitats with abundant food resources to balance the trade-off between foraging and hiding from predators (Anholt and Werner 1995). We suggest that variation in adaptive behaviors may not allow adult wood frogs to persist in Missouri under intense timber harvest or prolonged drought conditions. Optimal behaviors following timber harvest and during drought were the same as optimal behaviors within continuous forest and during average weather conditions. Therefore, adopting an alternative behavior following timber harvest or during drought will not increase the likelihood of survival for adults faced with these conditions.

Reduced survival was a cost of migration for adult wood frogs. We found high predation and desiccation risks near the aquatic habitat where annual breeding and the larval stage occurs. These ecological pressures explain why adult amphibians migrate away from breeding habitat during the nonbreeding season. Although increased exposure to predators due to movement activities can be a migration risk for many birds and mammals, amphibians seem to minimize this risk by migrating on rainy nights. The net distance amphibians migrate from wetlands have been used to define the habitat requirements of pond-breeding amphibians (Semlitsch and Bodie 2003, Rittenhouse and Semlitsch 2007*a*), and thus understanding this trade-off will enhance our ability to predict the space use requirements of local populations. Recent work documented that amphibians evacuate recently harvested timber stands (Semlitsch et al. 2008). This behavior may be a response to low survival probabilities within harvested stands. In addition, when timber harvest occurs between breeding and nonbreeding habitat this evacuation behavior may result in amphibians migrating greater distances from wetlands and thus may extend the amount of habitat required for the persistence of a local population.

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