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HOME RANGE CHARACTERISTICS OF SWAMP RABBITS (*SYLVILAGUS AQUATICUS*) IN SOUTHWESTERN INDIANA AND NORTHWESTERN KENTUCKY

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ABSTRACT. We used radio telemetry to estimate fall/winter home range size for five adult swamp rabbits (*Sylvilagus aquaticus*) in southwestern Indiana and northwestern Kentucky during the fall/winter months of 2007–2008, and compared that estimate to reported home range size estimates throughout the species' geographic range. Mean fall/winter 95% fixed-kernel home range size was 5.57 ha (SD = 3.91 ha) and 100% minimum convex polygon home range size was 2.98 ha (SD = 1.43 ha). Our estimate was smaller than previously reported in southwestern Indiana, but it was larger than other studies throughout the swamp rabbit's range. Differences among estimates may have been due to small sample sizes, methods used to calculate home range size, quality of habitat, and inclusion of locations during flood events. Daytime forms (n = 112) for eight rabbits included herbaceous vegetation (n = 28; 25.0%), brush piles (n = 27; 24.1%), cavities at the base of live trees (n = 17; 15.2%), downed hollow logs (n = 17; 15.2%), base of tree (n = 8; 7.1%) and miscellaneous (n = 15; 13.4%). Frequent use of cavities at the base of live trees is unusual and may be attributed to behavioral thermoregulation or insufficient brush cover. Our findings suggest natural resource managers in Indiana should pay careful attention to the quantity and quality of bottomland hardwood forest when evaluating swamp rabbit habitat.

Keywords: Swamp rabbit, *Sylvilagus aquaticus*, home range, southwestern Indiana

Swamp rabbits (*Sylvilagus aquaticus*) inhabit bottomland hardwood forests of the southeastern United States, with their northern range extending along the Ohio and Mississippi river drainages into extreme southwestern Indiana and southern Illinois (Chapman & Feldhamer 1981). Swamp rabbits are state-listed endangered mammals in Indiana (Simon et al. 2002) and have been extirpated from much of their historic range (Terrel 1972; Roy Nielsen et al. 2008; Whitaker & Abrell 1986). The decline is thought to be linked to the loss of bottomland hardwood forest and particularly to the lack of higher areas of good habitat (refugia) where they can escape flooding (Terrel 1972; Allen 1985; Whitaker & Abrell 1986).

Prior to 1969, records of swamp rabbits in Indiana included observations dating back to 1895 (see Terrel 1969; Mumford & Whitaker 1982) and four specimens collected in 1930 (Harrison & Hickie 1931). Subsequent to 1969, four studies have investigated the ecology, distribution, and status of swamp rabbits in Indiana (Terrel 1972; Whitaker & Abrell 1986; Conrad & Whitaker 1995; Roy Nielsen et al. 2008). Collectively, these studies documented a reduction in occupied range and a general decrease in population size with most rabbits isolated to Gibson and Posey counties (Roy Nielsen et al. 2008). Terrel (1969) conducted the only study of home range size of swamp rabbits in Indiana and used four different methods: snow tracking, dogs, telemetry, and trapping in combination with a minimum home range estimator (Haugen 1942). However, questions remain concerning the swamp rabbit and its home range requirements in Indiana, particularly whether the species' habitat needs, and therefore home range requirements, have changed appreciably in the intervening 40 years.

Swamp rabbits are one of the least studied lagomorphs in North America (Chapman & Feldhamer 1981). Home range size varies based on geographic area, habitat quality, and population density. Home range size estimates for swamp rabbits vary by season, data collection, technique used to estimate home range size, sample size, population density, and geographic location (Table 1). Techniques used to obtain locations include trapping (Toll et al. 1960; Mullin 1982), use of dogs (Lowe 1958;

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Table 1.—Reported swamp rabbit home ranges in the southeastern U.S. Sex: B = Both, F = Female, M = Male. Method: DOG = pursuit by dogs, SNT = Snow tracking, TEL = Telemetry, TRP = trapping. Estimator: FKR = 95% fixed kernel, MCP = minimum convex polygon, MHR = minimum home range, TSQ = trap squares.

Location	n	Sex	Method	Estimator	Season	Home range (ha)	Source
Arkansas	4	B	TEL	FKR	Annual	3.10	Zollner et al. 2000
	5				Spring/summer	4.30	
	5				Fall-winter	1.00	
	6				Flooded	4.90	
	6				Dry	1.20	
Georgia	7	B	DOG		Fall/winter	7.60	Lowe 1958
Illinois	6	B	TEL	MCP	Fall/winter	0.79	Kjolhaug & Woolf
	9				Winter snow	0.61	1988
	5				Flooded	0.60	
	4				Spring/summer	0.83	
	5				Annual	1.83	
Indiana	3	B	SNT	MHR	Fall-winter	4.10	Terrel 1969
	14		DOG			4.20	
	4		TEL			4.50	
	4		TRP			1.60	
Louisiana	8	M	TEL	MHR	Fall/spring	4.30	Gould 1974
	2	F	TEL			2.10	
Louisiana	Unk	M	TRP	MCP	Annual	1.50	Mullin 1979
	Unk	F				2.40	
Missouri	7	M	TRP	TSQ	Winter	2.40	Toll et al. 1960
	7	F	TRP			1.90	
	5	M	TRP	MCP		0.73	
	7	F	TRP			0.85	
	4	M	DOG			0.80	
	6	F	DOG			1.70	

Toll et al. 1960), radio telemetry (Gould 1974; Kjolhaug & Woolf 1988; Zollner et al. 1996), and a combination of techniques (Toll et al. 1960; Terrel 1969). Methods to calculate home range size include trap squares (Haugen 1942), maximum area method, minimum home range method (Mohr 1947; Mohr & Stump 1966), minimum convex polygon (Hayne 1949), and fixed-kernel home range (Worton 1989). Because of the variety of techniques used to estimate home range size, caution is required when comparing home range values among studies.

Home range size for swamp rabbits in fall and winter determined from telemetry locations at the species' northern range limit averaged 0.79 ha in Illinois (Kjolhaug & Woolf 1988) and 4.50 ha in Indiana (Terrel 1969). Elsewhere, home range size in fall and winter averaged 1.00 ha in Arkansas (Zollner 1993) and 4.29 ha in Louisiana (Gould 1974). The largest reported fall/winter home range size was 7.60 ha in Georgia (Lowe 1958).

We hypothesize that home range size should be larger in southwestern Indiana because habitat quality should decrease at the edge of a species' geographic distribution because of resource limitations and environmental conditions (Caughley et al. 1988; Brown et al. 1996; Borger et al. 2006). Further, higher quality habitats produce smaller home ranges (Harestad & Bunnell 1979; Tufto et al. 1996); and, conversely, species often require larger home ranges in lower quality (or marginal) habitats. The objective of this study was to estimate the size of home ranges of swamp rabbits and compare those estimates to previous studies in Indiana and throughout the swamp rabbit's range.

METHODS

Study site.—The study was conducted in Gibson and Posey counties in extreme southwestern Indiana, USA (N38°18′, W87°48′) and in the Sloughs Wildlife Management Area in Henderson and Union counties in northwestern

Kentucky (N37°48′, W87°33′). The mean rainfall for Indiana and Kentucky study sites is 109.5 cm. The mean maximum and minimum temperature during July is 31.6°C, 19.7°C respectively; with a January mean maximum temperature of 3.8°C and mean minimum temperature of −6.0°C. The predominant tree species of bottomland hardwood forest in southwestern Indiana include sweet gum (*Liquidambar styraciflua*), hackberry (*Celtis occidentalis*), sugarberry (*Celtis laevigata*), red elm (*Ulmus rubra*), shagbark hickory (*Carya ovata*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), silver maple (*Acer saccharinum*), butternut (*Juglans cinerea*), and northern red oak (*Quercus rubra*). A detailed description of the vegetation in the study areas is provided in Dumyahn (2009).

Study design.—Seven of 12 study sites trapped were selected in bottomland hardwood forests near the Wabash and Ohio rivers in southwestern Indiana and northwestern Kentucky. Site selection was based on preliminary capture success in areas with historic swamp rabbit populations. Five study sites were eliminated because no swamp rabbits were captured. The three study sites in Indiana are privately owned, while the four sites in Kentucky are on public land located within the Sloughs Wildlife Management Area.

Swamp rabbits were live-trapped with Tomahawk traps (model TLT106, National Live Trap Co., Tomahawk, Wisconsin, U.S.A.) periodically from January 2007 through February 2008. At each study site, a 300 × 300 meter grid (9 ha) was established and traps were first systematically placed approximately 20 m apart throughout the grid, then placed opportunistically in and immediately around each grid to take advantage of upland areas where rabbits concentrated during flooding, as well as in areas where rabbit sign was found. Traps were covered with tarpaper and baited with sweet corn, apples, apple juice, and alfalfa pellets. Captured swamp rabbits were weighed and measured, had sex determined, and received Nasco standard rototags (Nasco, Fort Atkinson, Wisconsin, USA) in the right ear. Adult swamp rabbits (i.e., > 1500 g) were fitted with very high frequency (VHF) radio collars equipped with mortality sensors (Model 80, Telonics, Inc., Mesa, Arizona, USA) and released. All animals were handled using protocols that are consistent with the guidelines of the American Society of Mammalogists (2007), and the protocols were approved by Purdue University Animal Care and Use Committee (PACUC# 07-032).

Locations of swamp rabbits were obtained by homing on the signal with a handheld, two element antenna and TR-5 receiver (model RA-14K, Telonics, Inc., Mesa, Arizona, USA). The animal's identity was confirmed from its radio frequency. Locations were recorded using a Trimble global positioning unit (Sunnyvale, California, USA) and corrected against local base stations. Estimated locations were entered into ArcView (Environmental Systems Research Institute, Inc., Redlands, California, USA). The Animal Movement extension (Hooge & Eichenlaub 1997) was used to determine 50% core areas (Kaufmann 1962; Samuel et al. 1985) and 100% minimum convex polygon home range (Hayne 1949) as well as the 50% core area and 95% fixed-kernel home range (Worton 1989) with a least square cross-validation smoothing parameter (Silverman 1986). Forms were recorded as either brush pile, form at base of tree, form near brush, herbaceous vegetation (> 0.5 m), cavity in live tree, hollow dead log, and open area.

RESULTS

Thirteen swamp rabbits (3M:9F:1 unknown) were captured 15 times in 3582 trap-nights at six sites (0.42 rabbits/100 trap-nights). Radio collars were attached to 12 rabbits classified as adult; the lone juvenile was released at capture site. There was an average of 14 (range = 1–82) locations per radioed rabbit. Only those rabbits with > 14 locations were used for fixed-kernel home range size estimate ($n = 5$) and > 7 locations for MCP. Mean 100% MCP home range size ($n = 5$) was 2.98 ha (SD = 1.43 ha) and the mean 95% fixed-kernel home range ($n = 3$) was 5.57 ha (SD = 3.91 ha) (Table 2). The mean 50% fixed-kernel core area was 0.79 ha ($n = 3$, SD = 0.74).

Home range estimates for rabbit #3 were based on 82 locations obtained over 397 days and examined seasonally. Swamp rabbit #3 had 55% of total locations and may bias estimates. However, fixed-kernel home range size during Year 1 for rabbit #3 was 5.89, 3.51, and 1.06 ha for winter, spring, and summer, respectively. Estimates during Year 2 were 3.77 ha in winter and 3.49 ha annually. MCP estimates for #3 in Year 1 were 2.67 ha

Table 2.—Swamp rabbit home range size estimates in southwestern Indiana reported in ha. 1: F = female, M = male. 2: MCP = minimum convex polygon estimate. 3: FKR = fixed-kernel home range estimate. * = insufficient locations.

Animal ID	Sex[1]	No. of locations	Home range estimate		
			100% MCP[2]	50% FKR[3]	95% FKR[3]
1	F	14	3.37	1.63	10.08
2	M	7	5.25	*	*
3	F	82	2.61	0.26	3.49
4	F	14	2.09	0.47	3.14
7	F	8	1.60	*	*
mean			2.98	0.79	5.57
SD			1.43	0.74	3.91

(winter), 1.88 ha (spring), 1.63 ha (summer). MCP estimates for #3 Year 2 were 2.13 ha (spring) and 2.61 ha annually. The 50% fixed-kernel core area was 0.41 ha for Year 1 winter, 0.13 ha spring, 0.60 ha summer, and 0.49 ha for Year 2 winter. There was only one occurrence of overlapping core areas with a single male swamp rabbit's core area overlapping two female swamp rabbits' core areas.

Descriptions of 112 forms were made for eight swamp rabbits (Table 3). The most common forms were in herbaceous vegetation (n = 28; 25%) within brush piles (n = 27; 24.1%). The next most common forms were in cavities inside of live trees and downed hollow logs (both n = 17; 15.1% each).

DISCUSSION

The documented average home range size that was larger than previously reported for swamp rabbits at this latitude (Terrel 1969; Kjolhaug & Woolf 1988). However, our estimate is within home range sizes reported across the species' geographic distribution (0.6 to 7.6 ha; Table 1). Previous research at the species' northern range limit revealed small home ranges, which is contrary to the hypothesis developed in the introduction. These observations suggest typical home range sizes at the northern limits of the swamp rabbits distribution, but not reaching the extremes that have been observed in places like Georgia. However, there is enough variation in the techniques used among studies that, when compiled with the small sample size in this study, it suggests that these comparisons should be interpreted with caution.

Terrel (1969) reported a fall/winter season home range size estimate for swamp rabbits in southwestern Indiana that is larger than the estimate in this study. Terrel obtained locations using radio telemetry and estimated home range size with trap squares and minimum home range. This study also used radio telemetry to obtain locations but used MCPs to estimate home range size. The trap squares

Table 3.—Descriptions of 112 daytime forms were made for eight swamp rabbits in southwestern Indiana and northwestern Kentucky.

Description	Swamp rabbit #								Total	%
	1	2	3	4	5	6	7	8		
Herbaceous vegetation		1	22	2			3		28	25.0
Brush pile			22		3		2		27	24.1
Cavities in live tree	3	2	11		1				17	15.2
Downed hollow log			16	1					17	15.2
Form at base of tree	2		2	2		2			8	7.1
Form near brush			3	3					6	5.4
Open area	1		2				1	1	5	4.5
Form next to hole	3								3	2.7
Hole in dead tree			1						1	0.9
Total	9	3	79	8	4	2	6	1	112	

technique used by Terrel (1969) overestimates home range size (Hayne 1949), which may account for the observed differences between studies.

Our home range estimates of swamp rabbits in winter were larger than those reported for swamp rabbits in southern Illinois (Kjolhaug & Woolf 1988). Both studies occurred at the northern extent of the species' range, had comparable sample sizes, and used telemetry locations to calculate MCP estimates. Kjolhaug and Woolf (1988) suggested their small home range estimates were due to high quality habitat and high population densities (two rabbits/ha), which was higher than those from previous studies.

In Missouri, Toll et al. (1960) reported average winter swamp rabbit home range size estimates similar to Kjolhaug and Woolf (1988) in Illinois but smaller than our 2.98 ha estimate in southwestern Indiana. Toll et al. (1960) did not report on rabbit density but described swamp rabbits as locally abundant in large areas of cutover bottomland forest. Studies in Missouri and southern Illinois may have occurred in higher density rabbit populations than did our study.

In south-central Arkansas, at the center of the swamp rabbit's range, Zollner et al. (2000) reported a fall/winter home range estimate considerably smaller than our estimate. This was perhaps attributed to a large home range (10.08 ha) of one individual (#1) and smaller sample sizes in this study. When telemetry locations were comparable (e.g., swamp rabbit #3) our estimates of annual home range size were similar to estimates provided by Zollner et al. (2000). Zollner et al. (2000) reported home range size increased during flood events, but we did not distinguish between locations obtained during inundated and dry conditions, which may explain differences between our estimates and theirs.

Home range estimates reported by Gould (1974) in Louisiana (Table 1) were determined by the minimum home range method and a weighted home range method. Mullin (1982), also in Louisiana, reported similar estimates using trapping and MCP estimators (Table 1). Our results are consistent with Gould (1974), but larger than those of Mullin (1982), who reported a high density of rabbits (0.6/ha lowland, and 0.8 ha upland).

We found no intrasexual overlap among home ranges, but documented two cases of intersexual overlap. The only overlap that occurred was a male swamp rabbit's core area overlapping that of two female rabbits. This agrees with research by Kjolhaug & Woolf (1988), who found no overlap of core areas of swamp rabbits, with the exception of a male overlapping the core area of two other rabbits. This suggests that swamp rabbits use their core area exclusively. However, because of the small sample size and the likelihood that rabbits were simply trapped far apart, results should be viewed with caution.

Frequent use of live trees as daytime rest sites (forms) was noted. Live trees were the third most frequently used form following herbaceous vegetation (> 0.5 m) and brush piles (Lowe 1958). Natural resource managers at the northern limits of swamp rabbit range should consider live standing trees with cavities when evaluating potential habitat. Swamp rabbits prefer selectively logged bottomland hardwoods (Terrel 1969) because foraging opportunities (i.e., browse) are more prevalent than in mature forests (Hurst & Smith 1986). Nonetheless, live, mature trees with cavities appear to be an important habitat component. Frequent use of live trees as forms may be a behavioral response to cooler temperatures at the northern extent of the species' range. Vertebrates can sense their surface and core temperature and will adjust both physiologically and behaviorally to existing temperature (Crawshaw 1980). Residing in live trees may aid the rabbit in thermoregulation by allowing it to conserve heat. In Indiana, swamp rabbits are at their most northern geographic extent and may be at the limit of cold temperature that this species can withstand. Alternatively, brushy cover, a commonly-used form, may be unavailable or less available in some habitats, thus forcing resident rabbits to use alternative structures. Swamp rabbits use old stumps, logs, vine tangles, cane patches, and open grassy areas as forms. These features allow rabbits to avoid predators by remaining motionless and providing opportunities for easy escape if needed. The absence of brush necessitates an alternative refuge that the live trees may provide.

In conclusion, swamp rabbit home range size estimates are larger in southwestern Indiana compared to other studies conducted at the

northern extent of the swamp rabbit's range. This may be because of the quality and quantity of habitat available for swamp rabbits in Indiana. It is likely that swamp rabbit habitat in Indiana lacks essential features like brushy cover that allow rabbits to avoid predators by remaining motionless and opportunities for escape. We recommend natural resource managers collect accurate home range data on local populations to guide management initiatives.

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