Home Range Use by Swamp Rabbits (Sylvilagus aquaticus) in a Frequently Inundated Bottomland Forest

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ABSTRACT.—Home range size of six swamp rabbits in south-central Arkansas was estimated by radio-telemetry from February 1991 through March 1992. The average home range size was significantly larger than previously reported estimates. This difference is partly attributable to the large number of observations per rabbit in our study, but may also be explained by our inclusion of numerous locations of swamp rabbits during periods of deep inundation. All of the individual rabbits tracked used different areas when the study site was flooded. These results provide the first quantitative description of the response of swamp rabbits to flooding.

INTRODUCTION

Throughout their range swamp rabbits (*Sylvilagus aquaticus*) are found in wet forested environments such as bottomland hardwood forests (Chapman and Feldhammer, 1981; McCollum and Holler, 1994). An important aspect of these environments is the disturbance associated with frequent flooding (Harris and Gosselink, 1990). Clearly, inundation has negative consequences for swamp rabbits (*e.g.*, increased embryo resorption [Conaway *et al.*, 1960]) increased starvation (Svhila, 1929) and increased mortality from hunting (Martinson *et al.*, 1961). To survive in such seasonally flooded environments resident animals must respond to changing water levels, *e.g.*, by moving to refugia during periods of inundation (Crawshaw and Quigley, 1990). The response of swamp rabbits to flooding has not been quantified. However, swamp rabbits have been observed resting on stumps surrounded by water (Lowe, 1958; Terrel, 1972) and home range size has been shown to decrease when flooding was common (Kjolhaug and Woolf, 1988). These observations suggest that swamp rabbits restrict their movements in response to inundation, although they are also known to inhabit adjacent upland habitats (Zollner *et al.*, 1996). It is unclear to what extent swamp rabbits use such neighboring habitat as refugia during inundation (McCollum and Holler, 1994), but Allen (1985) suggested that these areas may be crucial for the preservation of small isolated populations.

More broadly, the ecology of the swamp rabbit and the way it uses space is poorly understood (Lowe, 1958; Gould, 1974; Allen, 1985). Only two published studies have investi-

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gated the home range of this animal using radio-telemetry (Gould, 1974; Kjolhaug and Woolf, 1988) and they were conducted at the extreme southern and northern ends of the species' range, respectively. Other estimates of the size of home ranges of swamp rabbits are based on less reliable data such as trapping records and dog chases (Lowe, 1958; Toll *et al.*, 1960; Terrel, 1972; Mullin, 1979). This dearth of data is surprising because the swamp rabbit is a popular game species in the southern portion of its range and a species of conservation concern in the northern portion of its range. Thus, the present study had two objectives: (1) to quantitatively assess how an individual's home range changes in response to flooding and (2) to estimate swamp rabbit's home range size in south-central Arkansas.

METHODS

The study was conducted in Moro Bottoms Natural Area and adjacent private lands near Fordyce, Cleveland Co., Arkansas (33°47'N, 92°20'W). Moro Bottoms Natural Area contains a forest of bottomland hardwoods under the shared stewardship of the Arkansas Nature Conservancy and the Arkansas Natural Heritage Program (Smith and Zollner, *in press*). The area was ca. 70 ha; 40 ha was mature bottomland hardwoods. Second-growth forests of mixed upland pines and bottomland hardwoods occurred to the north and east of Moro Bottoms Natural Area for several miles. Additional second growth bottomland hardwoods occurred to the south and west of the study site for several miles. Immediately to the south of Moro Bottoms Natural Area was a 10 ha bottomland site that was intensively harvested in July of 1989. Sweetgum (*Liquidamber styraciflua*) dominated the overstory in the bottomland forests, whereas loblolly pine (*Pinus taeda*) dominated the overstory in the adjacent upland forests. Composition of overstory in all forests included oaks (*Quercus* spp.) and hickories (*Carya* spp.).

Between 60 and 145 traps were set and checked daily between 12 January and 26 June 1991. Captured rabbits were fitted with a 350 g radio-collar and released. After release a rabbit was allowed 1 wk to adjust to its collar and recover from the stress of capture, after which observations of movements began. Four rabbits were collared and tracked for both the spring/summer (15 April–1 Oct.) and fall/winter seasons (1 Oct.–15 April), a fifth rabbit was tracked only during the spring/summer season and a sixth rabbit was tracked only during the fall/winter season. All rabbits were adult females except for a single adult male (#740) that was only tracked during the spring/summer season. Monitoring of rabbits began on 22 Jan. 1991 and concluded on 5 Mar. 1992. Each rabbit's location was recorded once daily until death or transmitter failure. Diurnal observations occurred 5 d a week either between 0630 and 1200 or between 1200 and 1830 based on the flip of a coin. The other 2 d each week rabbits were located between 1830 and 0630. Starting times for nocturnal monitoring periods were selected from a random numbers table and triangulation stations (*see* below) were always visited in the same order. All locations used in analysis were considered temporally independent, based on the criterion that sufficient time elapsed between observations for the rabbit to be able to move from one side of its home range to the other (White and Garrott, 1990:147).

During the day we were typically able to locate each rabbit in a brush pile or thicket by walking around it with the antenna removed from the receiver. This was possible because the initial response of swamp rabbits to a threat is to remain motionless (Hamilton, 1955) and it allowed us to estimate the position of each individual within a few meters (always <5 m). However, to minimize disturbance to the rabbits, we did not attempt to confirm locations with visual observations. Nocturnal positions were determined using triangulation from a series of stations placed throughout the study area (Zollner, 1993). All nocturnal bearings were taken from stations within 250 m of the area where the animal was active.

Locations were not estimated more precisely at night because of logistic difficulty and increased animal activity (Gould, 1974).

The Universal Transverse Mercator (UTM) coordinates of the location of each swamp rabbit were used to estimate home range size and assess response to inundation. Each diurnal position was visited when the rabbit was not present and distance and bearing to a point on a transect were measured. UTM coordinates of the transects and the nocturnal triangulation stations were determined with a Trimble Pathfinder Professional (Trimble, Navigation Inc. Sunnyville, California) global positioning device. Ninety five percent fixed kernel estimates of home range size with smoothing selected by least squares cross-validation were generated using The Home Ranger program (Version 1.5; F. Hovey, 1999). For multimodal data such as ours, kernel techniques provide more accurate estimates of home range size (Seaman and Powell, 1996; Worton, 1989, 1995; Seaman *et al.,* 1999).

Seasonal home ranges (fall-winter and spring-summer; Kjolhaug and Woolf, 1988) were calculated only if >15 locations were available for an animal in a season. Annual home ranges were calculated for all animals for which seasonal home ranges were available in both seasons. Separate home ranges were also calculated for each rabbit using locations when the study area was inundated and when it was not. Locations were classified as inundated when the depth of water at a permanent depth gauge (Fisher and Porter Co. Series 8) in the center of the study area was >39 cm. This depth corresponded to conditions during which more than 90% of Moro Bottoms Natural Area was covered by at least 20 cm of standing water (Zollner, 1993). The gauge recorded the depth of water hourly throughout the study and flooding occurred during both seasons.

We used a *t*-test to test compare our estimates of annual home range with those reported in southern Illinois (Kjolhaug and Woolf, 1988). We used paired *t*-tests to compare the average fixed kernel estimates of home range size for our rabbits during inundated and dry times. We used the BLOSSOM software package (Slauson *et al.,* 1991) to develop Multiple Response Permutation Procedures (MRPP) comparisons of the portion of home range used during inundated and dry conditions for each rabbit. MRPP statistics are a distribution-free tool for testing whether two groups come from the same or different populations (Zimmerman *et al.,* 1985; Biondini *et al.,* 1988; Cade and Hoffman, 1990).

RESULTS AND DISCUSSION

Our 95% fixed kernel estimates of home range size were significantly larger ($t = 3.49$, $df = 3$, $P = 0.04$) than the home ranges reported for southern Illinois by Kjolhaug and Woolf (1988). However, these 95% kernel estimates were within the range of values (0.7–7.7 ha) of published swamp rabbit home ranges (Kjolhaug and Woolf, 1988). Comparison between our observations and previous work are provided to place our work in the context of existing knowledge, but they should be interpreted with caution because of differences in techniques used to collect location data, techniques used to estimate home range area and sample sizes.

Kjolhaug and Woolf (1988) attributed their small home ranges to the high quality of the habitat in their study area. However, browse (Zollner, 1993) and pellet surveys (Zollner *et al.,* 1996) suggest that habitat conditions are good for swamp rabbits in Moro Bottoms Natural Area and thus habitat quality can not explain our larger home range estimates. The patchy nature of good habitat (*e.g.,* windthrows; Smith and Zollner, in press) in the mature bottomland forest where our study was conducted may cause more movement and thus our larger home ranges. Additionally, our data were collected both at night and during the day. Sampling at night when nocturnal animals are more active can lead to larger home disappearing rapidly throughout the southeastern U.S. (MacDonald *et al.*, 1979; Harris, 1984; Smith *et al.*, 1993). Indeed, the limited remaining habitat already occurs as fragmented remnants in low elevation sites which are susceptible to inundation (Rudis and Birdsey, 1986). Thus, managers should consider both the landscape context and flooding history of an area when assessing whether it can support a viable population of swamp rabbits either by itself or in conjunction with adjacent refugia.

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TABLE 1.—Average (SE) estimates of home range size (ha) of swamp rabbits

	Annual (n = 4)	Spring–Summer (n = 5)	Fall–Winter (n = 5)	Inundated (n = 6)	Dry (n = 6)
95% Fixed kernel	3.1 (0.72)	4.3 (1.39)	1.0 (0.25)	4.9 (2.14)	1.2 (0.9)

range estimates (Holzman *et al.*, 1992). Finally, our home range estimates were influenced by the movements of rabbits in response to inundation of the study area.

There was no significant difference in home range size when the area was inundated ($t = 1.56$, df = 4, $P = 0.18$), although the tendency was for our estimates to increase during inundation (Table 1). Kjolhaug and Woolf (1988) described greatly restricted home ranges during flooded conditions, but performed no statistical analyses due to small sample sizes. These contradictory trends could be explained by different topographic or landscape contexts of our study sites. Additionally, the continuous record of water depth in our study area allowed us to analyze inundation year round on a per observation basis rather than as a single seasonal event (Kjolhaug and Woolf, 1988).

The MRPP tests showed that all of our rabbits used different areas when the bottoms were inundated than when the study area was not flooded (Table 2). During inundation two of the rabbits moved onto levees near the creek while the other four rabbits moved into adjacent uplands. This is the first quantitative assessment of swamp rabbit response to flooding and the best evidence that they do use adjacent uplands during flooding. It has been suggested that the preservation of small isolated populations of swamp rabbits may require the maintenance of suitable habitat to serve as a refuge from flooding (Allen, 1985; Whitaker and Abrell, 1986). However, pellet surveys in Alabama (McCollum and Holler, 1994) and Indiana (J. O. Whitaker, pers. comm.) failed to find evidence of swamp rabbit use of surrounding uplands, which may cause some to question the importance of adjacent uplands for swamp rabbits (McCollum and Holler, 1994). In this study telemetry documented that swamp rabbits moved into surrounding uplands during flooding in a study area where pellet surveys have also demonstrated swamp rabbit use of the adjacent uplands (Zollner *et al.*, 1996).

These tracking data, along with the significantly larger home range sizes, suggest that maintenance of suitable habitat that can serve as a refuge from flooding may be important at sites where prolonged heavy inundation is common. This may be particularly true of the northern extent of the species' range where small patches of suitable habitat are typically embedded in an inhospitable landscape (McCullom and Holler, 1994). However, this conclusion may apply broadly because forested bottomlands that swamp rabbits inhabit are

TABLE 2.—Multiple Response Permutation Procedure test of whether six swamp rabbits used different areas during inundated periods than during dry periods

	Rabbit 740	Rabbit 600	Rabbit 460	Rabbit 440	Rabbit 380	Rabbit 340
Number of locations when inundated	17	26	27	57	46	49
Number of locations when dry	135	175	29	221	209	218
MRPP test statistic (δ)	2.78	−64.89	−2.4	−10.48	−21.59	−17.49
P-value	=0.03	<0.0001	=0.03	<0.0001	<0.0001	<0.0001

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