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SPACING PATTERNS OF SUBADULT VIRGINIA OPOSSUMS (*DIDELPHIS VIRGINIANA*) AND HOME-RANGE ALLOMETRY

TROY A. LADINE

Edward J. Meeman Biological Station and The Department of Biology, The University of Memphis, Memphis, TN 38152
Present address: Department of Biology, Dana College, Blair, NE 68008

ABSTRACT—Elliptical home-range size estimations for subadult Virginia opossums (*Didelphis virginiana*) were calculated from mark-recapture data and computer analysis. Mean home-range size for 13 subadult opossums (nine males, four females) was estimated to be ca. 43 ha. Home-ranges that encompassed buildings were smaller than other home-ranges. Estimations of mean home-range size were compared with predictions of selected models to assess these models in predicting the sizes of home-ranges for subadult opossums. Selected models (McNab, 1963; Harestad and Bunnell, 1979; Swihart et al., 1988) varied in their prediction of subadult Virginia opossum home-range size based metabolic rate and trophic level.

Home-range relating to mammals was defined as the area covered by an individual in its normal activities of food gathering, mating and/or rearing of young (Burt, 1943). Home-ranges must be large enough to include adequate resources of food, shelter for rest and/or escape, and allow for access to potential mates. Factors limiting mammal home-range size include, but are not limited to, the size of the mammal, energy expenditure required to traverse the home-range, dispersion of food resources, and intraspecific competition (Brown, 1962).

McNab (1963) first formulated equations relating body size and trophic level of mammals home-range size. The slope of the double-log scaled relationship between body size and home-range size observed by McNab (1963) did not deviate significantly from the slope of 0.75 found by Kleiber (1961) relating basal metabolic rate to body size. McNab (1963) thus concluded home-range size correlated to basal metabolic rate. Subsequent studies have derived equations relating body size and trophic level to home-range size (Harestad and Bunnell, 1979; Swihart et al., 1988) in which the exponents were not correlated to basal metabolic rate. Equations that estimate home-ranges from weight of adults have the same general design: $A = CW^m$, where A = home-range size (ac or ha), C is a constant, W = body mass, and m = slope of the double-log linear relationship between home-range size and weight.

Reported home-range sizes of Virginia opossums (*Didelphis virginiana*) range from 4.9 ha for a juvenile female (VanDruff, 1971) to 108 ha for an adult male (Gillette, 1980) and are seasonally stable (Gillette, 1980). The Virginia opossum displays an omnivorous diet with food preference based on availability (McManus, 1974; Gardner, 1982; Seidensticker et al., 1987). Whereas most foods are arthropods and other invertebrates, fruits and nuts are eaten readily when in season. Based on the omnivorous diet, and the assumption that the trophic-level model (Harestad and Bunnell, 1979; Swihart et al., 1988) is correct, Virginia opossum home-range size should be intermediate compared to carnivores and herbivores. This study investigated the home-range size of male and female subadult opossums from mark-recapture data and compared the observed results to expected results from selected allometric models (McNab, 1963; Harestad and Bunnell, 1979; Swihart et al., 1988) of body weight and home-range size.

MATERIALS AND METHODS

Study area—The study was conducted at the 252 ha Edward J. Meeman Biological Station (Meeman) located ca. 20 km north of Memphis, TN (35°20′ N latitude, 90°01′ W longitude) on the third Chickasaw loess bluff. Topography varies from gentle (<3%) to steep sloping (> 45%) hills of loess deposit. Meeman is dissected by several permanent and intermittent streams; the trapping grid was within 100 m of seven permanent ponds. Meeman is surrounded on three sides by private lands and the fourth by the Shelby Forest Wildlife Management Area. Hunting is not allowed on the site, but does occur on the adjacent private lands and the Shelby Forest Wildlife Management Area.

Meeman vegetation is represented by a western mixed mesophytic forest (Braun, 1950; Miller & Neiswender, 1987) with patches of kudzu (*Pueraria lobata*) and several old fields dominated by red fescue (*Festuca rubra*) interspersed throughout the wooded areas (Fig. 1). Dominant canopy plants are sweet gum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), elms (*Ulmus* spp.), oaks (*Quercus* spp.), and hickories (*Carya* spp.). There is an extensive network of grape (*Vitis* spp.) and poison ivy (*Toxicodendron radicans*) vines throughout the canopy. The understory is dominated by spicebush (*Lindera benzoin*), paw-paw (*Asimina triloba*), and red buckeye (*Aesculus pavia*). Dominant ground-cover species are sweet cicely (*Osmorhiza* sp.), False Solomon's seal (*Smilacina racemosa*), poison ivy (*Toxicodendron radicans*), nettle (*Urtica* sp.), various woodland grass species, and seedlings of the dominant canopy and understory species. A detailed analysis of the habitat on the study site is provided by Ladine (1995).

Collection—A 5- by 10-trap grid was established with 50 folding Tomahawk live traps placed ca. 150 m apart. Traps were

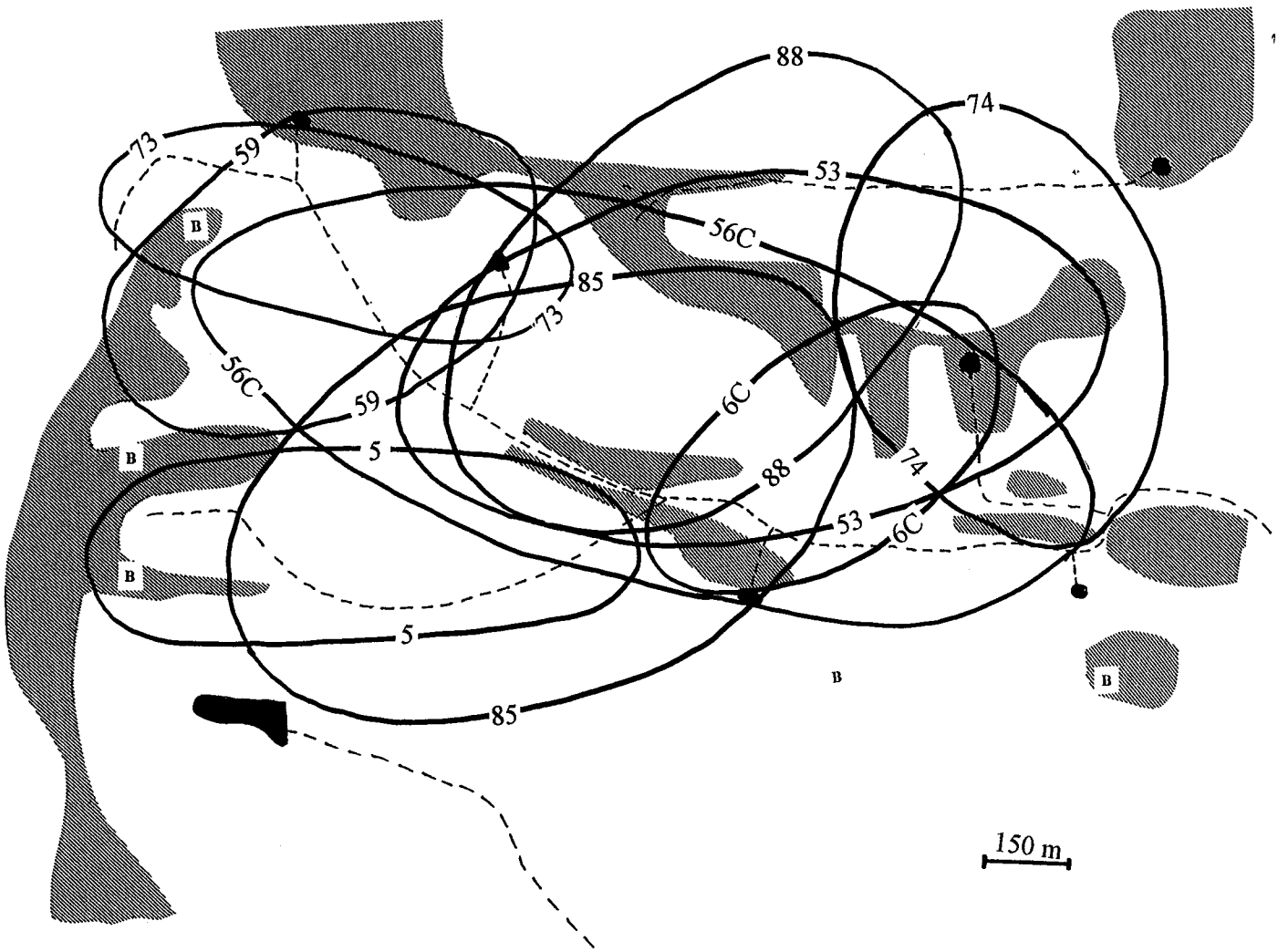

FIG. 1. Home ranges of subadult male opossums (*Didelphis virginiana*) overlayed on habitat, ponds, and building (B) locations. Home-ranges are indicated by solid lines with the identification number of each opossum interlaced in the line. All opossums except number 56C were captured in 1991. Dashed lines indicate intermittent or permanent streams. Patterned areas are regions of no tree cover, all other regions are wooded.

open 4 nights per week from 3 February 1991 to 31 January 1992, after which they were open 3 nights per week. Traps were baited with canned cat food. Capture data from 1 July 1991 to 31 January 1992 and 1 August 1992 to 31 December 1992 for home-range analysis of subadult opossums were collected. These dates coincided with the first capture of subadult opossums and the time when opossums were entering the adult age class.

All captured Virginia opossums were tagged in both ears with numbered rabbit tags (National Band and Tag Co., Newport, KY). Data collected from captured Virginia opossums included weight, sex, site of capture, and age class. Age class was determined by a combination of tooth eruption and tooth wear (Gardner, 1982). For this study the seven age classes of Gardner (1982) were placed into three categories; juveniles (<5 months old), subadults (5–7 months old), and adults (>7 months old). This age class was used for home-range analysis because adults tend to have larger home-ranges and will move over greater distances (see Ryser, 1992). The larger adult home-range and greater amount of movement could take the individual off the trapping grid resulting in an underestimation of home-range size.

Analysis—Home-ranges were calculated only for Virginia opossums captured a minimum of five times and at four different trap sites. Because fewer than 10 captures may result in underestimation of home-range sizes determined from mark-recapture data (FitzGibbon et al., 1995), home-ranges were estimated for only individuals captured a minimum of 10 times. Additionally, two capture sites had to be located away from the outer rows of traps.

Eisenberg (1981) suggested that home-ranges of sexually dimorphic species be analyzed separately for each sex. Because sexual dimorphism becomes evident in the subadult age class of Virginia opossums (Gardner, 1982), home-ranges for males and females were analyzed separately. Although mass is only one aspect of sexual dimorphism, mass is the aspect involved with the objective of this study. Thus, a comparison of the mass was conducted to assess the degree of sexual dimorphism in this population.

Computer program McPAAL, subprogram 95% ellipse (Cary, 1985) was used to estimate home-range sizes and overlay on the habitat of the study site. Home-ranges were compared to

TABLE 1. Weight, sex, and observed elliptical home-range sizes for subadult Virginia opossums (*Didelphis virginiana*) in western Tennessee. All individuals were captured during 1991 except for opossum identification numbers 56C and 59C.

Opossum identification number	Number of captures	Weight[1] (kg)	Sex	Home-range size (ha)
6C	18	1.04	♂	20.6
73	21	1.02	♂	21.8
5	23	2.73	♂	60.7
59	46	1.21	♂	32.2
74	48	1.55	♂	35.3
48	33	1.38	♀	37.2
73C	21	1.02	♀	40.9
88	43	1.40	♂	49.2
53	46	0.98	♂	57.5
85	45	0.90	♂	60.4
56C	27	2.39	♂	71.6
59C	12	1.08	♀	72.4
$\bar{X}_{♂}$	33 ± 16.4	1.47 ± 0.66	—	45.5 ± 18.6
$\bar{X}_{♀}$	21 ± 7.6	1.16 ± 0.19	—	50.1 ± 19.3
$\bar{X}_{total}$	30 ± 15.6	1.39 ± 0.58	—	45.0 ± 21.2

[1] Weight recorded at last capture.

models by McNab (1963), Harestad and Bunnell (1979), and Swihart et al. (1988) using goodness of fit statistics. All statistical analyses were performed with Statistical Analysis Systems software (SAS Institute Inc., 1989). Differences between observed home-range and the expected home-range size from selected models were tested using goodness of fit analyses.

RESULTS

Capture data of 12 subadult opossums, nine males and three females, met criteria for determining home-ranges. There were no significant differences between mean weight of subadult males and subadult females ($t_{10} = 0.779$; $P = 0.454$; Table 1).

Size of home-ranges for both sexes ranged from 20.6 to 72.4 ha (Table 1). Home-ranges of males overlapped extensively (Fig. 1). Home-ranges of females also overlapped, but the amount of overlap was not as extensive as for males (Fig. 2). There was no difference between male and female home-range size. Small sample sizes in 1992 prevented comparison between years.

Smallest home-ranges ($\bar{X} = 34.5 \pm 12.4$ ha, $n = 6$) were associated with human residences or other occupied buildings (Fig. 1 and 2). These home-ranges were located almost entirely within the wooded portions of the study site. Non-wooded areas within the study site had herbaceous vegetation growth greater than 80 cm mean height (Ladine, 1995). Mean herbaceous plant height within wooded areas was ca. 25 cm (Ladine, 1995). With the exception of the home-range of female 56C, the larger home-ranges did not encompass any human residences or occupied buildings. Mean size of home-ranges not encompassing buildings was 50.1 ± 19.3 ha ($n = 7$). Within the larger ranges there were substantial open areas, meadows, or large canopy gaps. All home-ranges contained permanent water sources. There was no significant difference in size between home-ranges that encompassed buildings and those that did not ($t_{11} = 1.696$, $P = 0.1118$).

Models differed in their ability to predict the home-range size of subadult Virginia opossums. The Harestad and Bunnell (1979) model closely predicted home-range sizes for all comparisons (Table 2). The McNab (1963) and the Swihart et al. (1988) models did not predict the observed home-range sizes (Table 2).

DISCUSSION

Virginia opossums' home-ranges overlap considerably (Gardner, 1982). There is considerable variation in home-range size and the degree of overlap of home-ranges throughout the range of the species (Gardner, 1982, Seidensticker et al., 1987). However, no data exist for the size of the home-range for subadult Virginia opossums. Nevertheless, the estimates of home-range size and overlap determined by this study fall within the range reported for the species throughout it's distribution (Gardner, 1982, Seidensticker et al., 1987).

Lack of difference in weight between males and females indicates that the sexual dimorphism in the species (Gardner, 1982) was not evident for weight in the subadults of this population. The lack of sexual dimorphism in subadults corresponded with the lack of difference in the size of the home-range size between sexes. The factor appearing to correlate most closely to home-range size was the presence of buildings. The tendency for Virginia opossum home-ranges encompassing occupied buildings to be smaller may be explained by the presence of a reliable food source. Macdonald (1983) proposed food patch dispersion as the principal factor determining home-range size in carnivores. Even though the size difference between home-ranges encompassing buildings and those not encompassing buildings was not significant, the difference may be of biological importance. The occupied buildings with the potential for reliable food resources could result in spatial variations in prey density. This spatial variation may lead to a rate-maximizing foraging strategy (Arditi and d'Acorogna, 1988) of the Virginia opossum. The rate-maximizing foraging strategy predicts the use of habitat within a homogeneous environment as if the habitat were patchy; thus, increasing their movements. Alternatively, movements could have been reduced during 1991 due to increased numbers of Virginia opossums on the grid (Ladine, 1995), resulting in a reduction in home-range size.

Underestimation of home-range size by two of the selected models (McNab, 1963; Harestad and Bunnell, 1979; Swihart et al., 1988) may be attributed to several factors. The nomadic tendencies of the Virginia opossum (Wiseman and Hendrickson, 1950; Brocke, 1970; Gillitte, 1980; Ryser, 1992) may be the primary factor. Other factors include, but are not limited to, difference in trophic level, method of estimation of home-range size, patchiness of the habitat, and statistical variation. McNab (1963) and Swihart et al. (1988) developed their models for carnivores, whereas Harestad and Bunnell (1979) developed their model, which best estimated the size of the home-range of subadult Virginia opossums, for omnivores. Home-ranges in the present study were estimated using mark-recapture methodology. Home-ranges from this type of study have been shown to result in larger estimations of home-range than radio telemetry estimations (Jones and Sherman, 1983). As already noted, patchiness may result in increased movements of individuals, thus increasing the home-range size. Additionally, previous models (McNab, 1963; Har-

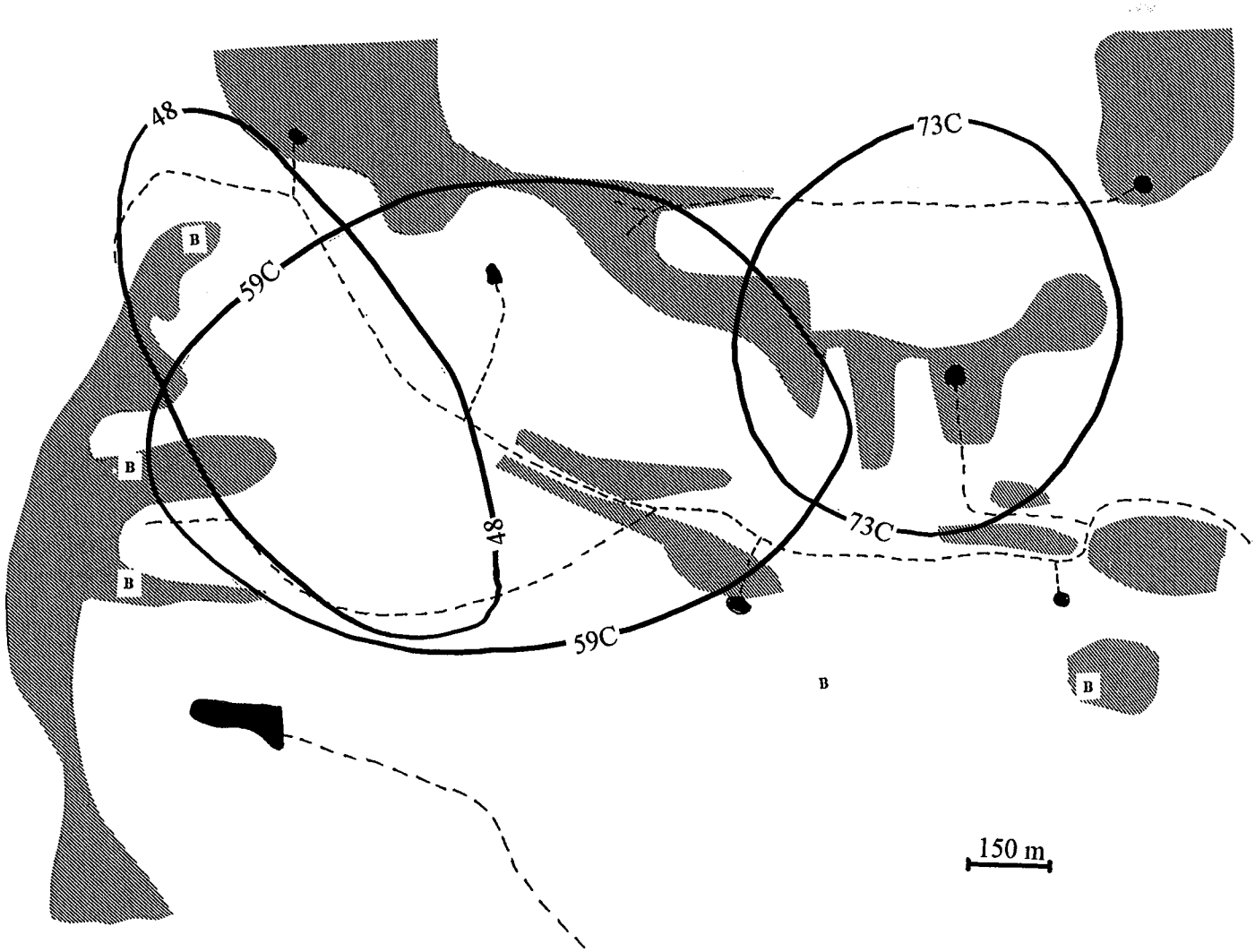

FIG. 2. Home ranges of subadult female opossums (*Didelphis virginiana*) overlayed on habitat, ponds, and building (B) locations. Home-ranges are indicated by solid lines with the identification number of each opossum interlaced in the line. Opossums 48, 6C, and 73C were captured in 1991; 44C and 59C were captured in 1992. Dashed lines indicate intermittent or permanent streams. Solid blocks indicate permanent ponds. Patterned regions are areas of no tree cover, all other regions are wooded.

TABLE 2. Equations for estimating home-range size, mean expected home-range size, mean observed home-range size, and chi-square (χ^2) values comparing observed (Obs) and expected (Exp) mean sizes of home-ranges of Virginia opossums (*Didelphis virginiana*). Sources of the models are listed according to the superscript number associated with the model (R). Values are in the units used in the original model.

Model	Tropic level	Home-range size											
		Males				Females				Species mean			
		Obs	Exp	χ^2	P	Obs	Exp	χ^2	P	Obs	Exp	χ^2	P
[1]R = 12.6W$^{0.71}$	C[4]	112.8	16.9	479.3	<0.001	124.5	13.6	450.8	<0.001	106.4	15.9	461.5	<0.001
[2]R = 0.059W$^{0.95}$	O	45.5	49.6	0.85	0.356	50.2	37.4	0.0	0.974	50.2	45.1	0.5	0.522
[3]R = 15.14W$^{1.26}$	C	45.5	25.4	7.23	0.007	50.2	17.3	23.0	<0.001	50.2	22.3	15.4	<0.001

[1] McNab (1963)—home-range size measured as, W = body weight in kg.
[2] Harestad and Bunnell (1979)—home-range size measured in ha, W = body weight in g.
[3] Swihart et al. (1988)—home-range size measured in ha, W = body weight in g.
[4] C = carnivore, O = omnivore.

estad and Bunnell, 1979; Swihart et al., 1988) were derived from data in which there was inherent variation around the estimated regression line. The results of the present study may reflect the inherent variation of estimating home-range size from models derived from body mass data.

The Virginia opossum is a versatile species that uses a number of food sources. This omnivorous feeding strategy is consistent with a nomadic lifestyle, and thus, a relatively large home-range size. Although the Harestad and Bunnell (1979) model predicted the subadult Virginia opossum home-range size, because of the nomadic lifestyle, models estimating home-range size of other age classes of Virginia opossums may need to accommodate nomadism and habitat use behavior.

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