

RESPONSE OF RACCOON SPATIAL AND SOCIAL BEHAVIOR TO
THE PRESENCE OF AN EXPERIMENTALLY CLUMPED FOOD
RESOURCE

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By

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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

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PRESENCE OF AN EXPERIMENTALLY CLUMPED FOOD RESOURCE

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John Donne states as part of his meditation XVII that “.....No man is an island, entire of itself; every man is a piece of the continent, a part of the main.....” This sentiment of one being part of an interconnected community is markedly true about the life of a thesis project. This research project and thesis would not have been as rewarding an experience without the support and help of my committee members, fellow graduate students, post doctor students, field technicians, family, and the raccoons of Baskett. I am extremely grateful to my advisor Dr. Matt Gompper for the patience, excellence, mentoring, freedom and coffee that he provided. I also want to provide infinite thanks to Walter and Lily and the animal companions for putting up with my ignoring them for extended periods.

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ABSTRACT

The spatial and behavioral ecology of raccoons (*Procyon lotor*) and many other putatively solitary species can fluctuate based on the availability and location of resources. Hallmarks of a more solitary existence include limited home range overlap and concurrent space use with conspecifics, and lack of social denning behaviors. Conversely raccoons exhibiting greater sociality or a more spatially aggregated local distribution also have greater overlap and conspecific co-occurrence values and higher frequencies of proximal or communal denning. The transition from a solitary to a social or group-living lifestyle can occur when clumped resources patches are available for extended periods, but detailed understanding of how raccoons shift from a solitary to an aggregated distribution is lacking. In this study I used an experimental approach to examine how raccoons respond to the addition of a predictable and abundant food resource. I contrasted raccoons inhabiting two adjacent sites on the University of Missouri Thomas S. Baskett Research and Education Area located 8 km east of Ashland

Missouri: both received similar food supplements, but one site received the food in a clumped fashion (via the creation of a permanent feeding station) while the other received the food dispersed to multiple sites that varied over time so that the food was neither spatially clumped nor spatio-temporally predictable. Radio telemetry data from adult raccoons were analyzed to assess the influence of the experimentally maintained clumped food source on home range spatial structure and social denning behaviors. Home range size did not differ between treatments sites or genders, but raccoons from the clumped resource site had home range overlap and probability of co-occurrence values were almost twice those of raccoons from the dispersed resource site. Communal denning, proximity of dens, and den reuse behaviors did not differ overall between the two sites, but clumped resource site raccoons moved shorter distances between subsequently used den sites and to utilize dens located within a smaller area. Differences in the patterns of overlap, co-occurrence, communal denning, proximal denning, and den reuse found in this study suggest that raccoons and perhaps other putatively solitary mesocarnivores are not truly solitary, but rather appear so only where resource availability induces territories occupied by just a single individual. Given sufficient resources or food patches, these species may exhibit a more social existence than previously reported.

Chapter

Effect of an Experimentally Clumped Resource on Raccoon (*Procyon lotor*) Home Range Structure.

ABSTRACT

Some species of carnivores fluctuate between a primarily solitary lifestyle and a group-living lifestyle, depending on resource availability. Understanding the ontogeny of this transition requires analyzing changes in space use. Radio telemetry data from 41 adult raccoons (*Procyon lotor*) were analyzed to assess the influence of an experimentally maintained clumped food source on spatial structure. Home range size, two-dimensional overlap, and volume of intersection (VI) values were compared between 22 raccoons with access to the clumped food resource and 19 raccoons on an adjacent control site that received similar food quantities, but for which food was distributed in a randomized and non-clumped pattern. No between-sex differences in home range size occurred within either food site, nor did differences in home range size occur between the two sites. However, the experimental site animals had two-dimensional home range overlap values 1.9 times greater than the control site animals and VI scores almost twice that of raccoons inhabiting the control site. Experimental site females had mean overlap and VI value 1.3 times greater than experimental site males. While a site's overall resource availability influences population size, the spatial clumping of resources facilitates the formation of local aggregations.

INTRODUCTION

Species in the order Carnivora are primarily solitary, with only 10-15% living in groups (Bekoff et al. 1984). Yet many of these putatively solitary species fluctuate between primarily solitary living, with little overlap of home ranges, and aggregated living with extensive overlap. This fluctuation depends on available resources (Bekoff et al. 1984, Moehlman 1986, 1989). The transition from a solitary to a social or group-living lifestyle can occur through the development of different types of aggregations. These aggregations include spatial groups (arrangements of adults where more than one individual routinely occupies the same general spatial-temporal location); population groups (individuals sharing a common home range); foraging groups (individuals grouping while searching for, hunting, or consuming food); and breeding groups (individuals grouping to form a reproductive unit) (Gittleman 1989). While these group types are non-exclusive, in most cases, the trigger for group formation is the presence or absence of abundant critical resources, in particular food (Bekoff et al. 1984, Atwood and Weeks 2003).

Understanding how these normally solitary carnivores react to resource availability to form spatial groups can provide researchers and resource managers with the knowledge to address a variety of habitat and species management questions (Atwood et al. 2009). The raccoon (*Procyon lotor*), a mid-sized, omnivorous and highly opportunistic carnivore, may be an excellent model species for understanding spatial dynamics and the ontogeny of social structure

in mesocarnivores. Raccoons show a high degree of plasticity in their space use and occupy different habitats as populations comprised of either solitary (Chamberlain and Leopold 2002) or highly aggregated individuals (Gehrt and Fritzell 1997, 1998). However, a detailed understanding of how raccoons shift from a solitary to an aggregated distribution is lacking. In this study I use an experimental approach to examine how raccoons respond to the addition of a predictable and abundant food resource. I contrast raccoons inhabiting two adjacent sites: both receive similar food supplements, but one site receives the food in a clumped fashion (via the creation of a permanent feeding station) while the other receives the food dispersed to multiple sites, with the location of the sites varying over time so that the food is neither spatially clumped nor spatio-temporally predictable.

Home range area, volume of intersection (VI) and home range overlap are metrics that can be used to measure the impact of clumped resources on space use. I use these three geometric aspects of home range structure to examine the responses of raccoon space use to a clumped resource. Home range size provides a direct two-dimensional measure of the extent of the landscape used by an animal during its normal activities. The size, shape and location of the home range provide a coarse scale or second order measure of an animal's resource selection (Johnson 1980). The presence of additional food, sometimes clumped, is often associated with decreased home range size in raccoons and other carnivore species (Gehrt and Fritzell 1997, 1998, Prange et al. 2004, Quinn and Whisson 2005). Furthermore the presence of predictable resources should

decrease the need for an individual to defend a large area, as a smaller area will include sufficient useable resource patches over time. Therefore, a larger home range size that might be necessary due to temporal fluctuations in resource availability is no longer necessary (Johnson et al. 2002). I predict mean home range size will be smaller for animals inhabiting a site with reliably available clumped resources.

Does home range overlap differ between animals that inhabit a site with clumped resources and those that inhabit a site that has a similar quantity of resource but whose distribution is not clumped? Along with home range size, home range overlap is a common method used to demonstrate the link between resource availability and group formation (Atwood and Weeks 2003), as the extent of overlap represents the proportion of an animal's home range containing additional individuals. Based on the concept that a predictable clumped resource would facilitate more than one individual using a locality without incurring costs to other individuals (Carr and Macdonald 1986, Macdonald 1983, Johnson et al. 2002), I predict that home range overlap values will be greater for the population inhabiting the site with clumped supplemental food.

While home range overlap indicates the number of different individuals occupying a geographical space, it does not directly describe the intensity of the joint space use. Thus, I also ask whether the intensity of use of individual home ranges and overlap areas differ between the two study populations as a function of resource clumping. Measuring the volume of home range overlap does not provide a temporal measure of the probability that an individual raccoon will

encounter conspecifics. Rather, kernel analyses allow quantification of an individual's probability of occurrence at each point in its home range (its utilization distribution; UD). The overlap of these UDs, quantifiable as a volume of intersection (VI) metric, allows the contrast of the extent of space sharing among animals based on the degree and intensity of use of areas of home range overlap (Kernohan et al. 2001). I predict that animals within the clumped-resource population will have higher mean VI values for their overlap areas than animals in the dispersed-resource population. Again, this prediction derives from hypotheses suggesting that a predictable clumped resource facilitates the use of a locality by multiple individuals without incurring additional costs to these individuals (Carr and Macdonald 1986, Johnson et al. 2002).

METHODS

Study Area

Field work occurred in and around the University of Missouri's Thomas S. Baskett Research and Education Center (hereafter, Baskett), located 8 km east of Ashland, MO USA (lat. 38.7N, long. 92.2W). Much of Baskett was previously used as farm and grazing lands, but has now reverted to the secondary mixed oak and hickory dominated forest communities found throughout much of central Missouri. Baskett is bisected east/west by a paved road (Route Y). Baskett is bounded on all sides by a mix of private and public (U.S.F.S. Mark Twain National Forest) lands. Radio telemetry locations collected during the course of this study covered approximately 15.75 km². This included data collected from 9 km² Baskett and an additional 6.75 km² of public and private lands immediately

adjacent to Baskett. With the exception of scattered rural dwellings, the habitats on these adjacent lands are similar to those found within Baskett. The study site was divided into two treatment areas (Figure 1). One area (hereafter the experimental site, ES) was contained within lands north of Route Y and one area (hereafter the control site, CS) within lands south of Route Y. Both areas contain a fifth order stream, several smaller perennial or intermittent low order-streams, as well as several ponds and small lakes.

Treatments

To simulate a persistent and abundant clumped resource, 18-36 kg of dry dog food were placed weekly at a single location on the ES from January 2006 through December 2008. Data generated from motion sensitive cameras showed the clumped food was heavily used by raccoons, often with multiple individuals visiting the location simultaneously (Monello 2009). The CS received the same amount of dog food as placed at the clumped resource site within the ES. However, instead of the creation of a clumped food patch at a single location, the food was subdivided into multiple small piles (ca 0.25 kg. ea.) which were placed at least 50 m apart in an irregular pattern throughout the study area. Placement of food in the CS was spatially randomized so that the placement of these small food piles was not predictable from week to week.

Capture and handling

Between May 2007 and June 2008 a total of 65 adult raccoons (37 ES, 28 CS) were captured and fitted with radio transmitters. Approximately equal numbers of females (18 ES, 14 CS) and males (19 ES, 14 CS) were collared at

each site. Procedures for trapping, anesthetizing, and handling raccoons followed University of Missouri Animal Care and Use protocol 3927. Raccoons were captured using Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk WI). Traps were placed along drainage courses, maintained dirt roads or trails. Depending on time of year, traps were baited with either a canned fish or sweet bait formulation of strawberry jam and mashed sugared donuts. Baited traps were checked daily between 0600 and 0800.

Raccoons were anesthetized with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine (1 mg/kg) (Belant 1995). Once anesthetized, the animals were removed from the trap and sexed, weighed and measured. Each animal was aged by tooth eruption, tooth wear and past capture history (Grau et al. 1970, Monello 2009). Raccoons were marked with numbered ear tags in both ears (#1005-1 Hasco Tag Company, Dayton KY). Animals age two years or greater were classified as adults and fitted with a radio transmitter collar (ATS, Isanti MN; Telonics, Mesa AZ). Collars weighed 65 grams and transmitted at frequencies between 150 and 152 MHz. Each collar was outfitted with a mortality signal that changed the collar pulse rate from 55 pulses per minute (ppm) to 110 ppm after 24 hours of immobility.

Data collection

Animal location data were collected by triangulation using a three-element hand-held Yagi antenna from fixed points throughout Baskett. Data were collected in one of two ways. A researcher would visit 2-3 fixed points within 10 minutes. An azimuth was collected for a single frequency until at least 2 azimuths

had been recorded. Alternatively, two or three individuals worked together to take simultaneous azimuths from two or three different fixed points. To ensure that data points represent all possible nocturnal activity zones, data were collected equally from each of four, three-hour periods (1800-2100, 2100-2400, 2400-0300, 0300-0600). To minimize biases in home range size estimations derived from a small sample size of location data, only animals with ≥ 30 locations spaced ≥ 2.5 hours apart were used to estimate UDs (Aebischer et al. 1993, Alldredge and Ratti 1986, Seaman and Powell, 1996)

Prior to beginning telemetry data collection a pilot study was conducted to measure the precision and accuracy of azimuth readings. Six radio collars (test transmitters) were each placed at 36 undisclosed locations (18 ES, 18 CS) for a total of 108 telemetry bearings. Transmitters were placed between 0 and 5 meters off the ground and between 200 and 1000 meters from telemetry stations. A GPS unit was used to record the UTM of both the test transmitter and the receiver location. The true bearing was then compared to the estimated bearing to calculate precision and accuracy (White and Garrott 1990). Data error was calculated with the program Location of a Signal (LOAS v 4.0, Ecological Software Solutions LLC, Hegymagas, Hungary). Test results indicated a mean bearing error of $2.5^\circ \pm SE 0.35$.

Data analysis

Bearing locations were converted to location estimates using a maximum likelihood estimate (MLE) in LOAS. Prior to and during conversion, bearings showing non-convergence were eliminated. A total of 1764 ($\bar{x} = 46 \pm SD 12$ per

animal) location estimates were derived from viable bearings. Road availability and site topography limited available triangulation points, so all bearings showing convergence were utilized even when between-angle bearings were less than 20° (Chu et al. 1989). During bearing conversion, biangulation was used when the third bearing was an obvious product of signal deflection. Data were pooled for analysis across seasons, as intra-seasonal sample sizes were small.

Plug-in smoothing methods were used to produce UD bandwidths for 95% and 50% fixed kernel home ranges (Gitzen and Millspaugh 2003, Kernohan et al. 2001, Seaman and Powell 1996, Worton 1995). The UDs were calculated using Matlab (Mathworks Inc., Natick, MA) with the kernel density estimator (KDE) folder attached. UDs were created and converted to rasters by applying inverse distance weighting point interpolations with ArcGIS 9.3 (ESRI, Redlands, CA) spatial analyst tools. Hawth's tools v3.2 (www.spatial ecology.com) was used to extract and define 95% and 50% isopleths. Isopleths were transformed into fixed kernel polygon (FKP) vectors for home range size and overlap analysis and remained as raster FKPs for VI analysis. Locations were projected using the NAD83 datum.

Composite mean home range values were compared between treatments (sites) and between genders. Differences were also tested for inter-gender within each treatment and intra-gender between treatments. Comparisons were done for both 95% and 50% FKPs. The home range core area was defined as the 50% FKP. The degree to which the clumped food addition may have influenced individuals within the ES was examined by noting whether or not the

location of the clumped food was included in the 95% and 50% FKPs. Based on the inclusion of the clumped food in the home range of an individual, animals were placed in 3 groups. Group 1 animals included the clumped food in their 95% and 50% FKPs. Group 2 animals did not include the clumped food in their 50% FKP but the location of the clumped food was within 500 m (approximately one mean core area diameter). Group 3 animals either had home ranges not including the clumped food, or did not include the clumped food location in their 50% FKP and were greater than one core area length from the clumped resource. To investigate any effects of the clumped resource on shared space use, home range overlap and VI score were tested for differences between groups.

Home range overlap was determined by calculating the area of intersection for every raccoon dyad. For each individual intersection the area was divided by the area of an individual's home range polygon to determine the proportion of a home range included in the overlap area. The VI index statistic measures the probability of co-occurrence in joint space use by comparing the shapes and locations of two or more UD's. An individual's UD is a three dimensional representation of how intensely it utilizes a given geographic area. The resulting quantity generated by overlapping UD's has a maximum value of 1 only when the space use pattern is identical for two individuals. With greater variation in space use patterns, the index score approaches 0 (Seidel 1992, Kernohan et al. 2001). VI index scores and co-occurrence UD's were generated in ArcGIS 9.3. Home range overlap and VI values for both 95% and 50% FKP

were derived between all individuals within their respective treatment areas. Animals with overlap and VI values of ≤ 0.01 were included when generating comparative statistics for 95% FKPs but were eliminated from subsequent 50% overlap and VI analyses. This approach was taken to avoid assumptions of inequality in movement opportunity in individual animals (95% FKP) and to not statistically overestimate 50% FKP between treatment differences. Overlap and VI values were tested for differences between treatment sites as a whole and for all possible combinations of inter- and intra-gender joint space use within and between treatments.

Tests for statistical differences were made using Wilcoxon and Kruskal-Wallis rank sum tests in program R ($\alpha = 0.05$). Home range size data was not transformed, but home range overlap and VI index calculations result in proportions which were arcsine square root transformed prior to analysis. Prior to reporting or graphing, any transformed data was back-transformed by squaring the sine of the number (Fleiss et al. 2003). Averages are presented throughout as mean \pm SE unless otherwise noted.

RESULTS

Home range and core area size

Forty-one (22 ES, 19 CS) of the 65 collared raccoons had the ≥ 30 telemetry points necessary for home range analyses. Thirty-four (18 ES, 16 CS) raccoons were radio tracked in both 2007 and 2008. Seven others (4 ES, 3 CS) were collared and tracked only in 2008 (Figure 2). Average distance between receivers and raccoons was 828 m \pm SE 36. The combined population of ES

and CS individuals had 95% FKP home range sizes between 0.75 - 4.26 km² and 50% FKP core area sizes between 0.15 - 1.09 km² (Table 1). Female mean 95% home range size was 1.70 km² ± SE 0.13 and 0.37 km² ± 0.03 for 50% FKP. Males mean 95% FKP home range size was 2.23 km² ± 0.20 and mean 50% home range size was 0.53 km² ± 0.05. For all individuals combined, male 95% FKP ($W = 132$, $p = 0.05$) and 50% FKP ($W = 112.5$, $p = 0.014$) home range estimates were significantly larger than those of females. No other inter- or intra-gender or site comparisons exhibited statistically significant differences in mean 95% or 50% FKP estimates.

Home range and core area overlap

The ES dyads had mean 95% FKP home range overlap scores (0.44 ± 0.01) 1.6 times greater than CS dyads (0.28 ± 0.01). These differences were driven principally by the disparity between ES and CS females. Females from the ES had over one and a half times the 95% FKP overlap of CS females ($p < 0.001$). ES females also differed significantly from CS females in their extent of overlap with males ($p < 0.001$). In contrast, the mean 95% FKP overlap scores among males were not significantly different between treatments ($W = 2285$, $p = 0.9196$) (Table 2). Within treatment sites, comparisons of male and female overlap values indicated ES females had slightly more overlap than ES males ($p = 0.05$), but on the CS, males had greater overlap values than females ($p = 0.01$). These inter-gender within sites differences were not present for the ES 50% core overlap values ($p = 0.47$), but persisted and strengthened for the inter-gender CS values ($p < 0.001$).

Compared to the mean 95% FKP scores there was less differentiation in mean home range overlap scores between populations for the 50% core FKP (ES: 0.14 ± 0.01 ; CS: 0.11 ± 0.01) (Table 2). Both the ES and CS populations had a greater number of non-overlapping dyads at the 50% core level, and mean overlap values were an average of 3 times lower. There was no male intra-gender dyad overlap difference for 95% FKP, but a difference was present in 50% core overlap ($W = 1309$, $p < 0.001$). CS males had nearly double the 50% core overlap of ES males (Table 2). Inter-gender dyad overlap was the only other joint space relationship that showed significant differences ($W = 22312.5$, $p = 0.001$) between treatments.

Probability of co-occurrence

The ES population had significantly higher composite mean 95% FKP VI scores (Table 2) than the CS population ($W = 27397.5$, $p < 0.001$), but as with 95% FKP overlap the female:female and female:male dyads were the only two individual comparisons that differed between treatment areas. Mean ES female:female and female:male VI scores were 1.5 to 2 times greater, respectively, than corresponding CS comparisons (ES_{F:F}: 0.24 ± 0.02 , CS_{F:F}: 0.15 ± 0.02 , ES_{F:M}: 0.23 ± 0.02 , CS_{F:M}: 0.10 ± 0.01). A weaker, but still significant, composite mean difference existed between treatments for 50% core FKP VI scores ($W = 77171$, $P = 0.05$). As with the 95% FKP VI scores, ES inter-gender scores were 2 times greater than the control site population, but male-male VI scores were greater for the CS treatment (Table 2). There were no within site differences between genders.

Clumped resource inclusion

All ES individuals except for four animals (3 males, 1 female) included the supplemental clumped food within their 95% home ranges. Overlap with the clumped food may have been missed for the four individuals, as all had putative home range polygons < 500 meters from the feeding site. Based on proximity to the location of the supplemental clumped food, Group 1 included 10 raccoons (5 males, 5 females), Group 2 was comprised of 6 individuals (3 males, 3 females), and Group 3 included 2 females whose 50% core areas were further than 500 m from the feeding site as well as the 4 (3M, 1F) individuals whose 95% FKP home ranges did not overlap the feeding site. Raccoons in groups 1, 2, and 3 had mean 95% FKP home range and 50% core overlap scores that differed significantly ($H_{95\%FKP} = 18.47$, $df = 2$, $p < 0.001$; $H_{50\%FKP} = 54.33$, $df = 2$, $p < 0.001$). For 95% FKPs, mean home range overlap was ca 30% greater for Group 1 individuals than Group 2 and 3 individuals. At the 50% FKP core level this difference was even greater (Figure 3). Female:female mean overlap and VI scores declined as separation from the location of the feeding site increased, but male intra- and inter-gender mean overlap scores were larger for Group 3 than Group 2. Similar patterns were also found between Groups 1, 2, and 3 for mean VI scores ($H_{95\%FKP} = 14.48$, $df = 2$, $p < 0.001$; $H_{50\%FKP} = 18.82$, $df = 2$, $p < 0.001$).

DISCUSSION

MacDonald (1983) advanced the Resource Dispersion Hypothesis (RDH) to explain how patterns in the availability of food or other limiting resources could predict the formation and dissolution of spatial groups among carnivores. The

underlying premise was that an individual's home range could support additional animals when the cost of the additional animal's presence was negligible (Johnson et al. 2002). Carr and MacDonald (1986) furthered the concept by demonstrating how increased habitat heterogeneity was conducive to spatial group formation, and Sandell (1989) showed how the spatial shifts in resource availability correlated with gender-related and temporal changes in home range size and overlap. Although there are few empirical tests of the RDH (Verdolin 2009), several field studies have found it provides a predictive framework for analyzing and understanding the spatial response of carnivores that occur in both solitary and aggregated populations (Valenzuela and Macdonald 2002, Eide et al. 2004, Macdonald and Sillero-Zubri 2004, Rosalino et al. 2005).

Observational studies examining the effect of clumped or aggregated resources on carnivore spatial dynamics report a decrease in home range size and an increase in intra-gender home range overlap (Fedriani et al. 2001, Hidalgo-Mihart et al. 2003, Moehlman 1986, 1989, Quinn and Whisson 2005). This effect is often greater in females than males (Erlinge and Sandell 1986, Sandell 1989). The results from this study varied subtly, however, from the above findings. While home range size and core areas of males were greater than those of females, I found no significant differences in home range or core area size for the two treatments. Nonetheless, greater home range overlap and probability of co-occurrence were found between most inter- and intra-gender ES dyads. These differences appear to be driven by increased overlap among ES females, as males from the two treatments had similar home range overlap and

VI scores. Additionally, *a posteriori* examination of the UDs generated from the VI scores revealed that peak areas of co-occurrence often occurred away from the location of the clumped resource, such that individuals with a more peripheral inclusion of the feeding site in their home range nonetheless demonstrated overlap and co-occurrence values comparable to individuals with inclusion of the feeding locale within 50% core FKPs.

Uniformity of raccoon home range and core area size independent of supplemental feeding seems to contradict previous findings. Such patterns might be expected in homogenous environments where resources are not patchily distributed (Baker and Harris 2004, Johnson 2002), a situation that my manipulations of resource availability and distribution aimed to prevent. However, the location of the ES food supplementation outside of peak occurrence portions of the core area UDs indicates that home ranges may have been modified to include the resource, a pattern observed in other studies of carnivores (Kolowski and Holekamp 2008). Modification of home range boundaries to include the resource without altering home range size may explain the lack of inter-gender and treatment differences. Thus home range and core area size may not be a sensitive metric for ascertaining the spatial response of ES animals to the clumped resource distribution if shifting of home ranges also occurred.

Although no difference was found in home range size, 95% home range overlap and co-occurrence patterns differed greatly between the ES and CS. The driving force behind this difference were ES females, whose home range overlap values with each other and with males were an average of 1.8 times greater than

those occurring among females from the CS population. Increased overlap is commonly observed in many resource dispersion studies, but the simultaneous occurrence of both intra- and inter-gender overlap is unusual (Eide et al. 2004, Davison et al. 2009, Fedriani et al. 2001). Differences in the extent of overlap and co-occurrence were less pronounced for 50% core areas, however, and only ES inter-gender dyads maintained a large significant difference for all joint space use comparisons. This suggests that extensive home range overlap does not always coincide with increased probability of co-occurrence even when habitat conditions allow spatial aggregations.

Although joint space use for females generally diminished as distance from the location of the feeding site increased, males did not follow the same pattern. Group 1 males had the largest intra- and inter-gender values, but Group 3 males also had extensive intra- and inter-gender overlap, with values higher than observed for Group 2 males. The RDH predicts that the presence of the clumped food source provides additional resources and thereby allows more animals to co-exist within each individual's home range area. As animals' core areas recede from the clumped resource, the probability of them encountering the resource diminishes and less overlap between animals is expected. The diminishing probability is a function not only of the distance from the resource, but also the temporal nature of the resource. Food was placed at the ES feeding site weekly, but generally persisted for no more than 3-4 days. Animals not visiting the feeding site immediately after supplementation would be less likely to benefit from its presence. Therefore males whose home ranges were more

distant from the location of the clumped resource may need to utilize additional foraging areas and their spatial arrangements display greater heterogeneity as the resources become more homogenous (Baker and Harris 2004, Bernstein et al. 1988). Thus, the overlap patterns of males more distant from the ES feeding site were similar to animals of both genders on the CS.

Gerht and Fritzell (1997, 1998) found only limited evidence of co-occurrence away from foraging sites among dispersing juvenile males. In light of those findings and because VI values diminished as the distance from the location of the feeding locale increased, it would be expected that the peak VI values would geographically fall on the feeding station. However, an examination of the UDs of dyads revealed that peak areas of co-occurrence were often not on the feeding station, but rather in locations closer to other potentially attractive and important resources such as water and den sites. Yet this does not negate the influence of the clumped resource, as mean values were twice those of CS dyads, and thus a much greater chance of co-occurrence existed on the ES.

The patterns of overlap and co-occurrence found on both the ES and the CS in this study suggests that raccoons and perhaps other putatively solitary mesocarnivores are not truly solitary, but rather appear so only where resource availability induces territories occupied by just a single individual. Given sufficient resources or food patches, these species may exhibit a more social existence than previously reported (see also Gehrt et al. 1998; Pitt et al. 2008). Optimal conditions and responses will vary from site to site, even for conspecifics (Davison et. al 2009), but in general home ranges demonstrating low dyad

overlap or low likelihood of co-occurrence may be indicators of habitats with limiting resources rather than a natural inclination of these animals to avoid overlap with conspecifics. Conversely a habitat rich in resources may facilitate smaller home ranges, higher densities and higher overlap among individuals.

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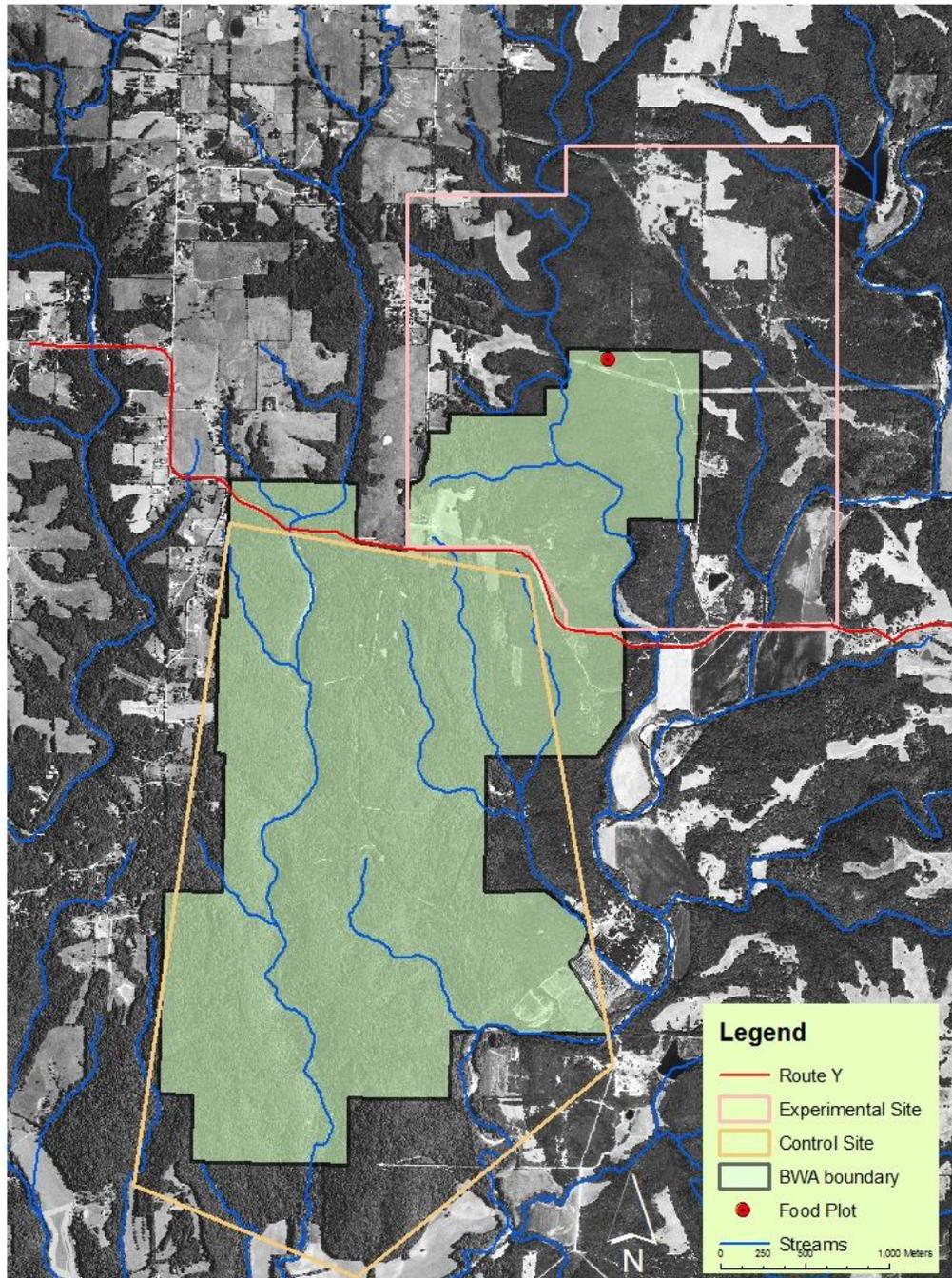


Figure 1. Map of study site and treatment areas. Study site is located 8 km east of Ashland, Missouri and includes all of Thomas S. Baskett Research and Education Center and portions of USFS Mark Twain National Forest.

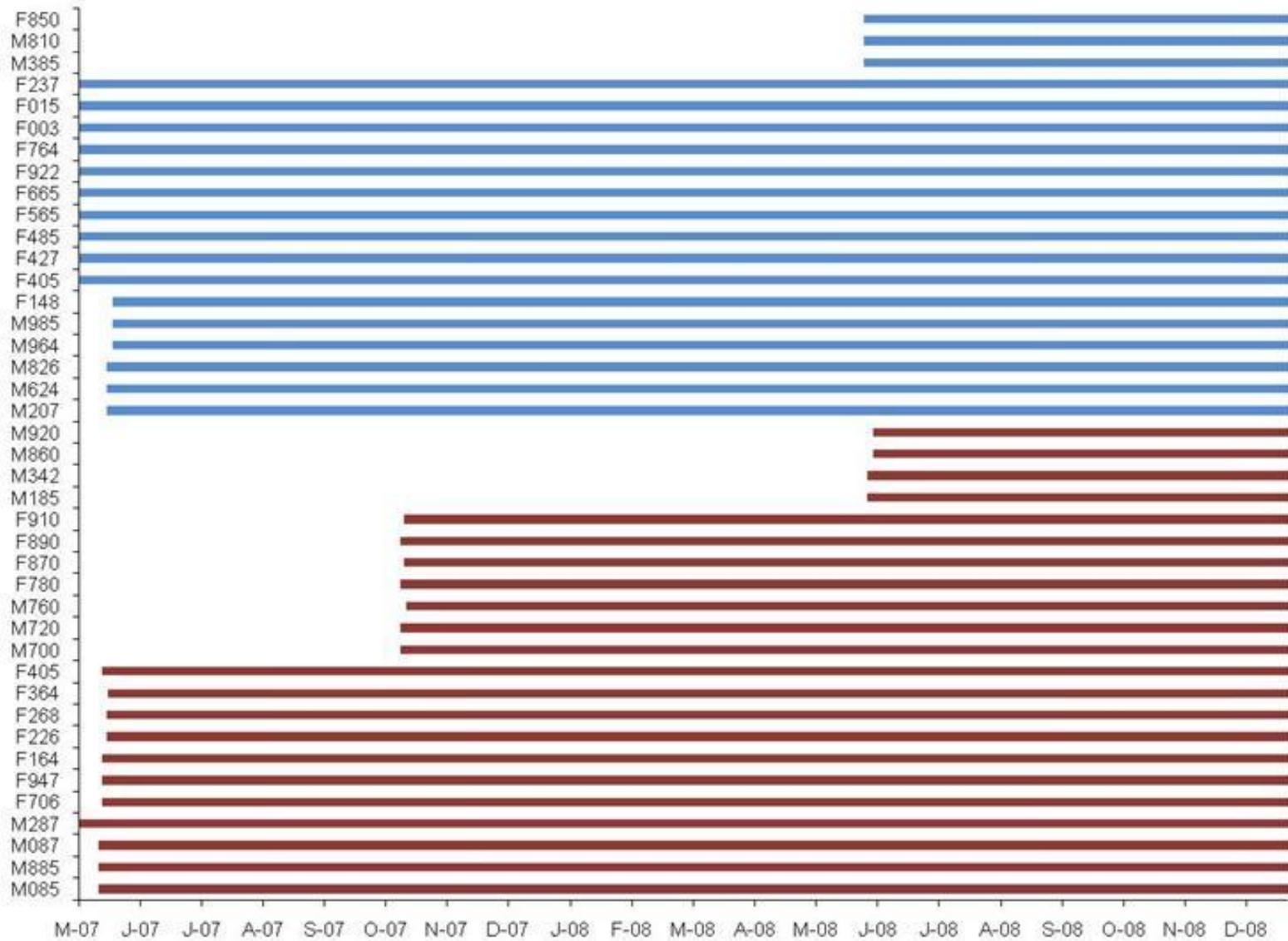


Figure 2. Monthly time line of radio tracking duration period for 19 control site raccoons (7M, 12F) and 22 experimental site raccoons (11M, 11F). Blue bars denote control site animals and red bars denote experimental site animals. Initial tracking began in May 2007 and extended through December 2008. Y axis shows gender and collars identification number of radio tracked animals.

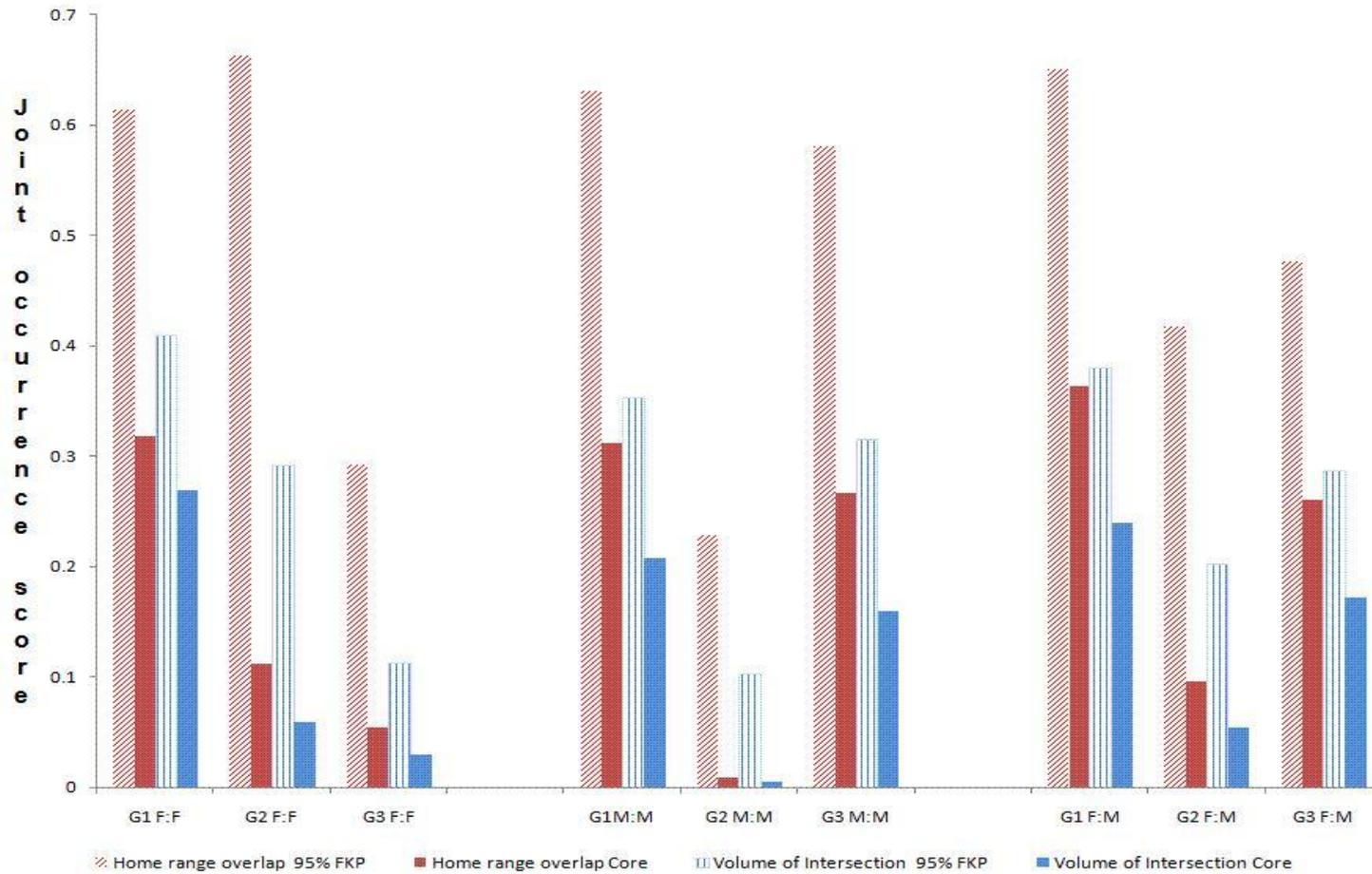


Figure 3. Comparison of joint space use scores for experimental site animals. Animals are subdivided by the extent of inclusion of the clumped resource in their home range. Group 1 (G1 5M, 5F) always included the clumped resource, Group 2 (G2 3M, 3F) excluded clumped resource from the 50% core area but were < 500 meters of the clumped resource. Group 3 (G3 3M, 3F) entirely excluded the clumped resource from their home range or their core areas were > 500 meters from the clumped resource. F:F denotes joint space use between female dyads, M:M between male dyads, and F:M inter-gender dyads.

Table 1. Home range size measured in km² of 95% fixed kernel polygons and 50% core areas for control site (CS) and experimental site (ES) raccoons from Thomas S. Baskett Research and Education Center, Ashland, Missouri. Data are further subdivided by gender. Final values combine ES and CS individuals.

Population	N	Max		Min		Mean (SE)	
		95% FKP	50% core	95% FKP	50% core	95% FKP	50% core
CS all	19	3.09	0.79	0.77	0.18	2.03 (0.17)	0.44 (0.04)
ES all	22	4.26	1.09	0.75	0.15	1.85 (0.18)	0.44 (0.05)
CS females	12	3.03	0.64	0.77	0.18	1.83 (0.19)	0.38 (0.04)
ES females	11	2.63	0.71	0.75	0.15	1.56 (0.19)	0.36 (0.05)
CS males	7	3.09	0.79	1.14	0.25	2.36 (0.29)	0.54 (0.05)
ES males	11	4.26	1.09	1.00	0.18	2.15 (0.29)	0.53 (0.07)
All females	23	3.03	0.71	0.75	0.15	1.70 (0.13)	0.37 (0.05)
All males	18	4.26	1.09	1.00	0.18	2.23 (0.20)	0.53 (0.05)

Table 2. Mean (SE) home range overlap and volume of intersection scores for experimental site (ES) and control (CS) raccoon dyads from Thomas S. Baskett Research and Education Center, Ashland, Missouri. Statistical values were generated using a Wilcoxon ranked sum test. F:F denotes joint space use between female dyads, M:M between males dyads and F:M inter-gender dyads.

Joint space use metric	Comparison group		Wilcoxon rank sum	
Home range overlap	ES All	CS All	W	P
95% FKP	0.44 (0.01)	0.28 (0.01)	106805	<0.001
50% Core	0.14 (0.01)	0.11 (0.01)	76962	0.06
Volume of intersection				
95% FKP	0.22 (0.01)	0.12 (0.01)	27397.5	< 0.001
50% Core	0.06 (0.01)	0.09 (0.01)	77171	0.05
Home range overlap	ES F:F	CS F:F	W	P
95% FKP	0.46 (0.02)	0.28 (0.02)	10317	< 0.001
50% Core	0.13 (0.02)	0.11 (0.02)	6941	0.21
Volume of intersection				
95% FKP	0.24 (0.02)	0.15 (0.02)	2475	0.001
50% Core	0.10 (0.02)	0.07 (0.02)	1818.5	0.16
Home range overlap	ES M:M	CS M:M	W	P
95% FKP	0.40 (0.02)	0.40 (0.04)	2285	0.92
50% Core	0.12 (0.02)	0.20 (0.03)	1309	< 0.001
Volume of intersection				
95% FKP	0.19 (0.02)	0.15 (0.03)	670	0.29
50% Core	0.07 (0.02)	0.09 (0.03)	355.5	0.05
Home range overlap	ES F:M	CS F:M	W	P
95% FKP	0.45 (0.02)	0.26 (0.02)	28970.5	< 0.001
50% Core	0.16 (0.01)	0.09 (0.01)	22312.5	0.001
Volume of intersection				
95% FKP	0.23 (0.02)	0.10 (0.01)	7621.5	< 0.001
50% Core	0.10 (0.01)	0.04 (0.01)	5715	0.01

Chapter 2

Raccoon Den Use as a Function of Experimental Manipulations of Resource Distribution

ABSTRACT

The presence of clumped food is often associated with changes in home range size and overlap and may affect other components of an animal's home range use. For example den use may be affected. I investigated the response of denning behaviors by raccoons (*Procyon lotor*) to a change in resource availability and distribution. The study site was divided into two treatments, each receiving 35 kg of supplemental food per week. An experimental treatment had the food placed in a large pile at the same location every week. The control treatment had multiple small piles (ca .25 kg. ea.) placed in an irregular non-repetitive pattern throughout the study area. Forty seven raccoons were radio collared and tracked over 2 years resulting in the location of 596 den sites, collectively used 694 times. Few quantitative differences were found between the two populations inhabiting the treatment areas for rates of den reuse, communal denning, spatial density of dens and den:den proximity. However on the experimental treatment site, a greater variety of individuals reused dens, denned communally, and denned closer together throughout the year. In contrast on the control treatment site communal denning primarily occurred October through December. A subset of 8 male raccoons, 4 from each treatment, was studied more intensively and showed differences in den reuse rates and the distance moved between den sites. Males on the experimental treatment site reused dens 27% of the time and moved an average of 504 meters between den sites. In

contrast, males on the control treatment site reused dens 10% of the time and moved an average of 659 meters between den sites. Collectively these differences, suggest the presence of the clumped resource altered the denning behavior of the raccoons.

INTRODUCTION

Dens are natural or man-made structures used by animals for parturition, diel rest, or extended protection against the weather. Dens are an important habitat component of an animal's home range selection and use (i.e. Johnson's [1980] second and third order selection), and the way in which an animal chooses and uses a den can be fundamental to its survival and reproductive success. Den sites are selected based on a combination of sociobiological needs and so selection may vary as a function of spatial and temporal requirements. Den site assessment and management have been applied as a means of assessing and adjusting animal population levels (Henner et al. 2004), and as a method for understanding social behavior (Doty et al. 2006, Frafjord et al. 2003).

Carnivore species often demonstrate both solitary and communal denning. Communal denning is the result of a variety of physiological, spatial and social behaviors (Endres and Smith 1993, Mohelman 1989). Thermoregulation against cold temperatures is an ascribed trigger for communal denning, but relatedness, protection from predators, reduced den availability, the broader social structure of the taxon, and proximity to forage patches are also attributed causes (Hwang et al. 2007, Loureiro et al. 2007, White 2007). Spatial shifts in resource availability often correlate with gender and with temporal changes in home range size and

overlap, and so the availability of food or other limiting resources may not only influence the formation and dissolution of spatial groups among carnivores, but also denning behaviors such as dispersion, location, rates of communal denning, den reuse, and the distance between successively used dens (Erlinge and Sandell 1986, Norbury et al. 1998, Quinn and Whisson 2005).

Here I use an experimental framework to examine potential links between the denning behavior of raccoons (*Procyon lotor*) and the distribution of resources. The raccoon is ubiquitous across much of North America, and the ecology of this species is amongst the best known of all mammals (Gehrt 2003). In raccoons, denning has been studied extensively from the standpoint of how landscape and habitat influence den site selection. Den site availability has been discounted as a primary effect on the first order aspects of raccoon distribution (Mech et al. 1966, Rabinowitz and Pelton 1986), but is potentially important for second or third order habitat selection, influencing the selection of location of home ranges and the relative use of areas within home ranges (Endres and Smith 1993, Henner et al. 2004, Huck et al. 2008, Waser and Jones 1983).

Little, however, has been published about potential links between third order spatial structure and denning behavior. Raccoons shift home ranges to maximize resource access (Chapter 1, Gerht and Fritzell 1997, 1998). Such resource-induced changes in home range size or location may also produce a corresponding change in denning behavior and changes in spatial patterns in the location of den sites. In this study I focus on the importance of clumped resource distributions for denning behavior. To simulate a resource distribution change an

experimental feeding site was created and maintained for 3 years. Raccoon denning behavior on this experimental treatment site was compared to a similar control site that received the same quantity of food additions but without the clumping of those foods. Clumped resources can induce decreases in home range size and increases in home range overlap in raccoon populations (Chapter 1), and these changes could alter both the short term availability of den locations and den site fidelity (Hauver 2008, O'Donnell and DeNicola 2006, Prange et al. 2004). I expected these changes to manifest themselves in differences between the experimental and control treatment populations in the following ways. Firstly there would be changes in the social use of dens, resulting in an increase in the amount of den reuse (including reuse of a den by a single animal and reuse of a single den site by multiple animals), an increase in communal denning, and an increase in the number of animals found denning in close proximity. Secondly, I expected that if overlap of core areas increased (Chapter 1) so would the number of animals utilizing den structures within a core area, thus resulting in an increasingly clustered dispersion of dens. Thirdly I expected that increases in this clustering of dens would be negatively correlated with the distance moved between subsequently used den locations.

METHODS

Study Area

Field work occurred in and around the University of Missouri's Thomas S. Baskett Research and Education Center (hereafter, Baskett). Baskett is located 8 km east of Ashland, MO USA (lat. 38.7N, long. 92.2W). Much of Baskett was

previously used as farm and grazing lands, but has now reverted to the secondary mixed oak-hickory forest communities found throughout much of central Missouri. Baskett is bounded on all sides by a mix of private and public land (Mark Twain National Forest). Radio telemetry locations collected during the course of this study covered approximately 15.75 km² (Chapter 1), which included the 9 km² Baskett and an additional 6.75 km² of public and private lands immediately adjacent to Baskett. With the exception of scattered rural dwellings, the habitats on these adjacent lands are similar to those found on Baskett. Raccoon densities on the study site are approximately 35 animals per km² and cross-site comparisons suggest the scale of the resource additives were insufficient to increase this density (Monello 2009).

Baskett is bisected east/west by a paved road (Route Y), and as such the study site was divided into two treatment areas (Figure 1). One treatment area (hereafter the experimental site, ES) was contained within lands north of Route Y and one treatment (hereafter the control site, CS) within lands south of Route Y. Both areas contain a fifth order stream, several smaller perennial or intermittent low order-streams, as well as several ponds and small lakes. Stand age and species diversity are similar on the two treatment areas (Belden and Pallardy 2009, Dijak and Thompson 2000, Fan et al. 2003).

Treatments

To simulate a persistent and abundant clumped resource patch, 18-36 kg of dry dog food were placed weekly at a single location on the ES from January 2006 through December 2008. Data generated from motion sensitive cameras

showed the clumped resource patch was heavily used by raccoons, often with multiple individuals visiting the feeding locale simultaneously (Monello 2009). The CS received the same amount of dry dog food as placed in the ES. However, instead of the creation of a clumped resource at a single location, the food was subdivided into multiple small piles (ca 0.25 kg. ea.) which were placed at least 50 m apart in an irregular pattern throughout the study area. Placement of food in the CS was spatially randomized so that the location of these small food piles was not predictable from week to week.

Capture and handling

Between March 2007 and June 2008 a total of 65 adult raccoons (37 ES, 28 CS) were captured and fitted with radio transmitters. Approximately equal numbers and proportions of females (18 ES, 14 CS) and males (19 ES, 14 CS) were collared. Raccoons were captured using Tomahawk box traps (Tomahawk Live Traps, Tomahawk WI). Traps were placed along drainage courses, maintained dirt roads or trails. Depending on time of year, traps were baited with either a canned fish or a sweet bait formulation of strawberry jam and mashed sugared donuts. Baited traps were checked daily between 0600 and 0800. Procedures for trapping, anesthetizing, and handling raccoons followed University of Missouri Animal Care and Use Protocol 3927.

Raccoons were anesthetized with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine (1 mg/kg) (Belant 1995). Once anesthetized, the animals were removed from the trap and sexed, weighed and

measured. Raccoons were marked with numbered ear tags in both ears (#1005-1 Hasco Tag Company, Dayton KY). Each animal was aged by tooth eruption, tooth wear and past capture history. Raccoons were classified into 5 age classes (Grau et al. 1970). Animals age two years or greater were classified as adults and fitted with a radio transmitter collar (ATS, Isanti MN; Telonics, Mesa AZ). Collars weighed 65 grams and transmitted at frequencies between 150 and 152 MHz. Each collar was outfitted with a mortality signal that changed the collar pulse rate from 55 pulses per minute (ppm) to 110 ppm after 24 hours of immobility.

Den site data collection

Dens were located by utilizing a hand held 3 element yagi antennae tuned to the collar's frequency. Frequencies were tracked until the exact den site was located and a hand-held global positioning system unit (GPS) was used to record Universal Transverse Meridians (UTMs) (NAD 83) for each den site. To minimize biases associated with over or undersampling particular individuals, two different sampling routines were used. Four animals from each study site (2 females, 2 males) were randomly selected without replacement to create a group of 8 individuals. Sampling groups remained static except for the removal of members due to death or collar loss. Groups falling below 5 in number were supplemented when additional animals were collared. Each group of 8 animals was sampled every 2 weeks between March 2007 and December 2008. Den sites were located between 0600 and 1800. All animals in a group were scanned for from study area roads on the initial sampling day of the two week period. Animals not

located or detected during the first sampling day were noted and repeatedly searched for during the two week period. Once located, individuals were not relocated until the next two week sampling period.

Between June and December 2008 a second sampling routine was also utilized. Eight males (4 ES, 4CS) were randomly selected, and thereafter den sites of these individuals were located for 2 successive days per week. Data collection procedures were the same for both routines, but once the second sampling routine began the 8 males were removed from the biweekly sampling.

Den type choice could potentially influence denning behaviors and located dens were classified as one of six types of den or diel resting sites: downed logs, snags, tree cavities, squirrel nests, rock crevices, and ground burrows. The presence of additional radio collared raccoons communally or proximally denning was determined by scanning for all assigned collar frequencies. I defined communal denning as the presence of more than one adult raccoon in a diel resting site and dens were considered proximal to another raccoon if they were within 100 meters of each other. Den sites were marked with plastic flagging and metal forestry tags. Tags were inscribed with the dates and collar frequency to facilitate the identification of future den site reuse by the same or different individuals.

Data analysis

Females reuse the same den for extended time periods during parturition and rearing (in Missouri, approximately March through August, Schwartz and

Schwartz 2001). Therefore, only dens reused by females outside of this period were included in analyses of den reuse, except where a den reuse location was originally detected outside of parturition. Daily dens locations for the subgroup of eight males were analyzed separately from the semi-monthly sampling routine. The mean number of locations for the primary sample routine individuals was 11.66 ± 2.8 and for the more intensely sampled 8 male subset the mean number of locations was 24.25 ± 3.85 . Prior to testing for differences in denning behaviors I calculated Pearson's correlations to evaluate potential interactions between the communal denning, den reuse and proximal denning (Doncaster and Woodroffe 1993, Endres and Smith 1993). A 2-way analysis of variance (ANOVA) was used to compare both den type and den behaviors between treatments, genders and years. A 2- way ANOVA was also used to test the eight male subset for differences in den type use and differences in denning behaviors between treatments,

Spatial dispersion of den locations was tested using the nearest neighbor tool in ArcGis 9.3 (ESRI, Redlands CA). Den site selection has been linked to resource configuration and availability and for carnivores in particular den dispersion may affect their social behavior (Henner et al. 2004, Loureiro et al 2007). Therefore patterns of dispersion of raccoon home ranges and core areas should also be observed in den locations (Levings and Traniello 1981, Pitt et al. 2008). Clark and Evans (1954) developed the nearest neighbor technique based upon the ratio between the observed mean nearest neighbor distance and the expected distance. The nearest neighbor ratio (NNR) can range from 0 (perfect

aggregation) to ≥ 2.15 (perfect uniformity). A value of 1 indicates a random dispersion pattern (Figure 2). Scores are validated or refuted using a Z test (Desmond et al. 2000, Levings and Franks 1982). One hundred percent minimum convex polygons (MCP) of den locations were generated to provide an area of the minimum enclosing boundary to assess spatial dispersion. NNR values were calculated annually and for combined years, subdividing the data by gender for each treatment. The subset of eight intensively monitored males was evaluated separately from the primary sampling procedure. Daily distance moved between den sites was calculated for the secondary sampling protocol subset of eight males. Calculations were accomplished with point distance tools in ArcGis 9.3 and compared using an ANOVA.

RESULTS

Den sites from a total of 47 animals (26 ES, 21CS) were analyzed. This included 28 animals (14 ES, 14CS) who were present throughout the study and 19 (12 ES, 7 CS) who were present for only one year of the study. Eighteen additional raccoons were also collared and located but did not result in enough den locations per animal to allow analysis. Dens were located 489 (261 ES, 228 CS) times over the course of the study. An additional 205 (100 ES, 105 CS) dens were located for the subsample of eight intensively studied males. Raccoons on the study site used all six types of natural structures for denning, but primarily denned in tree cavities (Figure 3, Figure 4). Diverse species of trees were utilized, including oaks (*Quercus spp*), hickories (*Carya spp*), Eastern red cedar (*Juniperus virginiana*), Eastern sycamore (*Plantanus occidentalis*), Basswood (*Tilia americana*), black walnut (*Juglans nigra*), sugar maple (*Acer sacchrum*),

and elms (*Ulmus* spp.). Empty fox squirrel (*Sciurus niger*) and gray squirrel (*S. carolinensis*) nests were also used throughout the year, as were snags and the numerous rock outcrops, crevices and cavities that occur in the extensive limestone karst formations in the area. Occasionally raccoons were found in ground hog (*Marmota monax*) burrows. No significant differences (ES:CS df = 46, $F = 2.01$, $p = 0.08$, ES 8 males:CS 8 males df = 11, $F = 0.016$, $p = 0.90$) existed in the extent of use of different structure types between treatments for either sampling routine (Figure 3, Figure 4). There were also no significant differences in the use of different structures for dens as a function of gender or year.

Excluding the eight male subset, communal denning, den proximity and den reuse did not differ by year between treatments (for all comparisons $p \geq 0.18$). Den reuse for females outside of the reproductive period and for males the entire year included both animals who reused their own dens (11 ES, 3 CS) and animals who used dens that had previously been used by other raccoons (6 ES, 1CS). CS animals only reused dens of the same gender, but 3 cases of mixed gender reuse were found on the ES. Seventeen ES raccoons (6M, 11 F) and 13 CS raccoons (5M, 8F) denned in proximity over the course of the study. While proximal denning did not differ between treatments, in 2007 the ES had 4 females that were found denning within 50m of each other repeatedly for a 13 week period. This grouping was not repeated in 2008, although two of the females denned in close proximity to different females and males for shorter periods. No such extended proximal incidents were detected on the CS.

Communal denning differed between genders. Males were found communally denning more frequently than females on both treatments ($df = 46$, $F = 6.19$, $p = 0.02$). Nine males (ES 5, CS 4) were found communally denning a total of 9 times (ES 5, CS 4) and 6 females (ES 4, CS 2) 4 times (ES 3, CS 1). One of the 5 CS communal denning events occurred in June while the remaining 4 events occurred late September through January. Four of the 8 ES communal dens were found between May and August and the remaining 4 between October and January. Three of the males (1ES, 2CS) were found communal denning again as part of the June through December 2008 intensive sampling protocol (Appendix A).

For the subset of eight intensively studied males there were neither significant interactions between individual denning behaviors, nor significant differences in rates of den reuse ($df = 7$, $F = 4.71$, $p = 0.07$) or communal denning ($df = 7$, $F = 4.56$, $p = 0.07$) than CS males. However, the 4 ES males had mean reuse and communal denning rates 2.4 times greater than the 4 CS males. The rate of communal denning was 11% for the 4 ES males and 3% for the CS males. Within both treatments males reused dens twice as often as they communally denned. The 4 ES males had a 20% rate of den reuse including one case of inter-gender den reuse, while den reuse was only 8.6% among the 4 CS males. For the 8 males neither treatment had any occurrences of proximal denning. One of the three CS male communal dennings events occurred in June and the other 2 events occurred in December, whereas 6 of the 11 ES communal

denning events occurred in July and August, 4 in September and 1 in December (Appendix B).

Within each sex, den dispersion generally did not differ between populations regardless of year (Table 1). Dens were uniformly dispersed for gender and year in both treatments with a mean NNR of $2.29 \pm \text{SD } 1.50$. NNRs also indicated uniform dispersion when single gender locations were combined for 2007 and 2008 except for ES females who had a clustered dispersion (0.67). Both treatments generated clustered dispersion values when 2007 and 2008 male and female dens were combined, but the ES dens differed from CS dens in that ES NNRs were clustered when genders were combined for any single year. All dens were clustered for the eight male subset regardless of treatment. Although dispersion differed little across year, gender and treatment, mean ES MCPs were 30% smaller than corresponding CS MCPs. Sequential inter-den movement distances were also smaller for the ES portion of the 8 male subset ($F = 4.089$, $p = 0.045$). ES mean sequential inter-den distance was $504 \text{ m} \pm \text{SD } 52.38$ and 659 m ($\text{SD} = 49.85$) for the CS. The maximum distance moved for any ES subset male was 1493 m and 1941 m, respectively.

DISCUSSION

Shifting resource availability and distribution is considered a primary factor initiating changes in social structure (Geffen et al. 1996, MacDonald 1983, Moehlman 1989). The presence of the clumped resource on the experimental treatment site was therefore expected to facilitate communal denning and other denning behaviors indicative of increased sociality under an assumption that

such behaviors bear little cost. Few quantitative differences were found between the treatments for rates of den reuse or communal denning, and for the spatial density and proximity of dens. However, for the population inhabiting the experimental treatment, a greater variety of individuals reused dens, denned communally, and denned closer together over all seasons of the year, and for the subset of intensively studied male raccoons, those inhabiting the experimental site showed mean den reuse rates 2.5 time larger than the control site individuals. The ES males also had decreased distances moved between subsequently used den sites. These differences suggest that the presence of a clumped resource altered the denning behavior of raccoons.

Given that extensive occurrences of communal denning in carnivores are generally only found in group-living species, are usually precluded among females during parturition, and can be sex specific (Bekoff et al. 1984, Ralls 2002), it was not surprising to find communal denning most often between males. Qualitative treatment site differences in communal denning were only found in the more intensively sampled eight male subset and not in the bi-weekly sampled raccoons. Communal denning among raccoons is most prevalent during the fall and winter, offering thermo-regulatory benefits, but has occasionally been noted in raccoon populations during the warmer months (Gerht and Fox 2004, Gehrt and Spencer 1990, Hauver 2008). Communal denning among CS individuals occurred mainly during the cooler months, while ES animals communally denned in all seasons.

Detection of differences between the treatment sites in the occurrence of social denning behaviors, though not gender correlated, was also limited to comparisons of the subset of data derived from the eight intensively sampled males. Den reuse was detected more frequently than communal denning. Reuse of a den by one or more individual is potentially a less costly response to clumped resource induced spatial aggregation than communal denning (Hoffmann and Gottschang 1977, Loureiro et al. 2007) and was found on both treatment sites more often in 2008 than 2007. This did not necessarily represent an increase in den reuse as about 25% of the dens reused in 2008 were first detected in 2007 and all of these were among females. Such occurrences of den reuse over time have also been reported in other studies and are attributed to the presence of clumped and consistent resources (O'Donnell and DeNicola 2006, Prange et al. 2003).

Positive associations of male raccoons at diel resting sites are not infrequent, but clustering of female diel locations is less well known (Hauver 2008, Pitt et al. 2008). Although temporally extended familial bonds have been shown to affect the makeup of spatial groups they do not usually extend beyond subsequent mating seasons, and when they do, are usually the result of an abundant and predictable resource (Eide et al. 2004, Ratnayeke et al. 2002). The smaller distances moved between successive den sites among the four ES male raccoons, the overall smaller MCPs enclosing den locations, and the lower NNR collectively indicate a clustered dispersion of ES raccoons, and provide additional support to the hypothesis that raccoon social and spatial behavior as it relates to

den use is a result of the extent to which resources are spatially and temporally predictable.

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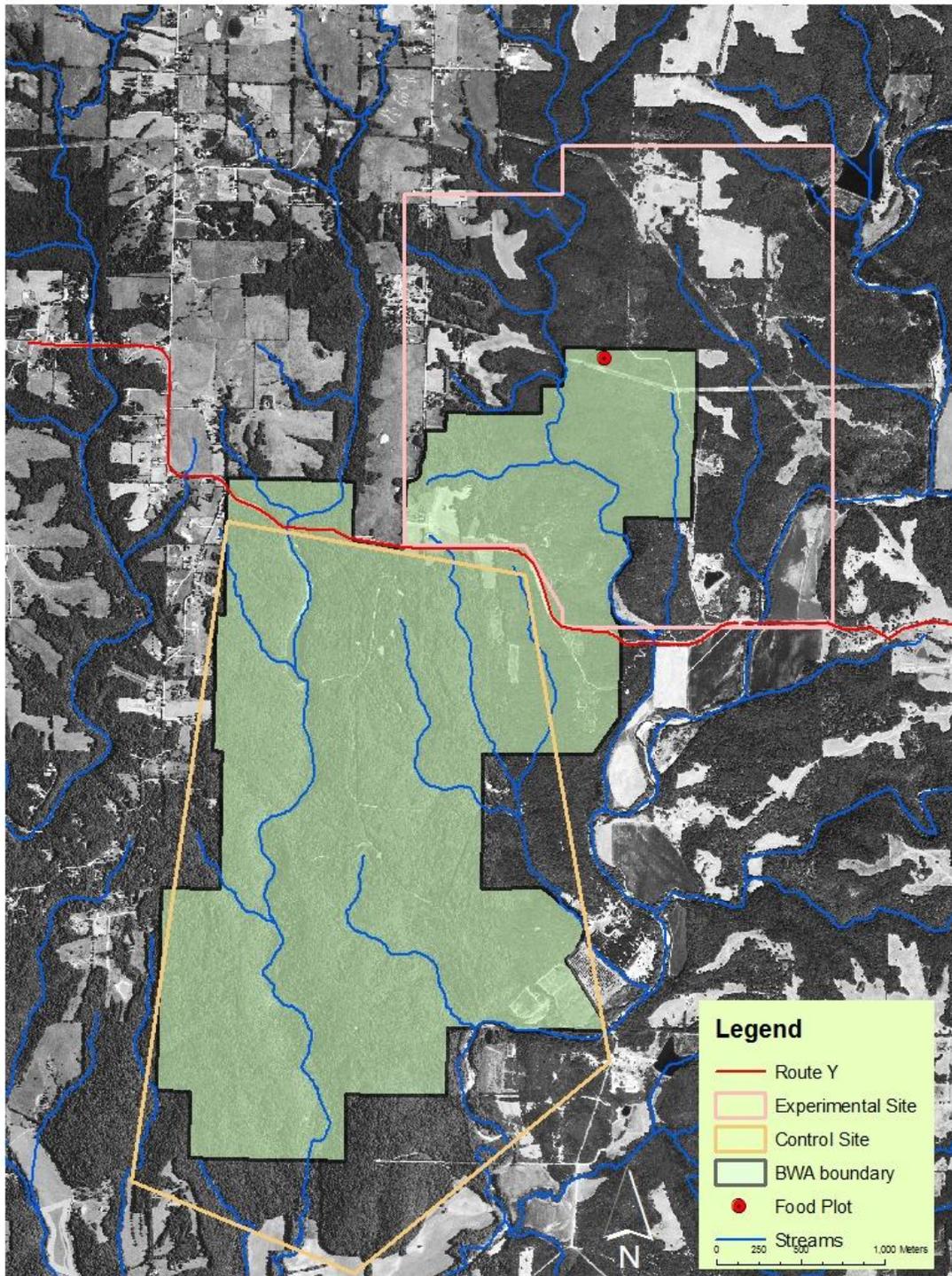


Figure 1. Map of study site and treatment areas. Study site located 8 km east of Ashland Missouri and includes all of Thomas S. Baskett Research and Education Center and portions of Mark Twain National Forest.

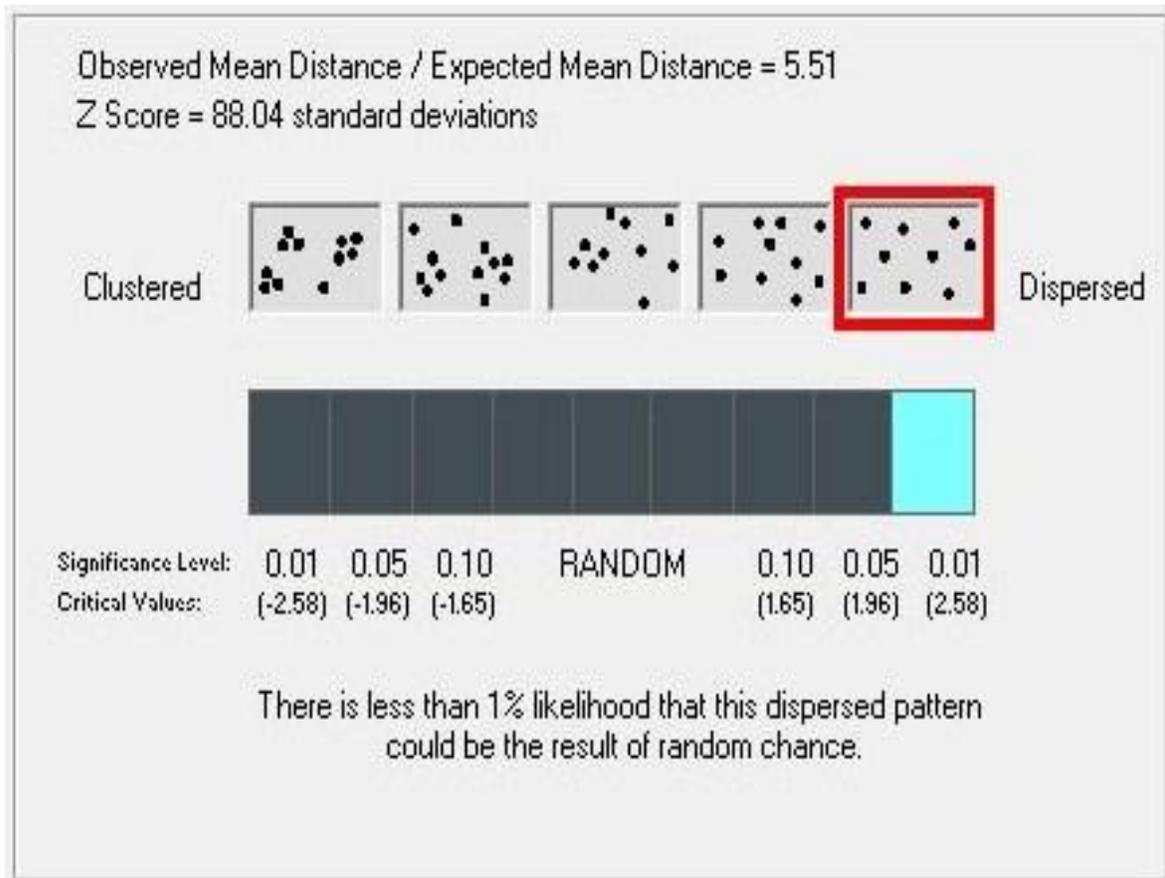


Figure 2. Example of ArcGIS generated output for nearest neighbor analysis used to reveal dispersion patterns in den locations. Based upon the Clark and Evans (1954) ratio between the observed mean nearest neighbor distance and the mean expected distance, the nearest neighbor ratio (NNR) is a measure of the dispersion. The NNR ranges from 0 (clustered) to ≥ 2.15 (dispersed). A value of 1 indicates a random dispersion pattern.

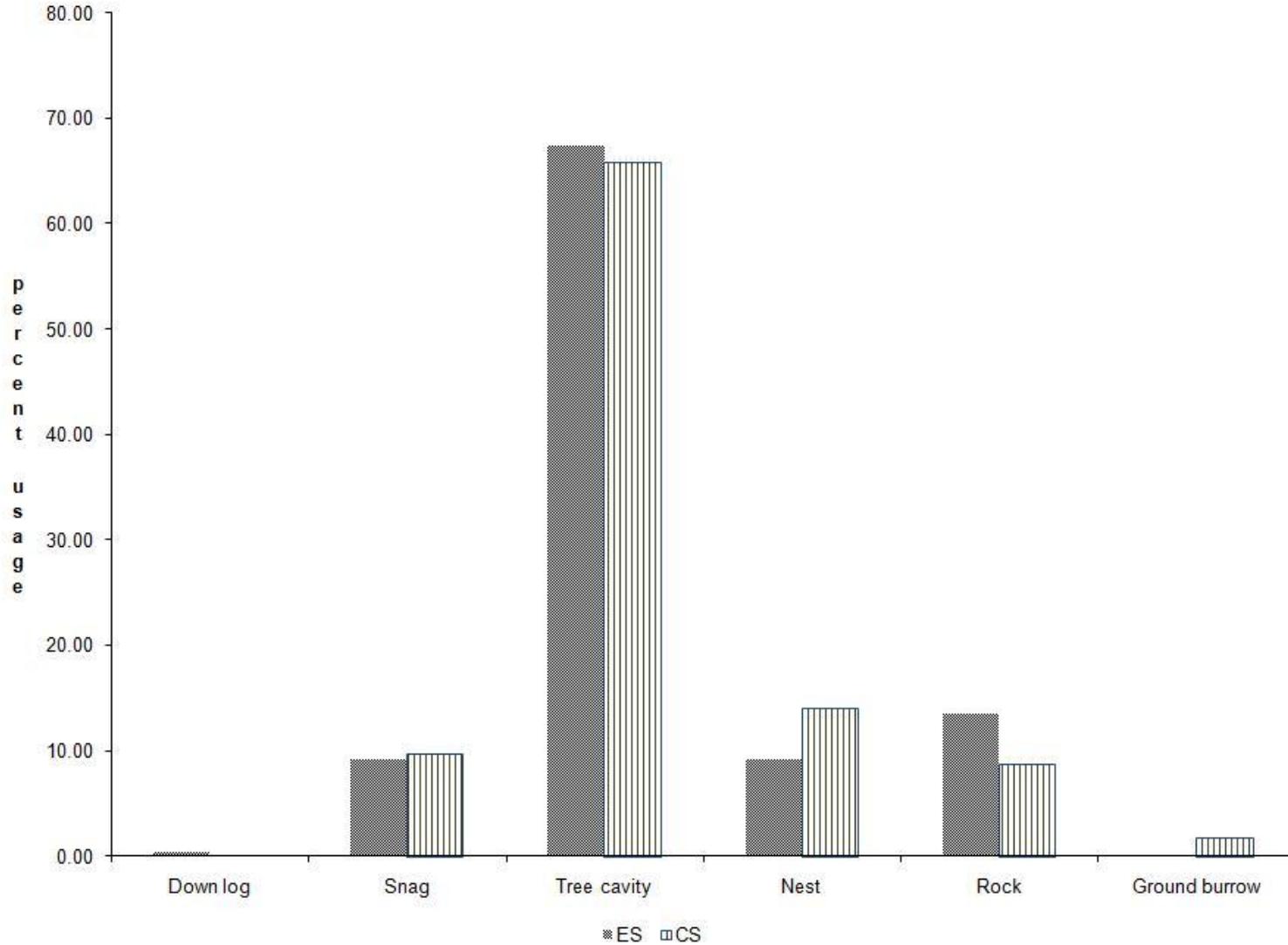


Figure 3. Percent usage of six types of den structures utilized by male and female raccoons on (ES) experimental and (CS) control treatment sites between March 2007 and December 2008. Solid bar depicts usage on the experimental treatment (ES) site and striped bar on the control treatment site (CS).

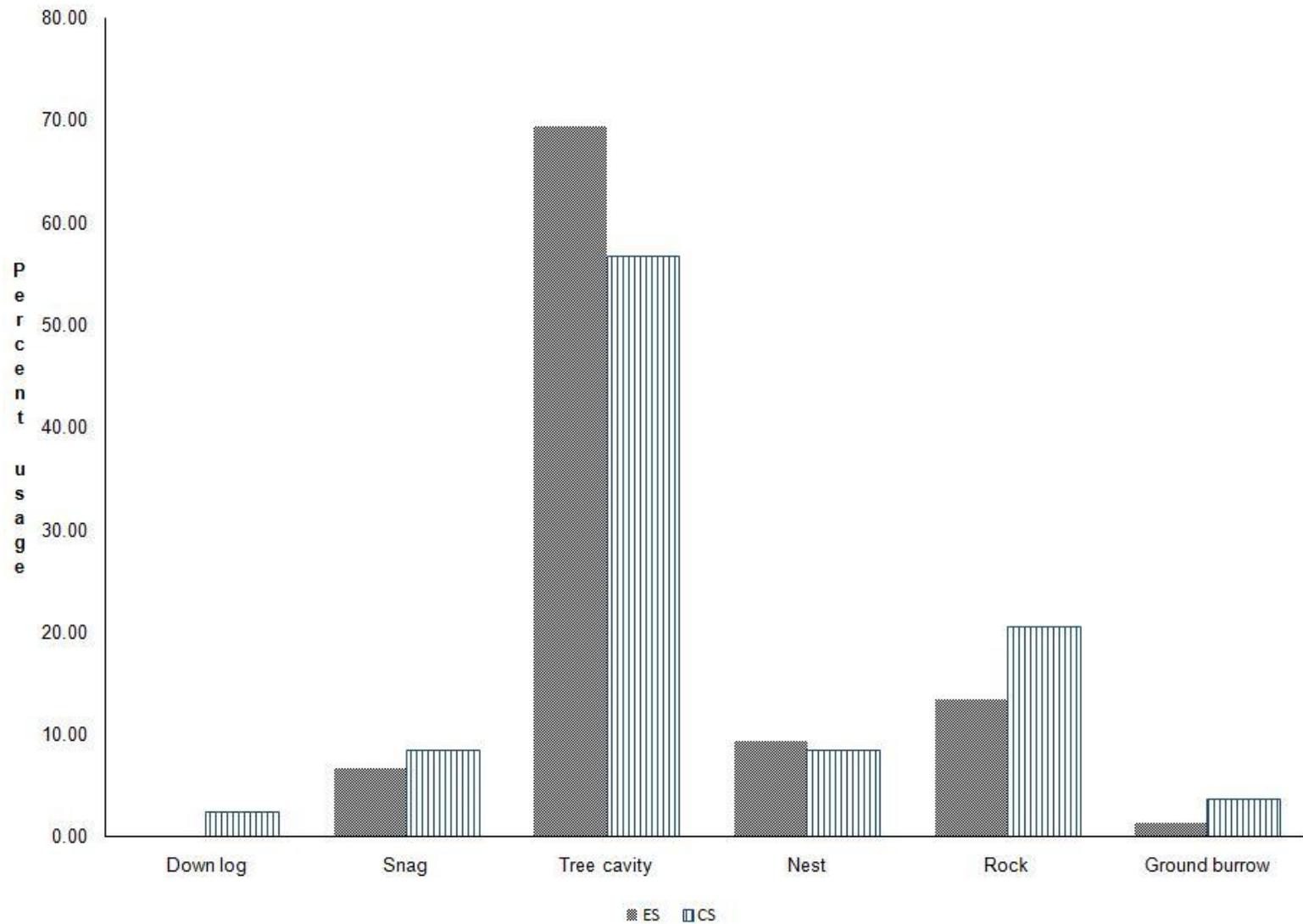


Figure 4. Percent usage of six types of den structures utilized by 8 male raccoons located two successive days per week between June 2008 and December 2008. Solid bar depicts usage on the experimental treatment (ES) site and striped bar on the control treatment site (CS).

Table 1. Spatial dispersion, nearest neighbor ratio (NNR), and dispersion of den area for male, female and combined gender den areas between March 2007 and December 2008. Data is subdivided for individuals inhabiting the (ES) experimental (ES) and the control site (CS) treatments. Subscript notated males were located two successive days per week between June 2008 and December 2008.

Year	Treatment	Female			Male			Combined Gender		
		Dispersion	NNR	Area	Dispersion	NNR	Area	Dispersion	NNR	Area
2007	CS	Uniform	1.13	4.18 km ²	Uniform	1.19	4.26 km ²	Random	0.98	5.20 km ²
	ES	Uniform	2.58	2.37 km ²	Uniform	1.22	2.28 km ²	Clustered	0.76	3.14 km ²
2008	CS	Uniform	1.07	1.47 km ²	Uniform	5.71	1.62 km ²	Random	0.96	2.56 km ²
	ES	Uniform	2.33	2.00 km ²	Uniform	3.20	2.47 km ²	Clustered	0.78	3.09 km ²
07 + 08	CS	Random	1.01	4.18 km ²	Uniform	1.16	4.37 km ²	Clustered	0.89	5.20 km ²
	ES	Clustered	0.67	2.91 km ²	Random	0.97	2.71 km ²	Clustered	0.62	4.63 km ²
2008	CS _{4 males}				Clustered	0.75	0.98 km ²			
	ES _{4 males}				Clustered	0.49	0.42 km ²			

Appendix A. Table of reused, proximal and communal dens for experimental and control site raccoons. ID indicates site, gender and collar frequency of individual (e.g. ESF706 is experimental site female 706). Age indicates age class based on tooth wear. Reuse indicates when den location was previously used by the same animal (self) or by another animal (ID given). Reused dens marked "Natal" indicates reuse of same den for extended period by a female during parturition (March through August). Individual occurrences appear more than once in table to provide age class information for each animal involved.

ID	Age	Reuse	Communal	Proximal	Date
ESF185	IV			ESF507	28-Sep-07
ESF445	II	Natal		ESF947,ESF065,ESF268	18-Mar-07
ESF445	II	Natal		ESF947,ESF065,ESF269	24-Mar-07
ESF445	II	Natal		ESF947,ESF065,ESF270	21-Apr-07
ESF445	II	Natal		ESF947,ESF065,ESF271	28-Apr-07
ESF445	II	Natal		ESF947,ESF065,ESF272	5-May-07
ESF445	II	Natal		ESF947,ESF065,ESF273	6-Jun-07
ESF507	IV			ESF185	28-Sep-07
ESF706	III			ESM885	14-May-07
ESF706	III	Self			6-Jun-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	18-Mar-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	24-Mar-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	21-Apr-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	28-Apr-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	5-May-07
ESF947	IV	Natal		ESF445,ESF065,ESF268	14-May-07
ESF947	IV	Self		ESF445,ESF065,ESF268	6-Jun-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	18-Mar-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	24-Mar-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	21-Apr-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	28-Apr-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	5-May-07
ESF065	IV	Natal		ESF947,ESF445,ESF268	14-May-07
ESF065	IV	Self		ESF947,ESF445,ESF268	6-Jun-07
ESF065	IV			ESF405	2-Oct-07
ESF226	II			ESM885	11-Sep-07
ESF268	III	Natal		ESF947,ESF445,ESF065	18-Mar-07
ESF268	III	Natal		ESF947,ESF445,ESF065	24-Mar-07
ESF268	III	Natal		ESF947,ESF445,ESF065	21-Apr-07
ESF268	III	Natal		ESF947,ESF445,ESF065	28-Apr-07
ESF268	III	Natal		ESF947,ESF445,ESF065	5-May-07
ESF268	III	Natal		ESF947,ESF445,ESF065	14-May-07
ESF268	III			ESM746	16-Oct-07
ESF364	III			ESM087	23-May-07
ESF1405	IV		ESF880		13-Dec-07
ESF880	III		ESF1405		13-Dec-07

Appendix A

ID	Age	Reuse	Communal	Proximal	Date
ESM326	II		ESM125		28-Apr-07
ESM326	II		ESM125		29-Apr-07
ESM326	II			ESM125	5-May-07
ESM746	II			ESF268	16-Oct-07
ESM885	III			ESF706	14-May-07
ESM885	III			ESF226	11-Sep-07
ESM087	II			ESF364	23-May-07
ESM125	II		ESM326		28-Apr-07
ESM125	II		ESM326		29-Apr-07
ESM125	II			ESM326	5-May-07
ESF706	III	Self			14-Dec-08
ESF947	IV	ESM700			11-Jul-08
ESF164	III			ESM087,ESM287	14-Nov-08
ESF268	III			ESF910	20-Jun-08
ESF268	III		ESM700		14-Oct-08
ESF870	IV	Self			21-Oct-08
ESF890	IV	Self			14-Dec-08
ESF910	III	Self			22-May-08
ESF910	III	Self		ESF268	20-Jun-08
ESF910	III	Self			8-Aug-08
ESM326	III	ESM700	ESM700		9-Jan-08
ESM326	III	ESM700			12-Jan-08
ESM087	III			ESM287, ESF164	14-Nov-08
ESM287	III			ESM087,ESF164	14-Nov-08
ESM700	II				9-Jan-08
ESM720	II		ESM760		7-Aug-08
ESM720	II		ESM760		30-Aug-08
ESM760	II		ESM720		7-Aug-08
ESM760	II		ESM720		30-Aug-08
ESM920	II	Self			17-Jul-08
ESM920	II	ESM345			9-Aug-08
CSF148	IV			CSM985	21-Sep-07
CSF405	III			CSM465	30-Oct-07
CSF485	IV			CSF015	6-Nov-07
CSF665	IV			CSM786,CSF003	18-May-07
CSF922	V			CSM207	18-Oct-07
CSF003	IV			CSF665,CSM786	18-May-07
CSF015	III			CSM985	31-May-07
CSF015	III			CSF485	6-Nov-07
CSM465	IV			CSF405	30-Oct-07
CSM786	III			CSM665,CSF003	18-May-07
CSM985	V			CSF015	31-May-07
CSM985	V			CSM964	21-Sep-07
CSM826	III		CSM964	CSM985	21-Sep-07
CSM826	III			CSM964	6-Nov-07

Appendix A

ID	Age	Reuse	Communal	Proximal	Date
CSM964	III		CSM826	CSM985	21-Sep-07
CSM964	III			CSM964	6-Nov-07
CSM207	III			CSF922	18-Oct-07
CSF565	III	CSF485			23-Nov-08
CSF665	IV			CSF764	17-Jan-08
CSF764	III			CSF665	17-Jan-08
CSF764	III	Self			29-Dec-08
CSM207	III			CSF922	9-Feb-08
CSM624	III		CSM385		6-Jun-08
CSM624	III	CSM826	CSM385, CSM826		24-Dec-08
CSM964	III		CSM826		26-Dec-08

Appendix B. Table of reused, proximal and communal dens for eight intensively sampled males experimental and control site raccoons. ID indicates site, gender and collar frequency of individual (e.g. ESF706 is experimental site female 706). Age indicates age class based on tooth wear. Reuse indicates when den location was previously used by the same animal (self) or by another animal (ID given). Individual occurrences appear more than once in table to provide age class information for each animal involved.

ID	Age	Reuse	Communal	Proximal	Date
ESM085	IV		ESM342		5-Jun-08
ESM085	IV		ESM342		10-Jun-08
ESM085	IV	Self			18-Jun-08
ESM085	IV	Self			25-Jun-08
ESM085	IV	Self			27-Jun-08
ESM085	IV	Self			2-Jul-08
ESM085	IV		ESM342		15-Jul-08
ESM085	IV	Self	ESM342		9-Sep-08
ESM085	IV	ESM342	ESM342		30-Sep-08
ESM085	IV	ESM342			11-Nov-08
ESM342	II		ESM085		5-Jun-08
ESM342	II		ESM085		10-Jun-08
ESM342	II	Self			25-Jun-08
ESM342	II	Self			9-Jul-08
ESM342	II		ESM085		15-Jul-08
ESM342	II		ESM085		9-Sep-08
ESM342	II	Self	ESM085		30-Sep-08
ESM342	II	Self			11-Nov-08
ESM342	II	Self			9-Dec-08
ESM700	II	ESM326			30-May-08
ESM700	II	Self			9-Jul-08
ESM700	II		ESF268		14-Oct-08
ESM700	II	Self,ESF268			21-Oct-08
ESM700	II	Self ESF268			4-Nov-08
ESM700	II	Self			9-Dec-08
ESM860	II	Self			30-Sep-08
ESM860	II	ESF780			14-Dec-08
CSM826	III	CSM385			19-Jun-08
CSM826	III	CSM385			20-Jun-08
CSM826	III	Self			27-Jun-08
CSM826	III	Self,CSM385			8-Jul-08
CSM826	III	Self			14-Oct-08
CSM826	III	Self	CSM624,CSM385		24-Dec-08
CSM826	III	CSM964			26-Dec-08
CSM385	V		CSM624		6-Jun-08
CSM385	V	CSM826	CSM826,CSM385		24-Dec-08
CSM810	II	Self			30-Sep-08
CSM810	II	Self			23-Nov-08

Appendix C. Matrices of home range overlap values based on 95% fixed kernel polygons for experimental site and control site raccoons. ID indicates site, gender and collar frequency of individual (e.g. ESF706 is experimental site female 706).

	ESF706	ESM085	ESF164	ESM185	ESF364	ESM885	ESF1405	ESM087	ESF890	ESM860	ESF947	ESM342	ESF226	ESM287	ESF780	ESM920	ESF268	ESM700	ESF870	ESM720	ESF910	ESM760
ESF706		0.22	0.30	0.57	0.45	0.38	0.56	0.47	0.45	0.47	0.38	0.10	0.62	0.30	0.70	0.32	0.30	0.20	0.22	0.30	0.41	0.32
ESM085	0.87		0.59	0.81	0.75	0.64	0.71	0.64	0.95	0.65	0.41	0.88	0.76	0.38	0.71	0.47	0.30	0.18	0.41	0.25	0.33	0.27
ESF164	0.62	0.34		0.88	0.89	0.66	0.84	0.86	0.84	0.88	0.40	0.37	0.88	0.64	0.59	0.28	0.26	0.08	0.09	0.34	0.49	0.39
ESM185	0.74	0.26	0.50		0.76	0.50	0.83	0.73	0.67	0.76	0.40	0.21	0.91	0.41	0.67	0.25	0.23	0.12	0.13	0.30	0.42	0.32
ESF364	0.58	0.24	0.50	0.75		0.45	0.79	0.70	0.65	0.67	0.36	0.21	0.78	0.43	0.54	0.20	0.11	0.03	0.09	0.25	0.29	0.26
ESM885	0.98	0.42	0.74	0.98	0.91		0.98	0.93	0.94	0.89	0.69	0.38	1.00	0.57	0.98	0.55	0.61	0.45	0.32	0.72	0.75	0.77
ESF1405	0.70	0.22	0.46	0.79	0.77	0.47		0.72	0.60	0.71	0.45	0.16	0.85	0.44	0.72	0.27	0.22	0.14	0.36	0.37	0.51	0.43
ESM087	0.74	0.25	0.59	0.88	0.84	0.56	0.90		0.61	0.83	0.44	0.18	0.90	0.52	0.73	0.27	0.22	0.15	0.15	0.39	0.51	0.44
ESF890	0.58	0.30	0.47	0.65	0.64	0.46	0.61	0.50		0.53	0.29	0.32	0.62	0.34	0.46	0.24	0.17	0.03	0.12	0.06	0.17	0.09
ESM860	0.61	0.21	0.49	0.75	0.67	0.44	0.73	0.68	0.54		0.33	0.15	0.72	0.43	0.54	0.20	0.17	0.08	0.08	0.22	0.38	0.25
ESF947	0.94	0.25	0.43	0.75	0.72	0.65	0.87	0.69	0.56	0.63		0.13	0.88	0.49	1.00	0.67	0.87	0.77	0.38	0.84	0.88	0.90
ESM342	0.24	0.52	0.37	0.39	0.38	0.34	0.29	0.28	0.59	0.27	0.13		0.34	0.17	0.10	0.20	0.08	0.00	0.20	0.02	0.04	0.00
ESF226	0.69	0.21	0.42	0.77	0.67	0.43	0.75	0.64	0.54	0.62	0.40	0.16		0.38	0.64	0.24	0.22	0.10	0.12	0.32	0.40	0.34
ESM287	0.69	0.22	0.64	0.72	0.77	0.51	0.81	0.77	0.62	0.77	0.46	0.17	0.79		0.64	0.27	0.29	0.15	0.17	0.38	0.57	0.45
ESF780	0.75	0.19	0.27	0.54	0.45	0.40	0.61	0.50	0.38	0.45	0.43	0.05	0.62	0.29		0.36	0.38	0.28	0.22	0.47	0.68	0.55
ESM920	0.89	0.33	0.34	0.53	0.42	0.59	0.59	0.48	0.52	0.43	0.76	0.24	0.60	0.32	0.94		0.82	0.72	0.61	0.72	0.76	0.78
ESF268	0.44	0.11	0.16	0.26	0.13	0.34	0.25	0.21	0.20	0.19	0.52	0.05	0.29	0.18	0.52	0.44		0.66	0.19	0.58	0.66	0.68
ESM700	0.34	0.08	0.06	0.15	0.04	0.29	0.19	0.16	0.04	0.10	0.52	0.00	1.00	0.11	0.44	0.44	0.76		0.27	0.56	0.51	0.58
ESF870	0.46	0.22	0.08	0.21	0.14	0.26	0.22	0.20	0.20	0.13	0.33	0.18	0.23	0.15	0.44	0.46	0.28	0.35		0.27	0.23	0.24
ESM720	0.40	0.08	0.20	0.30	0.26	0.37	0.39	0.33	0.07	0.23	0.45	0.01	0.38	0.22	0.58	0.35	0.53	0.44	0.17		0.91	0.93
ESF910	0.29	0.06	0.15	0.23	0.16	0.20	0.28	0.23	0.10	0.21	0.25	0.01	0.25	0.17	0.45	0.19	0.32	0.21	0.07	0.48		0.60
ESM760	0.30	0.06	0.16	0.23	0.19	0.28	0.32	0.26	0.06	0.18	0.34	0.00	0.29	0.18	0.48	0.26	0.43	0.32	0.11	0.65	0.80	

Appendix C

	CSF148	CSF405	CSF427	CSF485	CSF565	CSF665	CSF764	CSF922	CSF003	CSF015	CSF327	CSF850	CSM207	CSM624	CSM826	CSM964	CSM985	CSM385	CSM810
CSF148		0.02	0.09	0.07	0.13	0.25	0.14	0.02	0.23	0.20	0.35	0.12	0.02	0.28	0.30	0.33	0.57	0.33	0.60
CSF405	0.04		0.44	0.13	0.39	0.00	0.03	0.59	0.00	0.00	0.13	0.00	0.72	0.27	0.31	0.15	0.00	0.17	0.05
CSF427	0.17	0.46		0.66	0.32	0.35	0.47	0.28	0.33	0.48	0.28	0.38	0.46	0.31	0.36	0.35	0.18	0.20	0.05
CSF485	0.08	0.08	0.38		0.17	0.42	0.58	0.05	0.39	0.69	0.33	0.80	0.10	0.22	0.21	0.30	0.19	0.19	0.03
CSF565	0.22	0.35	0.27	0.26		0.12	0.20	0.13	0.11	0.16	0.59	0.02	0.25	0.57	0.51	0.50	0.15	0.55	0.20
CSF665	0.29	0.00	0.21	0.44	0.08		0.80	0.00	0.87	0.74	0.36	0.85	0.00	0.19	0.14	0.23	0.40	0.19	0.29
CSF764	0.13	0.01	0.24	0.51	0.12	0.68		0.00	0.72	0.71	0.35	0.84	0.01	0.19	0.13	0.21	0.26	0.19	0.13
CSF922	0.02	0.33	0.15	0.05	0.08	0.00	0.00		0.00	0.00	0.03	0.00	0.55	0.06	0.06	0.03	0.00	0.03	0.00
CSF003	0.21	0.00	0.16	0.33	0.06	0.70	0.69	0.00		0.57	0.31	0.73	0.00	0.15	0.10	0.16	0.36	0.16	0.21
CSF015	0.19	0.00	0.23	0.56	0.09	0.58	0.66	0.00	0.56		0.34	0.89	0.00	0.19	0.12	0.23	0.32	0.18	0.13
CSF327	0.35	0.07	0.15	0.30	0.36	0.31	0.36	0.03	0.33	0.37		0.34	0.04	0.43	0.43	0.47	0.57	0.58	0.33
CSF850	0.06	0.00	0.10	0.35	0.00	0.36	0.42	0.00	0.39	0.48	0.17		0.00	0.06	0.03	0.08	0.21	0.08	0.06
CSM207	0.03	0.59	0.36	0.13	0.22	0.00	0.01	0.79	0.00	0.00	0.05	0.00		0.15	0.18	0.07	0.00	0.07	0.00
CSM624	0.55	0.29	0.32	0.38	0.67	0.32	0.37	0.11	0.31	0.41	0.84	0.23	0.20		0.71	0.72	0.48	0.77	0.48
CSM826	0.58	0.33	0.37	0.38	0.61	0.24	0.27	0.11	0.22	0.26	0.85	0.11	0.24	0.72		0.72	0.49	0.84	0.50
CSM964	0.62	0.15	0.35	0.52	0.58	0.38	0.41	0.06	0.34	0.48	0.90	0.29	0.09	0.70	0.70		0.59	0.80	0.54
CSM985	0.50	0.00	0.08	0.15	0.08	0.31	0.24	0.00	0.34	0.31	0.41	0.37	0.00	0.22	0.22	0.27		0.32	0.46
CSM385	0.49	0.13	0.15	0.25	0.49	0.25	0.29	0.04	0.25	0.29	0.86	0.24	0.07	0.58	0.63	0.62	0.53		0.48
CSM810	0.60	0.03	0.03	0.03	0.12	0.26	0.13	0.00	0.23	0.14	0.33	0.12	0.00	0.25	0.26	0.28	0.52	0.33	

Appendix D. Matrices of home range overlap values based on 50% core area fixed kernel polygons for experimental site and control site raccoons. ID indicates site, gender and collar frequency of individual (e.g. ESF706 is experimental site female 706).

	ESF706	ESM085	ESF164	ESM185	ESF364	ESM885	ESF1405	ESM087	ESF890	ESM860	ESF947	ESM342	ESF226	ESM287	ESF780	ESM920	ESF268	ESM700	ESF870	ESM720	ESF910	ESM760	
ESF706		0.01	0.11	0.55	0.20	0.24	0.28	0.28	0.18	0.24	0.05	0.00	0.10	0.00	0.30	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESM085	0.07		0.04	0.08	0.02	0.11	0.03	0.00	0.20	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESF164	0.32	0.03		0.43	0.64	0.21	0.59	0.60	0.58	0.61	0.00	0.00	0.61	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESM185	0.84	0.02	0.22		0.40	0.31	0.50	0.50	0.42	0.48	0.00	0.00	0.30	0.00	0.47	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESF364	0.28	0.01	0.30	0.36		0.10	0.00	0.51	0.27	0.41	0.00	0.00	0.67	0.19	0.05	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
ESM885	0.90	0.08	0.27	0.76	0.28		0.35	0.37	0.60	0.35	0.19	0.04	0.17	0.03	0.63	0.71	0.00	0.00	0.00	0.00	0.03	0.00	0.00
ESF1405	0.45	0.01	0.32	0.52	0.00	0.15		0.62	0.56	0.53	0.00	0.00	0.59	0.13	0.08	0.05	0.00	0.00	0.00	0.00	0.11	0.00	0.04
ESM087	0.55	0.00	0.40	0.64	0.72	0.19	0.75		0.42	0.76	0.00	0.00	0.89	0.16	0.35	0.17	0.00	0.00	0.00	0.00	0.04	0.00	0.00
ESF890	0.25	0.06	0.27	0.38	0.27	0.22	0.48	0.30		0.28	0.00	0.00	0.17	0.01	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESM860	0.47	0.00	0.41	0.62	0.59	0.18	0.66	0.78	0.41		0.00	0.00	0.72	0.03	0.40	0.16	0.00	0.00	0.00	0.00	0.01	0.05	0.00
ESF947	0.15	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.23	0.16	0.91	0.61	0.00	0.36	0.24	0.18	
ESM342	0.00	0.36	0.00	0.00	0.00	0.03	0.00	0.00	0.04	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESF226	0.13	0.00	0.26	0.24	0.60	0.06	0.45	0.57	0.16	0.45	0.00	0.00		0.14	0.18	0.03	0.00	0.00	0.00	0.00	0.07	0.07	0.01
ESM287	0.00	0.00	0.32	0.00	0.33	0.02	0.19	0.19	0.02	0.04	0.00	0.00	0.27		0.00	0.02	0.00	0.00	0.00	0.00	0.09	0.00	0.05
ESF780	0.37	0.00	0.00	0.38	0.04	0.21	0.06	0.22	0.00	0.25	0.09	0.00	0.18	0.00		0.29	0.04	0.00	0.00	0.12	0.43	0.26	
ESM920	0.62	0.00	0.00	0.49	0.00	0.51	0.09	0.23	0.13	0.22	0.13	0.00	0.07	0.03	0.63		0.00	0.00	0.09	0.00	0.01	0.00	
ESF268	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.05	0.00		0.40	0.00	0.34	0.23	0.18	
ESM700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.00	0.57		0.00	0.13	0.04	0.04	
ESF870	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.05	0.00	0.00		0.00	0.00	0.00	
ESM720	0.00	0.00	0.00	0.00	0.10	0.01	0.13	0.03	0.00	0.00	0.20	0.00	0.10	0.07	0.17	0.00	0.39	0.11	0.00		0.80	0.90	
ESF910	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.05	0.00	0.04	0.00	0.23	0.00	0.10	0.01	0.00	0.30		0.70	
ESM760	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.05	0.00	0.00	0.02	0.17	0.00	0.10	0.01	0.00	0.42	0.86		

Appendix D.

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	CSF148	CSF405	CSF427	CSF485	CSF565	CSF665	CSF764	CSF922	CSF003	CSF015	CSF327	CSF850	CSM207	CSM624	CSM826	CSM964	CSM985	CSM810	CSM385
CSF148		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.21	0.01	0.11	0.34	0.73	0.06
CSF405	0.00		0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00
CSF427	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.01	0.00	0.00	0.00	0.00
CSF485	0.00	0.00	0.00		0.00	0.11	0.34	0.00	0.00	0.51	0.00	0.36	0.00	0.00	0.00	0.00	0.15	0.00	0.00
CSF565	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.13	0.26	0.42	0.00	0.00	0.14
CSF665	0.00	0.00	0.00	0.13	0.00		0.71	0.00	0.89	0.60	0.03	0.55	0.00	0.00	0.00	0.02	0.33	0.08	0.00
CSF764	0.00	0.00	0.00	0.27	0.00	0.49		0.00	0.42	0.84	0.03	0.81	0.00	0.00	0.00	0.02	0.30	0.00	0.00
CSF922	0.00	0.20	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
CSF003	0.00	0.00	0.00	0.00	0.00	0.58	0.41	0.00		0.28	0.00	0.21	0.00	0.00	0.00	0.00	0.08	0.00	0.00
CSF015	0.00	0.00	0.00	0.35	0.00	0.37	0.76	0.00	0.27		0.04	0.69	0.00	0.00	0.00	0.02	0.28	0.00	0.00
CSF327	0.08	0.00	0.00	0.00	0.03	0.02	0.03	0.00	0.00	0.04		0.00	0.00	0.42	0.20	0.37	0.35	0.00	0.38
CSF850	0.00	0.00	0.00	0.17	0.00	0.23	0.50	0.00	0.14	0.48	0.00		0.00	0.00	0.00	0.00	0.11	0.00	0.00
CSM207	0.00	0.40	0.04	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00		0.00	0.10	0.00	0.00	0.00	0.00
CSM624	0.34	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.81	0.00	0.00		0.31	0.43	0.45	0.18	0.63
CSM826	0.03	0.00	0.01	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.59	0.00	0.13	0.48		0.47	0.00	0.00	0.63
CSM964	0.23	0.00	0.00	0.01	0.50	0.03	0.04	0.00	0.00	0.05	0.91	0.00	0.00	0.57	0.41		0.49	0.09	0.45
CSM985	0.26	0.00	0.00	0.10	0.00	0.19	0.26	0.00	0.07	0.27	0.31	0.15	0.00	0.22	0.00	0.18		0.16	0.10
CSM810	0.70	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.04	0.20		0.01
CSM385	0.10	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.69	0.45	0.37	0.24	0.02	

Appendix E.

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CSF148	CSF148																		
CSF405	0.01	CSF405																	
CSF427	0.03	0.21	CSF427																
CSF485	0.02	0.02	0.19	CSF485															
CSF565	0.06	0.16	0.11	0.07	CSF565														
CSF665	0.13	0.00	0.09	0.25	0.03	CSF665													
CSF764	0.05	0.01	0.12	0.29	0.06	0.53	CSF764												
CSF922	0.00	0.33	0.07	0.01	0.04	0.00	0.00	CSF922											
CSF003	0.09	0.00	0.07	0.14	0.02	0.59	0.55	0.00	CSF003										
CSF015	0.06	0.00	0.13	0.44	0.03	0.52	0.64	0.00	0.35	CSF015									
CSF327	0.19	0.02	0.07	0.15	0.24	0.17	0.15	0.01	0.13	0.18	CSF327								
CSF850	0.02	0.00	0.05	0.35	0.00	0.34	0.37	0.00	0.23	0.45	0.08	CSF850							
CSM207	0.01	0.41	0.17	0.03	0.09	0.00	0.00	0.29	0.00	0.00	0.01	0.00	CSM207						
CSM624	0.23	0.07	0.11	0.08	0.28	0.08	0.09	0.02	0.08	0.08	0.35	0.02	0.05	CSM624					
CSM826	0.15	0.11	0.16	0.07	0.35	0.05	0.06	0.03	0.05	0.05	0.29	0.01	0.09	0.51	CSM826				
CSM964	0.09	0.01	0.06	0.05	0.11	0.04	0.05	0.00	0.03	0.05	0.10	0.01	0.01	0.23	0.20	CSM964			
CSM985	0.25	0.00	0.02	0.12	0.03	0.19	0.11	0.00	0.14	0.15	0.27	0.17	0.00	0.13	0.08	0.05	CSM985		
CSM385	0.24	0.04	0.07	0.07	0.33	0.09	0.09	0.01	0.08	0.09	0.52	0.03	0.02	0.39	0.47	0.12	0.18	CSM385	
CSM810	0.36	0.01	0.01	0.01	0.04	0.10	0.02	0.00	0.05	0.03	0.11	0.03	0.00	0.10	0.08	0.04	0.35	0.13	

Appendix F.

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CSF148	CSF148																		
CSF405	0.00	CSF405																	
CSF427	0.00	0.00	CSF427																
CSF485	0.00	0.00	0.00	CSF485															
CSF565	0.00	0.00	0.00	0.00	CSF565														
CSF665	0.00	0.00	0.00	0.08	0.00	CSF665													
CSF764	0.00	0.00	0.00	0.15	0.00	0.40	CSF764												
CSF922	0.00	0.20	0.00	0.00	0.00	0.00	0.00	CSF922											
CSF003	0.00	0.00	0.00	0.00	0.00	0.47	0.32	0.00	CSF003										
CSF015	0.00	0.00	0.00	0.00	0.00	0.38	0.67	0.00	0.17	CSF015									
CSF327	0.06	0.00	0.00	0.00	0.02	0.01	0.01	0.00	0.00	0.02	CSF327								
CSF850	0.00	0.00	0.00	0.16	0.00	0.21	0.34	0.00	0.06	0.36	0.00	CSF850							
CSM207	0.00	0.26	0.01	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	CSM207						
CSM624	0.16	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	CSM624					
CSM826	0.01	0.00	0.01	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.06	0.28	CSM826				
CSM964	0.03	0.00	0.00	0.00	0.08	0.00	0.01	0.00	0.00	0.01	0.10	0.00	0.00	0.17	0.10	CSM964			
CSM985	0.12	0.00	0.00	0.06	0.00	0.12	0.08	0.00	0.02	0.09	0.20	0.06	0.00	0.11	0.00	0.03	CSM985		
CSM810	0.36	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.10	CSM810	
CSM385	0.05	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.33	0.37	0.06	0.07	0.00	