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Authors: Wehtje, Morgan, and Gompper, Matthew E.

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Original article

Effects of an experimentally clumped food resource on raccoon *Procyon lotor* home-range use

Morgan Wehtje & Matthew E. Gompper

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. We analyzed radio-telemetry data from 41 adult raccoons *Procyon lotor* to assess the influence of an experimentally maintained clumped food source on spatial structure. We compared home-range size, two-dimensional overlap and volume of intersection (VI) values 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 non-clumped and spatially-temporally unpredictable 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 and volume of intersection (VI) scores that were nearly twice those of raccoons inhabiting the control site. These differences appear to be driven by increased overlap among females from the experimental site, as males from the two treatment sites had similar home-range overlap and VI scores. Collectively, these results indicate that the distribution of resources can significantly change the extent of spatial overlap among individuals, even when the mean home-range size of the population does not change. This further suggests that while a site's overall resource availability influences population size, the spatial clumping of resources facilitates the formation of local aggregations.

Key words: home-range, Missouri, Procyon lotor, raccoon, radio-tracking, resource dispersion, volume of intersection

Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, Missouri 65211, USA - e-mail addresses: mewffb@mail.missouri.edu (Morgan Wehtje); gompperm@missouri.edu (Matthew E. Gompper)

Corresponding author: Morgan Wehtje

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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 > 1 individual routinely occupies the same general spatio-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 & Weeks 2003).

Understanding how carnivores that are typically solitary 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 (e.g. Atwood et al. 2009). The raccoon *Procyon lotor*, a mid-sized, omnivorous and highly opportunistic

Carnivora is an excellent model species for understanding spatial dynamics and the ontogeny of social structure in meso-carnivores (Gaines et al. 2005, Ikeda et al. 2004). Raccoons show high plasticity in their space use and occupy different habitats as populations comprised of either solitary (Chamberlain & Leopold 2002) or highly aggregated individuals (Gehrt & Fritzell 1997, 1998). However, a detailed understanding of how raccoons shift from a solitary to an aggregated distribution is lacking. In this study, we use an experimental approach to examine how raccoons respond to the addition of a predictable and abundant food resource. We 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) whereas 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.

We examine the responses of raccoon space use, as measured by home-range size, the extent of overlap of home ranges among individuals and the volume of intersection (VI; Kernohan et al. 2001) among individuals. Home-range size provides a direct two-dimensional measure of the extent of the landscape used by an animal during its normal activities and, thus, provides a coarse scale or second order measure of an animal's resource selection (Johnson 1980). Because the area within the boundary of an individual's home range is generally used disproportionally (Burt 1943, Plowman et al. 2006), we derived and compared space use response for both 95% and 50% fixed kernel polygons (FKP). The core area (50% FKP) was defined as the most highly utilized part of the home range, and may reveal spatial dynamics that are not evident from comparisons between 95% FKP. Nonetheless, both areas are important for understanding landscape use (Plowman et al. 2006, Sandell 1989). We predict that mean 50% and 95% FKP home-range size will be smaller for animals inhabiting a site with reliably available clumped resources, as the presence of additional food, sometimes clumped, is often associated with decreased home-range size in raccoons and other carnivore species (Gerht & Fritzell 1997, 1998, Prange et al. 2004, Quinn & 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, and a larger home range, which might be required due to temporal fluctuations in resource availability, is no longer necessary (Johnson et al. 2002, Verdolin 2009).

Along with home-range size, home-range overlap is a common method used to demonstrate the link between resource availability and group formation (Atwood & Weeks 2003), as the extent of overlap represents the proportion of an animal's home range containing additional individuals. We predict that home-range overlap values will be greater for the population inhabiting the site with clumped supplemental food. Furthermore, 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 VI metric, allows the contrast of the extent of space sharing among animals, based on the intensity of use of areas of home-range overlap (Kernohan et al. 2001). We 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. These predictions are derived from the assumption that a clumped resource would facilitate more than one individual using a locality without incurring costs to other individuals (Macdonald 1983, Carr & Macdonald 1986, Johnson et al. 2002).

Methods

Study area

Our field work occurred in and around the University of Missouri's Thomas S. Baskett Research and Education Center (38.763N, 92.197W; hereafter Baskett), located 8 km east of Ashland, Missouri, USA (Fig. 1). Much of Baskett was previously used as farm and grazing lands, but has now reverted to the secondary mixed oak *Quercus* sp. and hickory *Carya* sp. dominated forest communities found throughout much of central Missouri. Baskett is bisected into a northern and southern portion by an east/west trending paved road and bounded on all sides by a mix of private and public lands (United States Forest Service Mark Twain National Forest). Radio-telemetry locations collected during the course of our study covered approximately 15.75 km^2. This included data collected from 9 km^2 Baskett and an additional 6.75 km^2 of public and private lands immediately

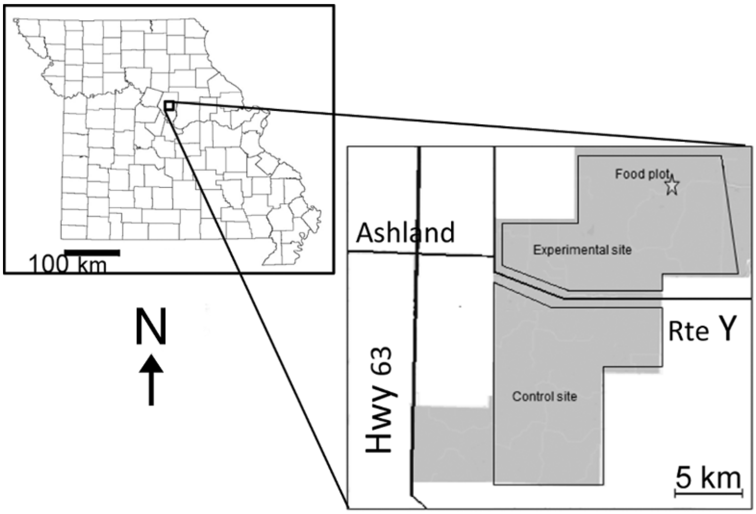

Figure 1. Location of the study area depicting control site, experimental site and food plot (star). The study site is in and around the University of Missouri's Thomas S. Baskett Research and Education Center, located approximately 8 km east of Ashland, Missouri, USA. Boundary polygons surrounding the experimental and control sites represent outer limits of trapping and/or raccoon home ranges. The dark lines represent major roads and the gray colour represents forested or public lands.

adjacent to Baskett. With the exception of scattered rural dwellings, the habitats on these adjacent lands are similar to those found within Baskett. Our study site was divided into two treatment areas. One area (hereafter the experimental site, ES) was contained within lands north of the paved road and the other area (hereafter the control site, CS) within lands south of the paved road. 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 that the clumped food was heavily used by raccoons, often with multiple individuals visiting the location simultaneously (Monello 2009). The CS received the same quantity 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 each) which were placed at least 50 m apart in an irregular pattern throughout the study area. Placement of food in the CS varied weekly so that the location of these small food piles was not predictable from week to week.

Capture and handling

Between May 2007 and June 2008, we captured and fitted 65 adult raccoons (37 in ES and 28 in CS) with radio-transmitters. We collared approximately equal numbers of females (18 in ES and 14 in CS) and males (19 in ES and 14 in CS) at each site. Procedures for trapping and handling raccoons followed the University of Missouri Animal Care and Use protocol 3927; details are given in Wehtje (2009). In brief, we captured raccoons using Tomahawk #207.5 box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). The captured raccoons were anaesthetized with ketamine hydrochloride (10 mg/kg) and xylazine (1 mg/kg; Belant 1995). Once anaesthetized, each animal was sexed and aged by tooth eruption, tooth wear and past capture history (Grau et al. 1970, Monello 2009). Raccoons were ear tagged (#1005-1 Hasco Tag Company, Dayton, Kentucky, USA), and animals ≥ 2 years of age were collared with ATS 1960 (ATS, Isanti, Minnesota, USA) or Telonics Mod210 (Telonics Inc., Mesa, Arizona, USA) model VHF radio-transmitters.

Data collection

Prior to collecting telemetry data on raccoons, we assessed the precision of azimuth readings (White & Garrott 1990). We placed six test radio-transmitters 0-5 m above ground and 200-1,000 m from telemetry stations at 36 locations (18 in ES, 18 in CS) for a total of 108 telemetry bearings. We compared the true bearing to the estimated bearing to calculate precision. We calculated data error using 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° ± SE 0.35.

We collected animal location data 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 two azimuths had been recorded. Alternatively, two or three individuals took simultaneous azimuths from different fixed points. To ensure that the data points represent all possible nocturnal activity zones, we collected data equally from each of four 3-hour periods (18:00-21:00, 21:00-24:00, 24:00-03:00 and 03:00-06:00). To minimize biases in home-range size estimations derived from a small sample size of location data, only animals with $\geq$ 30 locations spaced $\geq$ 2.5 hours apart were used to estimate UDs (Alldredge & Ratti 1986, Aebischer et al. 1993, Seaman & Powell 1996).

Data analysis

We converted bearing locations to true location estimates using the maximum likelihood estimate in LOAS. Prior to and during conversion, bearings showing non-convergence were eliminated. A total of 1,764 ($\bar{x}$ ± SD = 46 ± 12/animal) location estimates were derived from viable bearings (Wehtje 2009). Data were pooled for analysis across seasons, as intra-season sample sizes were too limited to contrast seasonal differences in home-range size. We used plug-in smoothing methods to produce UD bandwidths for 95% and 50% fixed kernel home ranges (Worton 1995, Seaman & Powell 1996, Kernohan et al. 2001, Gitzen et al. 2006). We calculated the UDs using Matlab (Mathworks Inc., Natiwick, Massachusetts, USA) with the kernel density estimator folder attached. UDs were created and converted to rasters by applying inverse distance weighting point interpolations with ArcGIS 9.3 (ESRI, Redlands, California, USA) spatial analyst tools. Hawth's tools v3.2 (available at: www.spatialecology.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. The 50% FKPs was calculated as an estimate of the home-range core area. Locations were projected using the NAD83 datum.

We determined home-range overlap 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 $\geq$ 2 UDs. An individual's UD is a three-dimensional representation of how intensely it utilizes a given geographic area. The resulting quantity, generated by overlapping UDs, has a value of 1 when space use patterns are identical for two individuals. With greater differentiation in space use patterns, the index score approaches 0 (Seidel 1992, Kernohan et al. 2001). VI index scores and co-occurrence UDs were generated in ArcGIS 9.3. Home-range overlap and VI values for both 95% and 50% FKPs were derived between all individuals within their respective treatment area. Within each treatment area, all animals were included when generating comparative statistics for 95% FKPs, but animals demonstrating no overlap in 95% FKPs were eliminated from the subsequent 50% FKP overlap and VI analyses to avoid overestimating differences in overlap and VI values for 50% FKPs between treatments (Millspaugh et al. 2004).

Differences in mean home-range use values were compared within and between treatments (sites) for all individuals combined, for each sex and for males vs females. Comparisons were done for both 95% and 50% FKPs using Wilcoxon ranked sum tests. Wilcoxon ranked sum tests were also used to detect differences in overlap and VI scores between and within populations. The degree to which the clumped food addition may have influenced overlap and VI within the ES was examined by assessing whether the location of the clumped food was included in the 50% FKPs. Based on the inclusion of the clumped food in the core area of an individual, ES animals were categorized in two groups. Group 1 animals included the clumped food in their 50% FKPs. Group 2 animals did not include the clumped food in their 50% FKP. Statistical analysis was conducted using Kruskal-Wallis rank sum tests. *Post hoc* analyses were performed using pairwise U-tests and studentized range statistics (Q) to determine which type of overlap and VI pairings differed.

Wilcoxon and Kruskal-Wallis rank sum tests were conducted in program R (available at: www.r-project.org), with values of $\alpha \leq 0.05$ considered as significant. Home-range size data were 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, transformed data were back-transformed by squaring the sine of the number (Fleiss et al. 2003). We present mean (± SE) values unless otherwise noted.

Results

Home-range and core-area size

Of the 65 collared raccoons, 41 (22 in ES and 19 in CS) had the $\geq$ 30 telemetry points necessary for home-range analyses. Of these, 34 (18 in ES and 16 in CS) raccoons were monitored in both 2007 and 2008, and seven others (four in ES and three in CS) were monitored only in 2008 (Wehtje 2009). The average distance between the receivers and raccoons was 828 ± 36 m. The combined population of ES and CS individuals had 95% FKP home-range sizes of 0.75-4.26 km^2 and 50% FKP core-area sizes of 0.15-1.09 km^2 (Table 1). For all individuals combined, male 95% and 50% home-range estimates were significantly larger than those of females (95% FKP: $W = 132$, $P = 0.05$; 50% FKP: $W = 112.5$, $P = 0.014$). However, both within (male vs female) and between treatments (male vs male and female vs female), no other comparisons were statistically different in mean 95% or 50% FKP estimates.

Home-range and core-area overlap

Mean 95% FKP home-range overlap of ES dyads (0.44 ± 0.01) was 1.6 times greater than that of CS dyads (0.28 ± 0.01). These differences were driven principally by the disparity between ES and CS females. Females from the ES (0.46 ± 0.02) had > 1.5 times the 95% FKP overlap of CS females (0.28 ± 0.02; $W = 10317$, $P < 0.001$). ES females (0.45 ± 0.02) also differed significantly from CS females (0.26 ± 0.02) in their extent of overlap with males ($W = 28970.5$, $P < 0.001$). In contrast, mean 95% FKP overlap scores among males were similar between the treatments (ES$_{M:M}$ 0.40 ± 0.02, CS$_{M:M}$ 0.40 ± 0.04; $W = 2285$, $P = 0.92$).

Compared to the mean 95% FKP scores there was little difference in mean 50% FKP home-range overlap scores between treatments (ES: 0.14 ± 0 .01; CS: 0.11 ± 0.01; $W = 76962$, $P = 0.06$). 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 three times lower (ES$_{95}$ 0.44 ± 0.01, ES$_{50}$ 0.0.14 ± 0.01; CS$_{95}$ 0.31 ± 0.03, CS$_{50}$ 0.13 ± 0.01). There was no difference in male:male dyad overlap for 95% FKP, but a difference was present in 50% core overlap. CS males had nearly double the 50% core overlap of ES males (ES$_{M:M}$ 0.12 ± 0.02, CS$_{M:M}$ 0.20 ± 0.02; $W = 1309$, $P < 0.001$). Female:male dyad overlap was the only other 50% FKP joint space relationship that showed significant differences between treatments.

Probability of co-occurrence

The ES population had significantly higher composite mean 95% FKP VI scores than the CS population (ES 0.22 ± 0.01, CS 0.12 ± 0.01; $W = 27397.5$, $P < 0.001$), and similar to 95% FKP overlap the female:female and female:male dyads were the comparisons differing between treatment areas. Mean ES female:female and female:male VI scores were 1.5-2 times greater, respectively, than the corresponding CS comparisons (ES$_{F:F}$: 0.24 ± 0.02, CS$_{F:F}$: 0.15 ± 0.02; $W = 2475$, $P = 0.001$; ES$_{F:M}$: 0.23 ± 0.02, CS$_{F:M}$:0.10 ± 0.01; $W = 7621$, $P < 0.001$). A weaker, but still significant, composite mean difference existed between treatments for 50% FKP VI scores (ES 0.06 ± 0.01, CS 0.09 ± 0.01B; $W = 77171$, $P = 0.05$). As with the 95% FKP VI scores, ES female:male scores were > 2 times greater

Table 1. Sizes (in km^2) of 95% and 50% fixed kernel polygons (FKP) home range for raccoons inhabiting Thomas S. Baskett Research and Education Center, Ashland, Missouri, USA. The data are subdivided by sex and by treatment (CS = control site and ES = experimental site).

Population	N	Mean 95% FKP (SE; range)	Mean 50% FKP (SE; range)
CS all	19	2.03 (0.17; 0.77 - 3.09)	0.44 (0.04; 0.18 - 0.79)
ES all	22	1.85 (0.18; 0.75 - 4.26)	0.44 (0.05; 0.15 - 1.09)
CS females	12	1.83 (0.19; 0.77 - 3.03)	0.28 (0.04; 0.15 - 0.64)
ES females	11	1.56 (0.19; 0.75 - 2.63)	0.36 (0.05; 0.25 - 0.71)
CS males	7	2.36 (0.29; 1.14 - 3.09)	0.54 (0.05; 0.18 - 0.79)
ES males	11	2.15 (0.29; 1.00 - 4.26)	0.53 (0.07; 0.15 - 1.09)
All females	23	1.70 (0.13; 0.75 - 3.03)	0.37 (0.05; 0.18 - 0.71)
All males	18	2.23 (0.20; 1.00 - 4.26)	0.53 (0.05; 0.15 - 1.09)

than those from the CS treatment ($ES_{F:M}$ 0.10 ± 0.01, $CS_{F:M}$ 0.04 ± 0.01; W = 5715, P = 0.01) and male:male 50% FKP VI scores were slightly higher for the CS treatment (ES 0.07 ± 0.02, CS 0.09 ± 0.03; W = 355, P = 0.05). Female:female scores did not differ between the two treatments (ES 0.10 ± 0.02, CS 0.07 ± 0.02; W = 1818, P = 0.16).

Clumped resource inclusion

Of the Group 1 ES individuals, 10 (five males and five females) included the supplemental clumped food within their 50% home ranges. Group 2 excluded the clumped food resource and was comprised of 12 individuals (six males and six females). Mean 50% FKP core overlap and VI scores differed significantly ($H_{overlap} = 33.31$, df = 5, $P < 0.001$; $H_{VI} = 12.88$, df = 5, P = 0.02) between Group 1 and Group 2 animals. *Post-hoc* analysis revealed female:male overlap and VI scores were higher in Group 1 than in Group 2 (overlap: $P < 0.001$; VI: P = 0.03). Group 1 female:female overlap was greater than that of Group 2 females, but VI scores did not differ between the two groups (overlap: P = 0.03; VI: P = 0.90). Male:male overlap and VI did not differ between the two groups (overlap: P = 0.27; VI: P = 0.61).

Discussion

Previous studies of the effect of clumped or aggregated resources on carnivore spatial dynamics report a decrease in home-range size and an increase in home-range overlap among same sex individuals (Moehlman 1986, 1989, Fedriani et al. 2001, Hidalgo-Mihart et al. 2004, Quinn & Whisson 2005). This effect is often greater in females than in males (Erlinge & Sandell 1986, Sandell 1989). Our findings, despite increased food availability and patchiness, seem to subtly contradict these previous findings. Rather than shrinking, home ranges may have been modified or shifted to include the resource, a pattern observed in studies of carnivores where resources are either less heterogeneous or seasonally limited (Edwards et al. 2009, Kolowski & Holekamp 2008). Modification of home-range boundary morphology to include the clumped food resource without altering overall home-range size is supported by the ES food supplementation site falling outside peak occurrence portions of the core area UDs. Johnson et al. (2002) suggest that an increase in a singular type of resource abundance may not enable a home range to shrink, because a larger area is still needed to encompass other critical resources. Our manipulations only involved one type of critical resource (food), and the temporal and spatial availability of other resources, e.g. diurnal rest sites, natal dens and water, may explain the lack of between-treatment differences in home-range size. Thus home-range and core-area size may not be a sufficiently sensitive nor dynamic metric for ascertaining the spatial response of animals to the manipulation of only one critical resource.

Increased joint space use is commonly observed in many resource dispersion studies and is influenced by the temporal and spatial variance of resource abundance (Fedriani et al. 2001, Eide et al. 2004, Davison et al. 2009). Thus while our finding of increased overlap and co-occurrence is not unexpected what is unusual is the simultaneous and contrasting manifestation of differences in both within- and between-sex overlap and co-occurrence. While ES female:female and female:male overlap and VI scores are the primary source of differences between the two treatment sites, male:male overlap and VI scores were greater for CS males than for ES males. Gerht & Fritzell (1997, 1998) correlated increased levels of male:male joint space use among raccoons with critical resource areas supporting aggregations of females. Those findings were mirrored in the spatial overlap of the CS males. In contrast, peak areas of overlap and co-occurrence between ES males 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 (Wehtje 2009). While female philopatry may explain some measure of female:female overlap and co-occurrence differences between the treatment sites, it is unlikely to explain the sustained significant ES inter-gender difference between the treatments for all joint space use comparisons (Hauver et al. 2010, Ratnayeke et al. 2002).

A more comprehensive explanation of the between treatment and between clumped resource inclusion group differences can be found by applying the Resource Dispersion Hypothesis (Macdonald 1983). The Resource Dispersion Hypothesis 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 (Johnson et al. 2002). This enhanced co-existence may also facilitate increased social tolerance among con-specifics and further explain the sustained higher levels of inter-gender overlap and co-occurrence (Carr & Macdonald 1986). As animals' core areas recede from the clumped resource, the probability of them encountering the resource diminishes and less overlap and co-occurrence 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 just 3-4 days. Animals not visiting the feeding site immediately after supplementation would be less likely to benefit from its presence. Therefore animals whose home ranges were more distant from the location of the clumped resource may need to utilize additional foraging areas and their spatial arrangements would display less congruence as resources become more homogenous (Bernstein et al. 1988).

The patterns of overlap and co-occurrence found on both the ES and the CS in our study suggest that raccoons and perhaps other putatively solitary mesocarnivores are not truly solitary, but rather may become more aggregated and perhaps more social as a function of resource availability and heterogeneity (Gehrt et al. 2008, Pitt et al. 2008, Smith et al. 2008). The conditions that underpin the spatial distribution of individuals within a population will vary from site to site, even for conspecifics (Davison et al. 2009), but in general for species in which aggregation has been observed, home ranges demonstrating low dyad overlap or low levels of co-occurrence may be indicators of habitats with limiting or spatially homogenous resources rather than a natural inclination of these animals to avoid overlap with conspecifics.

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