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1 **Title page**

2 Quality and overlap of individual core areas are related to group tenure in female spider monkeys

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Abstract

In species with a high degree of fission-fusion dynamics group members may differ in the use of the group home range to reduce food competition. Such differential use may result in distinct individual core areas. We studied core area quality and overlap among 21 female spider monkeys belonging to the same group over a period of 4 years. Core areas ranged between 62 and 161 ha with a mean overlap of 56% between any given two females. Only a small portion (mean = 3ha) of each individual core area was used exclusively. No single part of the home range was used as core area by all females, and only an area of less than 1 ha was used as part of the core area by 20 of the 21 females. The time a female spent in the group (i.e. group tenure) was associated with characteristics of the core areas: the longer the group tenure, the better the quality of her core area. In addition, the longer the time two females spent together in the same group, the larger the overlap between their individual core areas. As this result was obtained while controlling for the time two females spent together in the same subgroup, females may reduce direct competition by using the same resource at different times. In sum, spider monkey females' group tenure plays a central role in the quality and overlapping patterns of their individual core areas.

Keywords: Home range, core area, spider monkeys, tenure, immigration

Introduction

Core areas are the parts of the home range most frequently used [Burt 1943]. Because they constitute the areas in which spatial activity is concentrated, core areas are expected to contain biologically relevant features in greater densities than the rest of the home range [Kaufman 1962; Leuthold 1977]. Several studies support this view as muriquis' (*Brachyteles hypoxantus*) core areas contained a greater number of large trees than other home range areas [da Silva Junior et al. 2009], more decayed logs were in the core areas of western red-backed voles (*Myodes californicus*) than in other parts of the home range [Thompson et al. 2009], white-handed gibbons' (*Hylobates lar*) core areas had the highest densities of food trees [Asensio et al. 2014], and European wolves' (*Canis lupus*) core areas overlapped mainly with the forest habitats used by its major prey species, red deer [Findo & Chovancova, 2004]. Similarly, spider monkeys' (*Ateles geoffroyi*) core areas contained high densities of feeding trees, sleeping sites, and patches of old-growth forest [Asensio et al. 2012a, Ramos-Fernandez et al. 2013]. Because of the concentration of biologically relevant features, core areas are commonly thought to represent the optimal area that an individual or a group needs to survive and reproduce [Binghan & Noon 1997; Powel 2000; Samuel et al. 1985]. Core areas are thought to be associated with the presence of fundamental resources, but the notion of being the optimal area required for survival has been challenged because other parts of the home range may also contain necessary resources [Buchanan et al. 1997; Asensio et al. 2012a]. In addition, core areas may be operationally defined using different methods (e.g. kernels, minimum convex polygon) and parameters (e.g. different percentages of kernels) creating potentially erroneous variation [Downs et al. 2012].

Individuals living in cohesive groups must share the same locations, and interindividual differences in space use would be minimal depending mainly on group spread [Bode et al. 2012; Smith et al. 2005; Warburton & Lazarus 1991]. This pattern is unlikely in species with a high degree of fission-fusion dynamics, in which individuals belonging to the same group fission and fuse into subgroups of variable composition [Aureli et al. 2008]. Under these circumstances, individuals may have distinct core areas as different individuals can occupy different areas of the group home range at the same time.

Food is a main source of competition among female mammals as feeding efficiency is expected to be closely linked to reproductive success [Emlen & Oring 1977; Trivers 1972]. Therefore, female space use is highly influenced by the availability and distribution of resources [e.g. Benson et al. 2007; Murray et al. 2007; Pellerin et al. 2010], and females should compete for better quality habitat whenever possible [Sterck et al. 1997]. For example, in chimpanzees (*Pan troglodytes*), which exhibit a high degree of fission-fusion dynamics [Nishida & Hiraiwa-Hasegawa 1987; Stumpf 2011], females have individual core areas that appear to mediate reproductive success [Williams et al. 2002] and long-term residents attack new immigrant females in high-quality core areas [Kahlenberg et al. 2008; Miller et al. 2014]. Food quality differences across core areas have been associated with variation in reproductive success as chimpanzee females with core areas containing more preferred foods had elevated ovarian hormone production, shorter inter-birth intervals, and higher infant survivorship [Emery Thompson et al. 2007].

Like chimpanzees, spider monkeys (*Ateles* spp.) are characterized by female dispersal and a high degree of fission-fusion dynamics [Aureli & Schaffner 2008; Shimooka et al. 2008;

Symington 1990]. They prefer evergreen primary forest and relatively high canopy levels [Chapman 1988; DeGama-Blanchet & Fedigan 2006; Wallace 2008] where higher densities of food trees are found [Asensio et al. 2012a; Ramos Fernandez et al. 2013]. Spider monkeys do not use their home range homogeneously focusing their activities in core areas [Asensio et al. 2012a; Campbell 2000; Chapman 1990; Shimooka 2005; Spehar et al. 2010; Symington 1988; van Roosmalen, 1985] that may vary depending on changes in resource availability [Asensio et al. 2012b; Nunes 1995; Wallace 2006]. Although there is variation in the size and overlap of individual core areas across spider monkey populations [Wallace 2008b], overall there are similarities with chimpanzees regarding individual core areas and aggression patterns. Spider monkey females concentrate their ranging in individual core areas distributed throughout the group home range [Symington 1988]. Asensio et al. [2008] documented aggression by long-term resident females to recently immigrated females during feeding in spider monkeys; thus, females may compete for high-quality core areas, like in chimpanzees.

The aim of our study was to examine space use of spider monkey females and the potential competition for high-quality habitat by investigating differences in their individual core areas. We analyzed whether the location of individual core areas and female tenure in the group are associated with the quality of female core areas. In addition, we examined which socioecological factors, such as habitat quality, the degree of association in subgroups between individual females and the time females lived together in the group, could better explain the size of the overlap between individual core areas.

Methods

Study site and study individuals

The study was carried out at the Santa Rosa sector of the Guanacaste Conservation Area, situated in northwestern Costa Rica (10º 50'N, 85º 38'W). The Santa Rosa sector comprises 108 km^2 of tropical dry forest from the foothills of volcanic mountains down to the Pacific coastal plain (0–300 m elevation). Santa Rosa sector consists of a highly seasonal forest with a severe dry season between December and May and a wet season during the rest of the year when most of the annual rainfall occurs (900-2500 mm) [Janzen 1986].The original vegetation was continuous dry forest consisting mainly of semi-evergreen trees [Janzen 1983, 1986], but over the past 400 years much of the upper plateau was cleared by anthropogenic activities [Fedigan &Jack 2001]. The study site is a mosaic landscape with various stages of forest regeneration surrounding occasional fragments of old evergreen mature and riparian forest [Arroyo-Mora et al. 2005].

Our research conforms to the American Society of Primatologists principles for the ethical treatment of primates and permission to conduct research was granted by the Costa Rica Ministry of Environment and Energy (MINAE) and adhered to the legal requirements of Costa Rica.

We investigated one group of spider monkeys (*Ateles geoffroyi*) that varied in size (25-34 individuals) due to birth, immigration, and disappearance during the study period. Twelve adult females were already present in the group (since 2003) at the start of our study and 9 additional females immigrated into the group over the next 4 years. The monkeys were well habituated to being followed by researchers and could be individually recognized from pelage and facial patterns as well as sex and size.

120

121 Data collection

122 The study was carried out between January 2005 and December 2008 for 48 consecutive months.
123 We followed subgroups during the entire course of the daylight hours balancing observations
124 between mornings and afternoons. Spider monkey subgroups were followed for a total of 521
125 days, of which 73 were all-day subgroup follows. Individuals were considered in the same
126 subgroup when they were at a distance of ≤ 50 m from at least one other subgroup member
127 [Aureli et al. 2012], following a chain rule [cf. Ramos-Fernandez 2005]. Fission occurred when
128 one or more individuals from the followed subgroup were not observed at a distance of ≤ 50 m
129 from at least one current subgroup member for more than 30 minutes. Fusion occurred when one
130 or more individuals not belonging to the followed subgroup came to a distance of ≤ 50 m from
131 any member of the followed subgroup [Asensio et al. 2009]. Different subgroups could be as far
132 as 2 km apart from each other, and some individuals were not observed together in the same
133 subgroup for several months (unpublished data). We randomly selected which subgroup to
134 follow after a fission event.

135 Every 30 minutes we recorded the location of the followed subgroup using the track point
136 setting on a handheld global positioning unit (GPS Garmin GPSMAP 76CSX) from roughly the
137 center of the subgroup. Geographical coordinates were collected using the coordinate system
138 (datum) WGS84 and projected into Universal Transverse Mercator (UTM, Zone 16N) units. A
139 total of 5381 30-minute subgroup location points during 2691 sampling hours were collected
140 during the study, with a mean (± SD) of 1344 (± 301.4) points per year. A subgroup location
141 point was considered as a location point for each female present in the subgroup. Due to the high

142 degree of fission-fusion dynamics of the study group, females were not equally present in the
143 followed subgroups, being sampled on average in 1863 (± 287) location points, with a minimum
144 of 165 and a maximum of 3715 points. To determine the minimum number of location points
145 needed to generate individual core areas we followed a bootstrap procedure running 50 iterations
146 (with replacement) at every 10-location-point increment (10 location points, 20 location points,
147 30 location points and so on) for each female using the Animal Movement Extension in Arcview
148 3.2 [Environmental Systems Research Institute, Redlands, CA, USA; Hooge and Eichenlaub
149 2000]. We found that a minimum of 120 location points was sufficient to reach an asymptote of
150 the area-observation curve (Figure 1; Odum & Kuenzler 1955). Hence, all the 21 females were
151 used in the analyses. The location of food trees where the monkeys of the followed subgroup fed
152 for at least 5 minutes was also recorded with the GPS and their diameter at breast height (DBH)
153 was measured.

154

155 Core area estimation

156 We used the fixed kernel method to determine the core area for each female. Kernel method
157 produces probability utilization distributions of space use patterns with smaller percentages
158 representing the most used areas based on a set of animal locations [Worton 1989]. Each location
159 is assumed to have a "weight" in the form of a bivariate normal kernel controlled by a smoothing
160 factor [Samuel et al. 1985]. The smoothing factor was calculated by the least squares method.
161 The inflection point in the utilization distribution of kernel contours was used to determine core
162 areas following Harris et al. [1990]. We plotted contour values at 5% increments from 5% to
163 95% contours against the percentage of area enclosed. Contour area values were calculated using

the "fixed kernel density estimator" of Hawth Tools for ArcGIS [Beyer 2004]. Then, we fitted an exponential regression function ($y = e^{bx}$) forced through the origin to the data. We used the resulting regression coefficient 'b' to determine the point (x) where the slope of the exponential regression curve was 1, i.e. where there was a slope discontinuity, by solving $x = [\ln (1/b)] / b$ for each individual set of locations. The use of an interval of 30 minutes between location points was considered as an acceptable compromise between inappropriate subsampling and loss of biologically relevant information while seeking independence of data points [De Solla et al. 1999; Willems & Hill 2009].

A biologically relevant method to establish individual core areas in species characterized by a high degree of fission-fusion dynamics is 1) to consider that all subgroup members share the same location [cf. Spehar et al. 2010] and 2) to use a weighted value of each individual location by taking into account the research effort. To control for differential research effort across locations, we divided the study site in 25x25 m square cells and identified the cell in which each location was found. We then divided the number of times a female was observed in a location cell by the number of times the study spider monkeys were observed in that location cell. For example, if one female was observed in a given cell twice and spider monkey subgroups were followed in such a cell 10 times, the weighted value of that particular location for that female was 0.2 (2/10). Accordingly, we calculated each female's core area by specifying the appropriate weighted value to the input points in the density estimate of the "fixed kernel density estimator" tool.

Data analysis

185 Overlap intensity among individual female core areas was defined as the relative use of
186 the home range as individual core area. We determined overlap intensity by overlaying all
187 individual core areas and identifying sections covered by a different number (ranging from 0 to
188 21) of individual core areas [cf. Ramos-Fernandez et al. 2013]. The resulting figure provides a
189 visual representation of the overlap intensity among individual core areas. To quantify such
190 overlap intensity we estimated an overlap index (*oi*) per each female using the formula:

$$oi = \frac{\sum_{i=2}^{j} t_i o_i}{nA}$$

191 where *j* is the number of overlapping areas in a given female core area, *t* is the number of times
192 that each area overlapped with other females core areas, *o* is the overlap area size, *n* is the
193 number of females (i.e. the maximum number of times any region of a core area can be
194 overlapped), and A is the corresponding female core area size. Overlap values could range from
195 0 to 1 with values close to 1 indicating high overlap and values close to 0 indicating none or low
196 overlap. We also examined the size of core area and the sum of DBH of the food trees within it
197 as a function of the overlap intensity.

198 In addition, we calculated the proportion of the group home range (509 ha, calculated as
199 the overlay of seasonal home ranges across the 4 years [Asensio et al. 2012b], which also
200 matches the overlay of all individual home ranges), corresponding to the overlay of all individual
201 female core areas. The degree of core area exclusivity was the proportion of each female's core
202 area that did not overlap with other females' core areas.

203 A General Linear Model (GLM) was used to investigate how a female's core area quality
204 (continuous dependent variable) was affected by her group tenure (i.e. the amount of time a

female had spent in the group). The distance of the female to the center of the group home range was added as another independent variable to control whether the potential effect of tenure on core area quality could simply be due to shorter-tenure individuals using peripheral areas of the group home range (which may be of lower quality) more often than longer-tenure individuals. The distance of the female to the center of the group home range was calculated as the distance between the geometrical center (i.e. the centroid) of the group home range [509 ha; Asensio et al. 2012b] and that of the core area of each female. Both centroids were calculated using the "calculate geometry" tool in ArcGIS. Group tenure of each female was calculated as the number of months the female was present in the group from 2003 (i.e. from when all monkeys were individually recognized) until the end of this study (maximum 72 months). As a proxy for the quality of each female's core area we used the sum of DBH of the food trees within the core area. Given that the study area covered during subgroup follows did not change over the 4-year study period and 200 observation days were sufficient to find an asymptote in the number of food trees used by spider monkeys in the entire home range, we considered these food trees as representative of the food sources available to the study group [Asensio et al. 2012a]. Furthermore, we used another GLM to test the effect of a female's group tenure (controlled by the female's distance to the center of the group home range) on the density of food trees in her core area. Such a food tree density was viewed as a proxy of core area effectiveness since it is less energy costly for a female to range in a smaller than a larger core area with the same number of food trees. The parameters of the GLM tests and their standard errors were estimated with the weighted generalized estimating equations. All data sets followed a normal distribution with homogeneity of variance.

227 To examine the factors affecting the size of the overlap between pairs of individual core
228 areas (dependent variable) a linear mixed model (LMM) was employed with dyadic tenure,
229 dyadic association index and habitat quality in terms of the sum of DBH of the food trees in the
230 overlap as independent variables. Dyadic tenure was defined as the number of months two
231 females were together in the group during the study period. Dyadic association index reflected
232 the proportion of time two individuals were together in the same subgroup. Following Cairns and
233 Schwage (1987), we calculated dyadic association index (I_{AB}) as follows:

$$I_{AB} = \frac{\#AB}{\#A + \#B + \#AB}$$

234 where *#AB* is the number of 30-minute subgroup location points in which individuals *A* and *B*
235 were present in a subgroup together, *#A* the number of subgroup location points in which *A* was
236 present without individual *B,* and *#B* the number of subgroup location points individual *B* was
237 present without individual *A.* We only took into account the period in which both females of any
238 dyad were present in the group to calculate *#A* and *#B.*

239 Core area overlap between each pair of females was calculated by using the percentage of
240 the Minta index (Minta 1992):

$$Minta\ index = \frac{A \cap B}{\sqrt{AB}}$$

241 where $A \cap B$ is the size of the overlapping area between the two individual core areas *A* and *B*
242 and $\sqrt{AB}$ is the geometric mean of the two core area sizes. A percentage of the Minta index of
243 100 indicates complete overlap between the two individual core areas, whereas 0 signifies that
244 the two core areas do not overlap at all. The sum of the size of the two individual core areas was

added in the LMM to control for its potential effect on the overlap area size. The individual identities were fitted as random factors to control for data dependency and between-subject variance as the same individual belonged to several dyads. The assumptions of normality and homogeneity of variance in the random errors were not violated The Akaike information criterion was used to select the best explanatory model (Tabachnick & Fidell 2007). All analyses were performed in PASW/SPSS version 20.0 for windows (IBM Corp., USA). An alpha level of $P \leq 0.05$ was set for all analyses.

Results

Spider monkey females had individual core areas ranging in size between 62 and 161 ha (mean ± SD = 138 ± 24 ha) with a mean overlap of 56 % (± 22) between any given two females. The intermediate degree of overlap was confirmed by a mean overlap index of 0.61 (± 0.10). The overlay of all individual core areas accounted for an area of 350 ha, covering 69% of the group home range. Female core areas occupied the most central position of the group home range and all together included 97% of the known food trees (Figure 2). No single part of the home range was used as core area by all females and only an area of less than 1 ha was used as core area by 20 of the 21 females (Figure 2 and 3). In 18% (63 out of 350 ha) of the overlay of all individual core areas there was no overlap between core areas (Figure 3), reflecting the small size of each individual core area that was used exclusively by a given female without overlap with other females' core areas (3 ± 3 ha; 3 ± 2% of the individual core area). The variation in overlap intensity among the 21 females' core areas was characterized by a steep decrease of the core area sizes as the overlap intensity increased (Figure 3), indicating a differential use of the space across

267 females. Areas with especially high overlap intensity contained the highest values of cumulative
268 DBH of food trees (Figure 4), with a sudden drop within areas used by more than 18 females,
269 likely due to the small size of these areas (Figure 3).

270

271 Core area quality

272 The study group home range contained 677 food trees (1.3 per ha) for a total of 38,985
273 cumulative DBH with a mean (±SE) of 395 (±30) food trees (2.8 ± 0.15 per ha) and 22,855 (±
274 1,625) cumulative DBH per female core area. The best model explaining variation in individual
275 core area quality included only group tenure (Table 1). The quality of individual core areas
276 significantly increased with group tenure ($F_{1,21} = 11.7$, $P = 0.002$, Figure 5). Similarly, only
277 group tenure was included in the best model explaining core area effectiveness (Table 2). Female
278 group tenure was positively associated with the density of food trees in her core area ($F_{1,21} =$
279 9.59, $P = 0.005$, Figure 5).

280

281 Core area overlap

282 The best model explaining variation in overlap between two female core areas included all
283 independent variables (Table 3). Specifically, there was a positive effect of dyadic tenure ($F_{1,178}$
284 $= 28.1$, $P = 0.0001$; Figure 6), dyadic association index ($F_{1,159} = 62.5$, $P = 0.0001$; Figure 7) and
285 the sum of DBH of the food trees in the overlapping area ($F_{1,178} = 57.7$, $P = 0.0001$; Figure 8).

286

Discussion

Our findings confirm that in spider monkeys adult females have individualized core areas as their high degree of fission-fusion dynamics allows different spatial use for each adult female. The overlap between the core areas of any given two adult females was on average 56%, which was further confirmed by an intermediate value of the overlap index of 0.61. However, an exclusive use of individual core areas was rare, with on average only 3 ha (3%) not overlapping with any other female's core area. Similarly, Spehar et al. [2010] found little evidence of exclusive core area use by individual spider monkeys (*A. belzebuth*), although the range estimator they used was the grid cell count, which likely overestimated core area size [Powell 2000]. The overlay of all individuals' core areas covered a large portion of the group home range. This result is in agreement with Symington's [1988] finding of the existence of core areas distributed throughout the group home range of *Ateles paniscus chamek*. Despite the relative high overlap between pairs of females and low individual core area exclusivity, we did not find a single area of the home range in which all 21 study individual females' core areas overlapped, and the size where the core areas of 20 females overlapped was less than 1 ha. Overall, this pattern indicates that females are to some extent spacing themselves out within the group home range, but without any substantial exclusive use of core areas. This finding agrees with what Wrangham (1979) reported for chimpanzee females at Gombe, but at the same site Williams et al. (2002) found a pattern of small overlapping core areas between chimpanzee females with resident females having high core-area fidelity. Emery Thompson et al. (2007) show that resident chimpanzee females at Kibale occupied core areas containing the most preferred foods. This supports the notion of exclusive core areas being only relevant at times of food scarcity, when defending an exclusive core area with critical food may become beneficial [van Roosmalen, 1985; Wallace, 2006].

Group tenure was a good predictor of core area quality. The time spent in the group may mediate competition for resources among females as the longer a female was in the group the better quality her core area, although we need to use caution in interpreting this finding as some females were already in the group at the beginning of the study and thus it was not possible to know their exact group tenure. The flexibility of fission-fusion dynamics creates opportunities for spatial patterns to differ among group members, allowing longer-term resident females to outcompete new immigrants for better quality areas. In a heterogeneous landscape where food availability varies across the habitat, such as the dry forest biome of the study site [Frankie et al. 2004], females are expected to compete for access to high quality areas [Sterck et al. 1997], which could be reflected in differential reproductive success as shown in chimpanzees [Emery Thompson et al. 2007; Kahlenberg et al. 2008]. We do not have data on reproductive success, but in another spider monkey species (*A. paniscus chamek*) the females most vulnerable to aggressive displacements had the longest interbirth intervals [Symington 1988], although the study was probably not sufficiently long to obtain a reliable dataset on interbirth intervals. In our study group aggression was typically directed by longer-term resident females against newly immigrant females at food trees (Asensio et al. 2008). It would have been interesting to know whether the most vulnerable females of Symington's (1988) study were newly immigrants, and whether such aggression occurred within high-quality core areas.

Core area overlap between pairs of adult females was best explained by the association index, dyadic tenure, quality of the overlapping area, while controlling for the combined size of the two core areas involved. The positive effect of the association index is not surprising as the more time females spend together in the same subgroup the more likely their individual core areas overlap. This is similar to what is found in other mammals in which the degree of

interaction between individuals is correlated with their spatial overlap [*Giraffa camelopardalis*, Carter et al. 2013; *Artibeus watsoni*, Chaverri et al. 2007; *Tursiops truncatus*, Frère et al. 2010]. The dyadic tenure, i.e. the time two individuals spent simultaneously in the group without being necessarily together in the same subgroup, independently had a similar effect. This suggests that in addition to using the same area because they are in the same subgroup, females with longer dyadic tenure are also intensively using the same areas when they are not together. Thus, females could reduce competition by fissioning into smaller subgroups and avoid the simultaneous use of resources. However, they are more likely to use the same resources as longer-known partners (i.e. long dyadic tenure), albeit at a different time, resulting in larger overlap of their core areas. In the best model there was also a positive effect of habitat quality in the overlapping area. This effect suggests that females more often use high-quality areas intensively used by others. It is important to note that the study group had a higher female immigration rate (9 in 72 months: 2.2 females per year) than other spider monkey groups (0.7 females per year: Shimooka et al. 2008). It is possible therefore that the high demographic fluidity, due to this higher female immigration rate along with a previously unreported high fluidity of males [Aureli et al. 2013], affected female ranging and association patterns.

In conclusion, the flexibility of spider monkeys' fission-fusion patterns creates opportunities for differential space use resulting in individual female core areas, but with a low degree of exclusive use. Group tenure played a central role in the quality and overlapping patterns of these core areas. Our findings suggest that despite the possibility of fissioning, spider monkey females still compete for access to distinct but overlapping high-quality core areas. Future research should examine whether, like in chimpanzees, having better quality core areas results in fitness benefits for spider monkey females.

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524

525

Figure legends

Table 1. GLMs used to explain core area quality with their corresponding AIC values.

Table 2. GLMs used to explain core area effectiveness with their corresponding AIC values.

Table 3. LMMs used to explain dyadic core area overlap with their corresponding AIC values.

Figure 1. Example of the relationship between location sample size and home range size for a female with more than 3,000 location points.

Figure 2. The overlay of the 21 individual female core areas and known food tree locations (marked by circles, which size represents the relative tree size according to its DBH). Different colors from dark green (from only one female) to dark red (up to 20 females) illustrate the gradient of overlap intensity among core areas. The outer dashed polygon represents the overlay of the seasonal home ranges across the 4 years of the study (509ha; Asensio et al. 2012b).

Figure 3. Core area size as a function of the overlap intensity of the females' core areas.

Figure 4. The sum of food tree DBH as a function of the overlap intensity of the females' core areas.

Figure 5. Depiction of the relationship between group tenure (in months) for the 21 females and core area quality (expressed as the sum of food tree DBH in cm) and core area effectiveness (expressed as the density of food trees per ha). The best fitting lines are presented for illustrative purposes.

Figure 6. Depiction of the relationship between dyadic tenure (in months) and core area overlap (%). The best fitting line is presented for illustrative purposes.

Figure 7. Depiction of the relationship between dyadic association index and core area overlap (%). The best fitting line is presented for illustrative purposes.

Figure 8. Depiction of the relationship between the sum of food tree DBH (in cm) and core area overlap (%). The best fitting line is presented for illustrative purposes.

Table 1

Model	**AIC**
Tenure*	429
Tenure*, Distance to the group center	431
Distance to the group center	437

*$p<0.05$

Table 2.

Model	**AIC**
Tenure*	41.9
Tenure*, Distance to the group center	43.5
Distance to the group center	49

*p<0.05

Table 3.

Model	**AIC**
Tenure*,Association index*,DBH*,Sum of core areas*	-362
Tenure*,Association index*,Sum of core areas*	-360
Tenure*,Association index*,DBH*	-328
Tenure*,Association index*	-324
Tenure*,DBH*,Sum of core areas*	-316
Association index*,DBH*,Sum of core areas*	-313
Tenure*,Sum of core areas*	-311
Association index*,DBH*	-310
Tenure*,DBH*	-279
DBH*,Sum of core areas*	-272
Tenure*	-263
DBH*	-262
Association index*,Sum of core areas*	-246
Sum of core areas*	-240
Association index*	-194

*$p<0.05$

Figure 1.

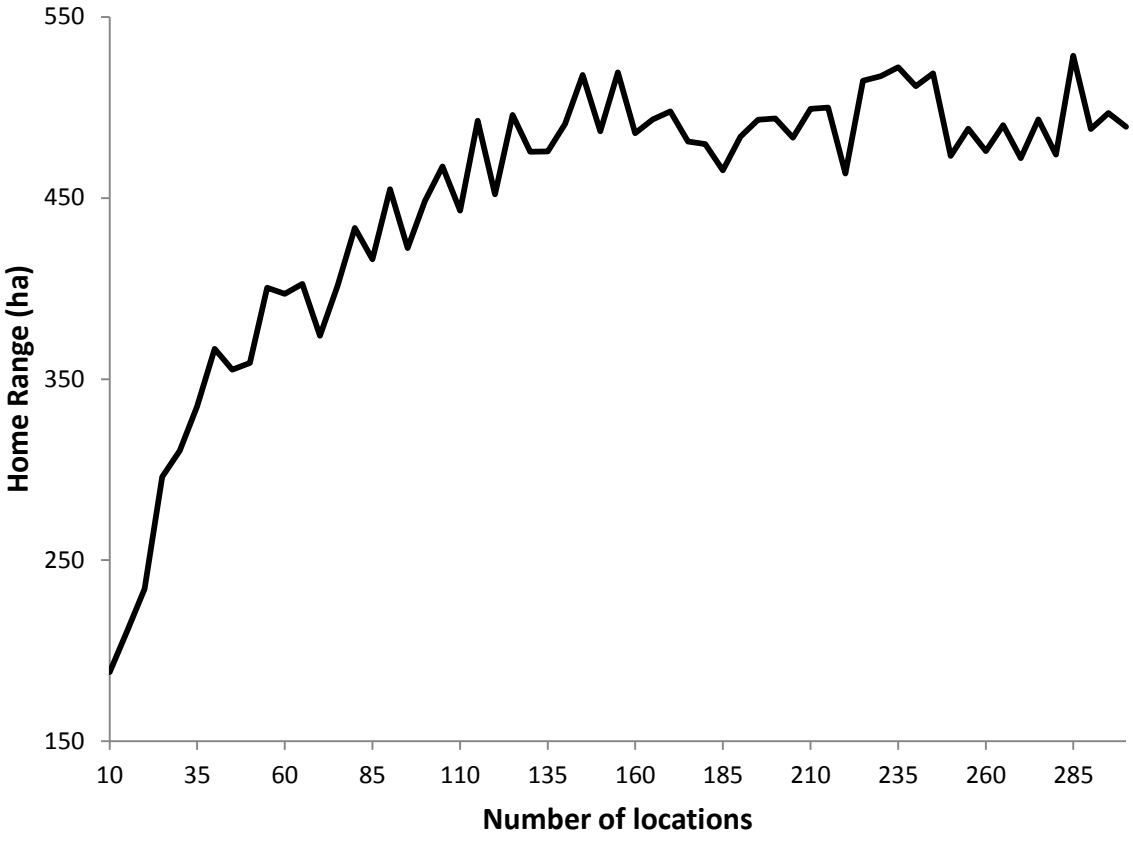

550
450
350
250
150
Home Range (ha)
10
35
60
85
110
135
160
185
210
235
260
285
Number of locations

Figure 2

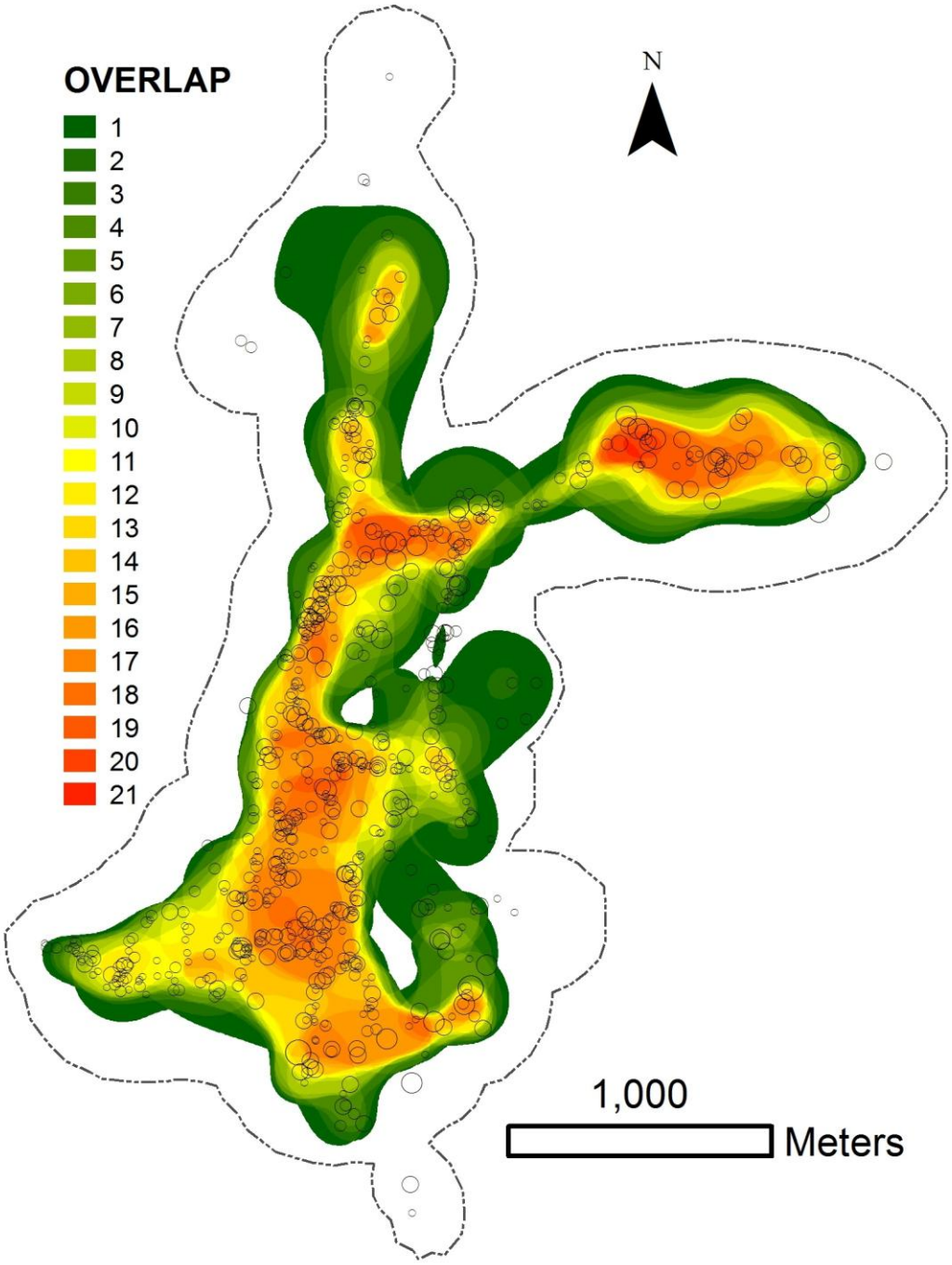

OVERLAP
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
N
1,000
Meters

Figure 3

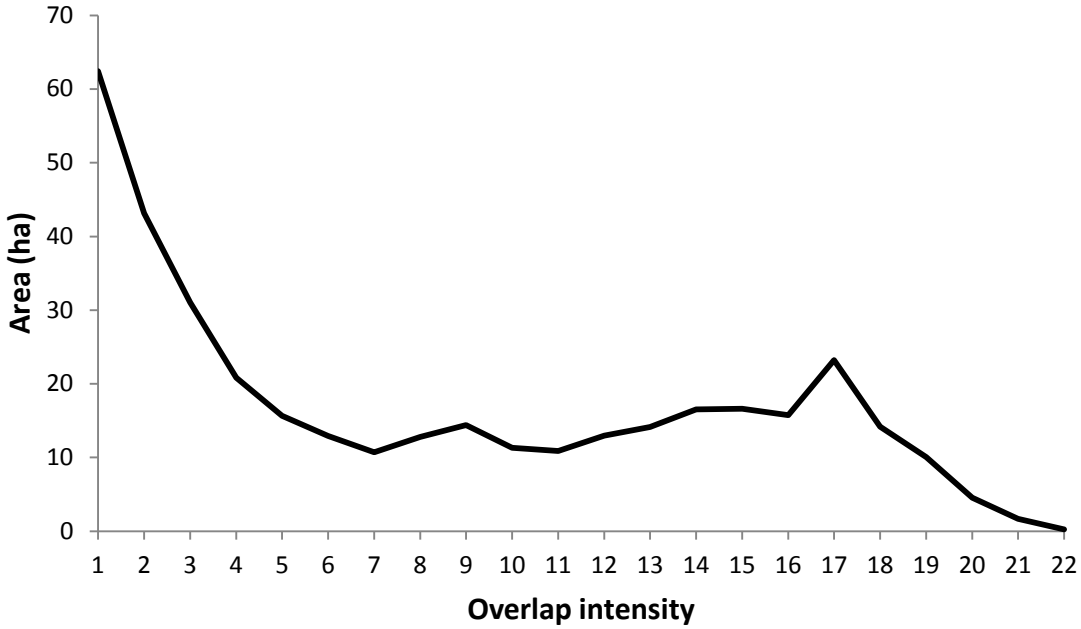

70
60
50
40
30
20
10
0
Area (ha)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Overlap intensity

Figure 4

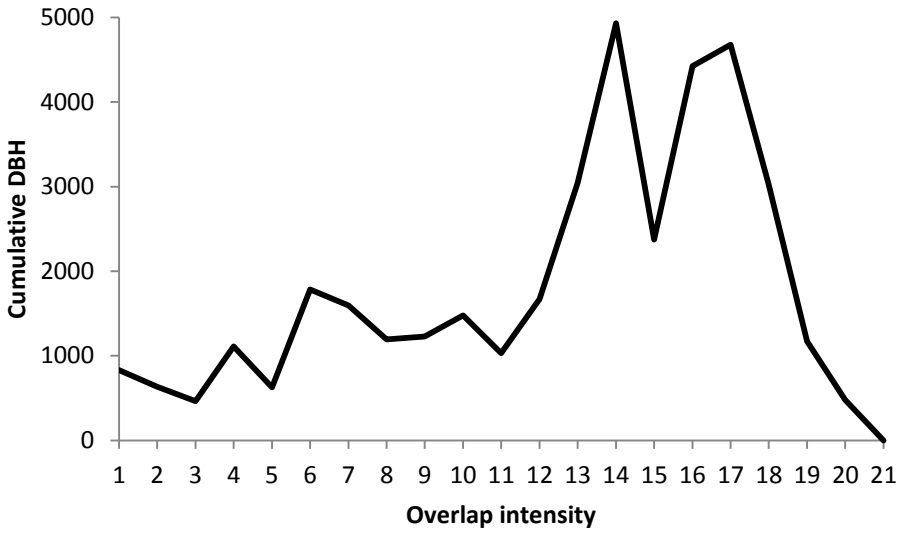

5000
4000
3000
2000
1000
0
Cumulative DBH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Overlap intensity

Figure 5

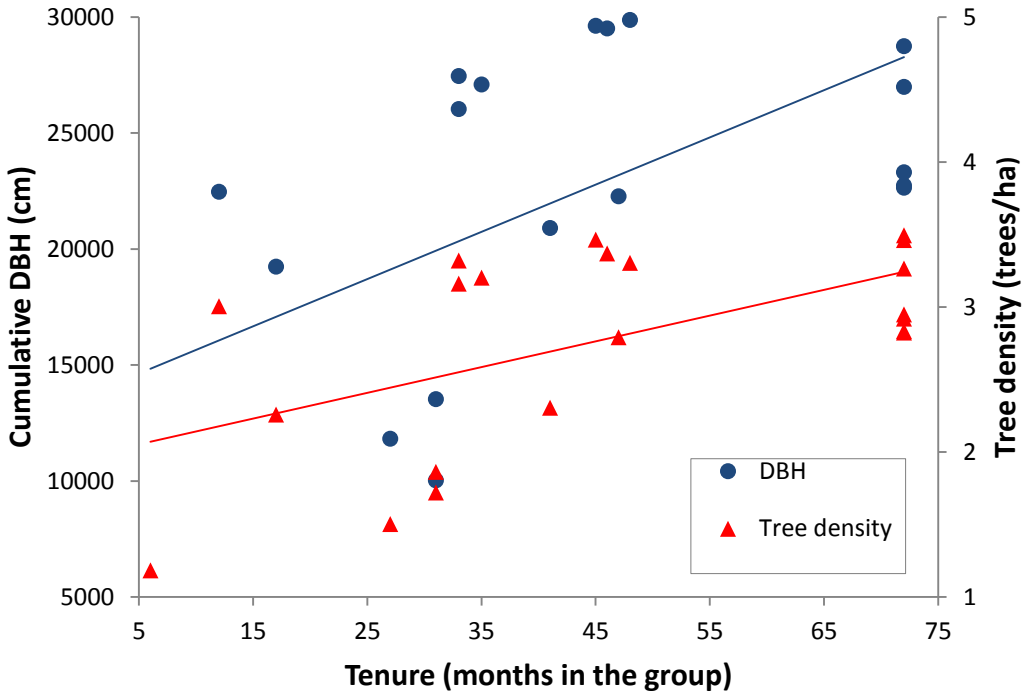

30000
25000
20000
15000
10000
5000
5
4
3
2
1
Cumulative DBH (cm)
Tree density (trees/ha)
5
15
25
35
45
55
65
75
Tenure (months in the group)
DBH
Tree density

Figure 6

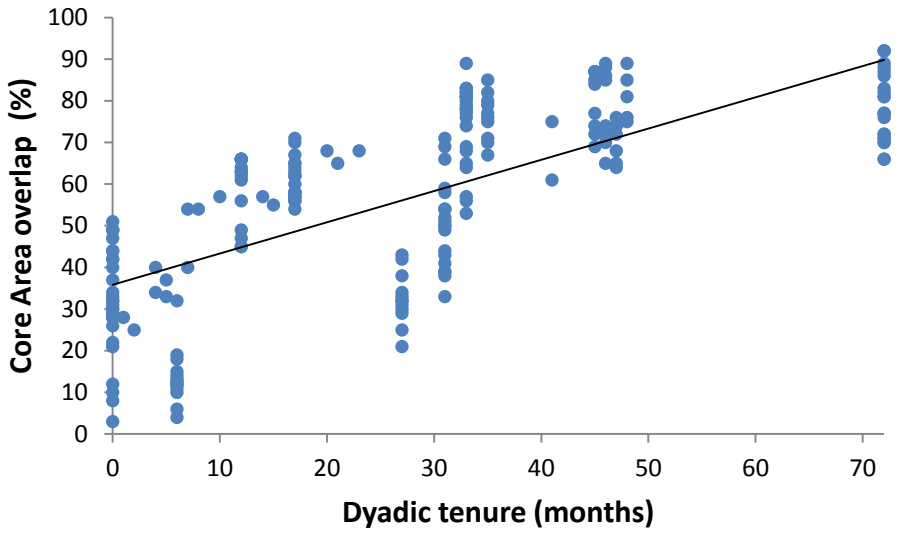

Core Area overlap (%)
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Dyadic tenure (months)

Figure 7

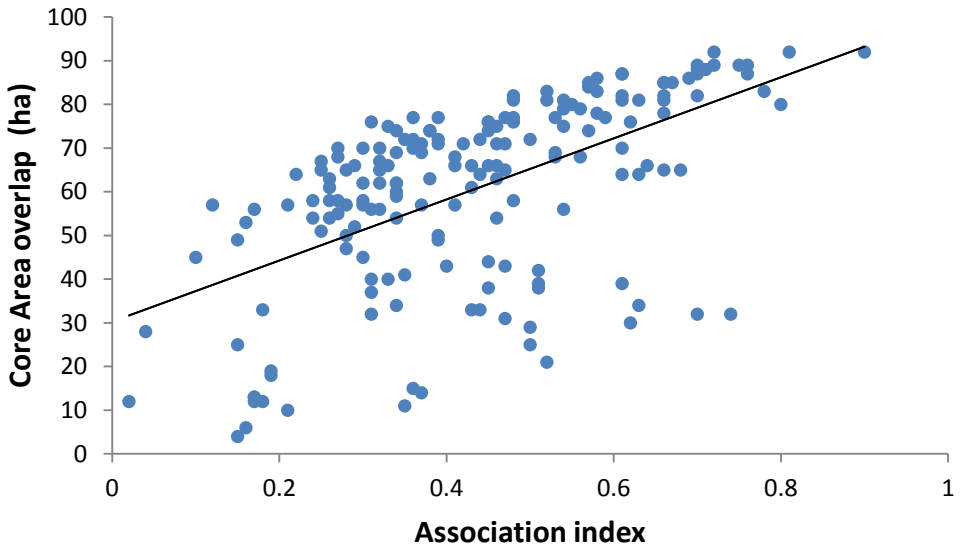
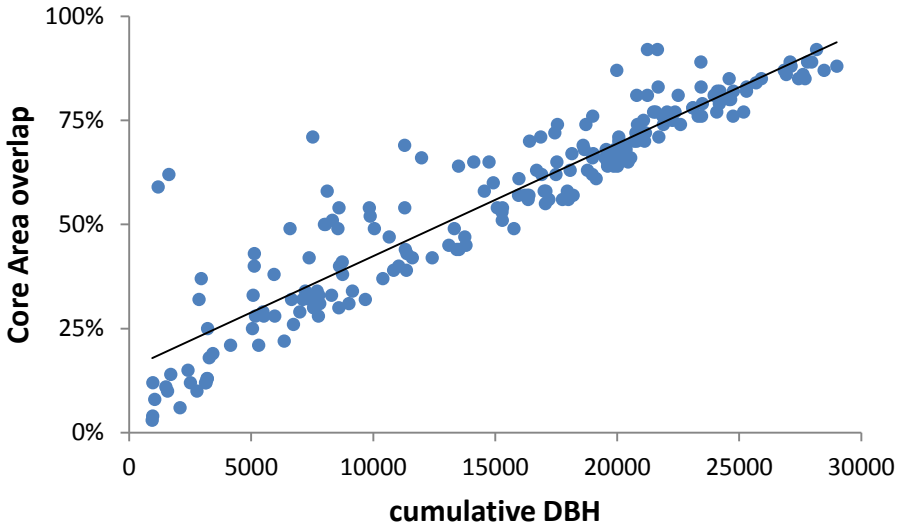

Core Area overlap (ha)
100
90
80
70
60
50
40
30
20
10
0
0
0.2
0.4
0.6
0.8
1
Association index

Fig 8


100%
75%
50%
25%
0%
Core Area overlap
0
5000
10000
15000
20000
25000
30000
cumulative DBH