Journal of Mammalogy, 96(1):120–128, 2015
DOI:10.1093/jmamma/gyu012

Socio-spatial organization and kin structure in ocelots from integration of camera trapping and noninvasive genetics

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Kin selection theory predicts that under certain conditions animals will tolerate related individuals in their home ranges. We examined the relationship between spatiotemporal overlap and genetic relatedness in ocelots (*Leopardus pardalis*) to determine if kin selection plays a role in structuring ocelot populations. We used 3 years of camera trapping to examine the spatial organization of an ocelot population on Barro Colorado Island in Panama. We also placed camera traps on ocelot latrines to match photographs of individual ocelots with microsatellite genotypes from feces. Strengths of spatiotemporal overlap between individual ocelots were calculated using a half-weight association index based on how often individuals were photographed at the same camera within 30 days of one another. We calculated relatedness between individuals based on 11 variable microsatellite loci. Male ocelots overlapped with ≤ 11 females, and females overlapped with ≤ 7 males. We detected no clear evidence of strict intersexual territoriality in either sex. Mean overlap among males was more than 5 times greater than overlap among females; however, spatiotemporal overlap was strong between some female pairs. Overall, overlapping individuals were more related to one another than was the sample population as a whole, consistent with the hypothesis that kin selection influences ocelot spatial organization. This finding was driven by relatedness among overlapping females, and by relatedness among overlapping individuals of opposite sex, but not by overlapping males.

Key words: Barro Colorado Island, genetic relatedness, *Leopardus pardalis*, ocelot, space-use overlap, spatial organization

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Space use by individual animals is dictated by the need to acquire the resources necessary to maximize fitness such as food, mates, or den sites. Consequently, the spatial organization of individuals at the population level is determined by intraspecific competition for these resources, as well as by the abundance and dispersion of the resources themselves (Clutton-Brock and Harvey 1978; Macdonald 1983; Sandell 1989; Nicholson et al. 2011; Lührs and Kappeler 2013). If the fitness benefits of defending these resources outweigh the costs, then animals will defend exclusive territories. Conversely, if the fitness costs of territory defense outweigh the benefits, individuals should overlap in their use of space (Davies and Houston 1984). At low population density the cost of territoriality may be low because there will be few competitors from which a home range must be defended. At high population density, however, the cost of defending a territory from many competitors may be high, resulting in overlap in space use among individuals. The amount of overlap may in turn be determined by the dispersion of resources in the environment. If resources are heterogeneously distributed in the environment as is common in most natural systems (Johnson et al. 2002), then when conditions are favorable, multiple individuals may share resources

within a given area at little cost to each other (i.e., the resource dispersion hypothesis—Macdonald 1983; Carr and Macdonald 1986). This outcome does not negate all competition between individuals that overlap however, especially during times of resource shortage (Johnson et al. 2002).

If individuals overlap in their space use and are competing for shared resources, one mechanism that could minimize fitness costs due to competition is kin selection. Kin selection theory predicts that organisms will be more tolerant of competition from relatives than from unrelated individuals because when relatives share limited resources, inclusive fitness benefits offset the individual fitness costs of competition (Hamilton 1964; Wade and Breden 1987). Female philopatry and male dispersal are typical among mammals (Greenwood 1980) including solitary carnivores (Waser and Jones 1983), thus relatedness among individuals sharing space is often higher among females than among males. Relationships between spatial overlap and genetic relatedness have been investigated for many mammals including carnivores (Kitchen et al. 2005; Moyer et al. 2006; Nicholson et al. 2011); however, such relationships for small solitary felids are poorly understood and seldom investigated (but see Janečka et al. 2006) because solitary carnivores are generally elusive, and are thus difficult to study in the wild. By integrating 2 noninvasive techniques, we developed a novel approach to gain new insight into this relationship for a solitary felid.

We examined the relationship between spatiotemporal overlap and genetic relatedness in an ocelot (*Leopardus pardalis*) population to determine if spatial structure was consistent with predictions arising from kin selection theory. We worked on Barro Colorado Island, an island in the Panama Canal that offers a unique opportunity to investigate this relationship because it has the highest ocelot density ever reported (> 1.5 individuals/km^2—Rodgers et al. 2014), likely due to an abundant prey base, and release from competition from larger predators (Moreno et al. 2006). Studying such a population is particularly interesting because it provides insight into the dynamics and flexibility of socio-spatial organization at one extreme of the population density spectrum. Ocelots, like most felids, are typically described as solitary and territorial (Sunquist and Sunquist 2002); however, reported patterns of spatial overlap between individuals vary. As is the norm for most carnivore species (Sandell 1989), all ocelot studies report intersexual overlap in which males overlap with several females. As for intrasexual overlap, studies have reported that both female and male ocelots maintain exclusive territories (Tewes 1986; Emmons 1988; Laack 1991), males maintain exclusive territories with female home ranges overlapping one another (Ludlow and Sunquist 1987), or intrasexual overlap within both sexes (Dillon and Kelly 2008). This plasticity in spatial organization could be the result of differences in population density or differences in resource dispersion (Sandell 1989). Alternatively, observed differences between ocelot populations could be an artifact of small sample sizes from telemetry studies that only followed a portion of the population, thus underestimating true spatial overlap (Sandell 1989; Dillon and Kelly 2008).

We had 2 goals in this study. First, we investigated patterns of intersexual and intrasexual overlap between individuals to gain insight into spatial organization of ocelots in a high-density population. We hypothesized that ocelots would overlap in their use of space both between and within each sex and would not defend territories because of the high cost of defending a home range from many competitors at high population density. To test this hypothesis, we conducted a camera-trap study of the ocelot population on Barro Colorado Island for 3 years. Camera trapping enabled us to sample the entire adult population in our study area throughout the study period, which would have been logistically unfeasible with radiotelemetry. To our knowledge, this is the 1st study to examine overlap in space use in a carnivore species with camera trapping.

Second, we evaluated whether kin structure was evident within the population to determine if genetic relatedness plays a role in structuring ocelot spatial organization. Space use for females is most strongly tied to allocation of resources necessary for rearing offspring, whereas for males, the most important resource is likely access to females (Clutton-Brock and Harvey 1978; Sandell 1989). We hypothesized that for both sexes inclusive fitness benefits can reduce costs of sharing these resources with overlapping individuals. As a result, individuals should be more tolerant of sharing space and resources with relatives than with nonrelatives. Therefore, we predicted that individuals of the same sex that overlap in their use of space would be more closely related than individuals of the same sex in the population as a whole. Finally, we hypothesized that individuals would avoid overlapping with relatives of the opposite sex to avoid inbreeding (Pusey 1987). Therefore, we predicted that relatedness between males and females that overlap with one another would be low. To test these predictions, we used a novel approach that integrated camera trapping with noninvasive genetics.

Materials and Methods

Study site.—Field work was conducted on Barro Colorado Island, a 1,543-ha island in the Panama Canal waterway, at a research station operated by the Smithsonian Tropical Research Institute (Fig. 1). Barro Colorado Island (9°10′N, 79°51′W) sits within Gatun Lake, an artificial body of water created in 1912 by the damming of the Chagres River to create the Panama Canal, and is part of the protected 54-km^2 Barro Colorado Nature Monument. Vegetation is tropical moist forest, and topography is dominated by hills that reach a maximum elevation of 165 m above sea level. Mean temperature is 27°C with an average annual precipitation of 2,600 mm, with 90% of rainfall occurring from May to November (Leigh 1999). Forest cover on the island is a mix of old growth forest and mature secondary forest > 80 years old, all of which is suitable habitat for ocelots.

Spatiotemporal overlap.—We measured spatial overlap between individual ocelots using an array of 17 Reconyx PC900 and RC55 trail cameras (Reconyx Inc., Holmen, Wisconsin), from 6 February 2010 to 31 December 2012. Cameras were placed along trails to maximize capture probability, and

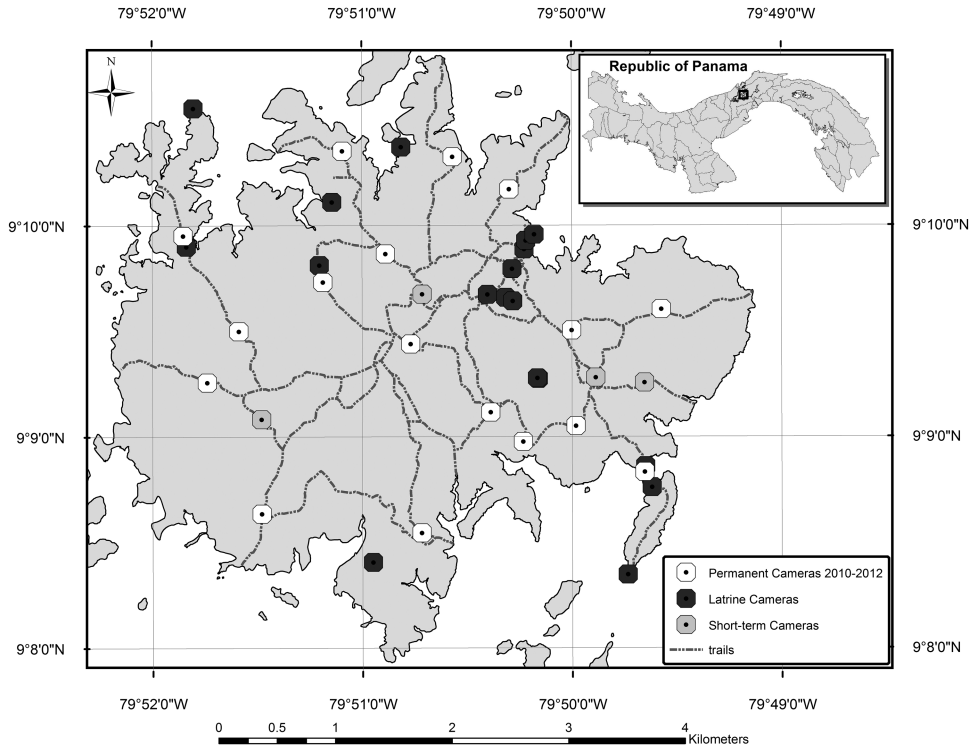

Fig. 1.—Map of Barro Colorado Island, Panama, showing the locations of camera traps placed along trails and at ocelot (*Leopardus pardalis*) latrines.

distributed evenly throughout the island so that gaps between cameras that could contain an ocelot home range were unlikely (Fig. 1). Cameras were checked at least every 6–7 months, and replaced or repaired if no longer functioning. Some gaps in data collection arose for most cameras due to flooding, tree falls, or ant colonization, especially during the wet season; however, on average all cameras were active for > 60% of the 3-year study period, and these monitoring gaps were accounted for in the analysis. We added 4 additional cameras to the array for shorter periods in 2011 and 2012. We identified individual ocelots from photographs based on unique spot patterns (Trolle and Kery 2003). Each camera station consisted of 1 camera and thus could photograph only one side of an animal at a time. For all individuals, however, we observed right and left sides in the same photo sequence at least once either before or during our study period, allowing us to pair right and left profiles for individual identification.

To quantify the degree of spatiotemporal overlap between individual ocelots, we used the program SOCPROG (Whitehead 2009) to calculate the strengths of association between individuals based on how often they were photographed at the same camera traps. We used a half-weight association index (Cairns and Schwager 1987) in which pairwise association values can range from 0 (individual A and individual B were never photographed at the same camera) to 1 (individual A and individual B were photographed at the same camera during every 30-day sampling period in which both individuals were photographed at least once). This index can be conceptualized as the proportion of time during the study that a pair of individuals spent using the same area, and thus as a measure of spatiotemporal overlap. The half-weight association index has historically been used in the study of gregarious animals, for example, as a measure of association based on how often 2 individuals are observed in the same social group. For our analysis we replaced group with camera, providing a novel method to examine association between solitary animals. The half-weight association index was also chosen over other related association indices, because it is unbiased by missing data (Whitehead 2008), which is important given gaps in data collection due to occasional camera trap failure. The choice of 30-day sampling periods was a balance between being long enough to contain sufficient data (median for females was 1.7 photo captures/30 days; median for males was 3.5 photo captures/30 days) and being short enough to be biologically meaningful (i.e., individuals in the same area within 30 days of one another could compete for the same resources). We restricted these analyses to 18 individuals present in the study area all 3 years, and who were either adults or subadults in 2010 and mature adults in both 2011 and 2012 to avoid bias from including juveniles still inhabiting their natal range.

Next, we tested whether observed spatiotemporal associations between individuals differed from a null model in which associations between individuals were random. Because association index values between individuals are nonindependent, we used the Bejder et al. (1998) permutation test in SOCPROG to permute our matrix of association values within samples (Whitehead 2008). We ran 20,000 permutations of our matrix with 1,000 trials per permutation. We used the difference in the coefficient of variation (*CV*) between our observed association matrix and randomly generated association matrices as a

test statistic to determine if our observed data differed from random. A nonrandom matrix would be expected to have significantly greater variation than random (Whitehead 2008). We also used this test to determine which pairs of individuals showed associations or disassociations greater than random expectations. Last, we used a Mantel test (Mantel 1967) with 10,000 random permutations to determine if males had significantly larger mean association index values than did females.

Scat surveys.—Ocelots commonly defecate at latrine sites used by multiple individuals of both sexes (Moreno and Giacalone 2008; Rodgers et al. 2014). These latrines are typically located in large cavities or overhanging buttresses of large trees, underneath buttresses of fallen trees, or underneath human structures. All scats used in this study were found at such latrines. Seven latrines were located during searching from 16 March to 15 April 2011, 5 of which were still active in 2012. To find additional latrines in 2012, we walked all 39.5 km of trails on Barro Colorado Island (Fig. 1) a minimum of 3 times (once every 33 days) from 29 January to 6 May. In addition, we walked > 390 km of random, off-trail transects throughout the island in search of latrines. Once a latrine was located all scats were removed, and it was revisited every 4–7 days to collect additional scats until 6 May 2012. Additionally, 18 cameras were placed on ocelot latrines between 29 January and 5 May 2012 to photograph defecating ocelots in order to match photographed individuals with genotypes from noninvasive genetics.

Genotyping.—We extracted DNA from 80 scats using the Qiagen QIAamp DNA stool mini kit (Qiagen, Valencia, California) following the manufacturer's recommendations (QIAamp DNA Stool Handbook, 2nd edition, April 2010). For species identification, we amplified a 126-bp fragment of the mitochondrial gene ATP6 by polymerase chain reaction (PCR) using primers ATP6-DF3 and ATP6-DR1 following conditions from Chaves et al. (2012). PCR products were sequenced on an Applied Biosystems 3730xl DNA analyzer, and resulting sequences were compared to reference sequences using the online tool DNA Surveillance Carnivora (Chaves et al. 2012).

To identify individuals and determine genetic relatedness, we initially screened 22 microsatellites originally developed for the domestic cat *Felis catus* (Menotti-Raymond et al. 1999). To avoid linkage disequilibrium, we selected these loci for their broad distribution throughout the genome based on linkage maps for the domestic cat (Janečka et al. 2011). The family Felidae has > 95% chromosomal conservation among species (Davis et al. 2009) so we assumed genomic position of loci to be shared between the ocelot and domestic cat genomes. Of these initial 22 loci, we ultimately chose the 11 loci used in our study (Supporting Information S1) based on success of amplification, degree of variability, and ease and clarity of allele scoring.

To identify individuals, all scat samples were initially genotyped at 4 microsatellite loci (FCA075, FCA077, FCA088, and FCA132). We then genotyped one sample from each identified individual at an additional 7 loci (FCA008, FCA117, FCA124, FCA126, FCA171, FCA229, and FCA082) for relatedness analyses (see Supporting Information S2 for PCR conditions). As DNA from noninvasively collected fecal samples is often low quality and prone to genotyping errors such as allelic dropout and false alleles (Taberlet et al. 1999; Broquet et al. 2007), we used a multiple tubes approach (Taberlet and Fumagalli 1996) whereby each sample was genotyped 3–9 times until reliable consensus genotypes were obtained. Genotypes were considered reliable if a minimum of 3 identical heterozygote profiles, or 5 identical homozygote profiles, were observed. Probabilities of individual identity (Waits et al. 2001) and checks for deviation from Hardy–Weinberg equilibrium were calculated using the program GENALEX (Peakall and Smouse 2006).

To determine the sex of ocelots from scat samples, we used felid-specific primers that amplify a 200-bp segment of the AMELY gene (Murphy et al. 1999), which is only present on the Y-chromosome of males (see Supporting Information S2 for PCR conditions). PCR amplifications were performed in triplicate along with male and female positive controls and a negative control, and PCR products were visualized on agarose gel. Samples were identified as male if they showed amplification of the Y-linked marker for all 3 replicates, and were identified as female if no amplification was observed.

Genetic relatedness analyses.—To determine if individuals who overlapped in their space use were more closely related than the population as a whole, we first used our microsatellite genotype data to calculate pairwise relatedness between all sampled individuals using the regression estimator of Lynch and Ritland (1999) with the program COANCESTRY (Wang 2011). This estimator calculates relatedness coefficients (R) between pairs of individuals based on the number of identical alleles the 2 individuals share by descent, while also taking into account allele frequencies in the entire sampled population. R values can range from −1 to 1, with positive R values indicating 2 individuals are more related than expected by chance, and negative R values indicating the opposite. We then tested if mean R values of individuals who overlapped in their use of space were larger or smaller than mean R values in the sampled population as a whole for all individuals, as well as for males and females only. To test for significance, we used COANCESTRY to carry out 1,000,000 bootstrapping permutations, and then compared our observed values with the distribution of permuted values. Due to our moderate sample sizes (n = 13 individuals identified from noninvasive genetic sampling), we used an alpha of 0.10 to balance type I and type II errors. Because genotypes were only obtained from a segment of the population, and not all genotyped individuals could be matched with photographed individuals, we defined overlapping pairs as individuals that used the same latrine during our scat sampling period, or for ocelots with genotype-photograph matches, as individuals who were photographed at the same camera during the same 30-day period.

Results

Spatiotemporal overlap.—We recorded 2,376 independent photograph sequences of ocelots during 12,015 camera-trapping

nights, including 126 sequences of juveniles and 2,250 sequences of adults or subadults. We identified 37 individuals including 19 females, 15 males, and 3 kittens that disappeared before sex could be determined. For our analyses of spatiotemporal overlap we used 19 core individuals (7 males and 12 females) chosen because they were adults in all 3 years, with the exception of 2 males and 2 females who were subadults in 2010 but mature adults by 2011. All other individuals were born, died, or disappeared during the study period, and were excluded from analyses to avoid biasing of overlap results. The 19 core individuals accounted for 2,004 independent photo sequences, with individual males captured a median of 123 times (range 106–300), and individual females captured a median of 60 times (range 28–312).

Male ocelots overlapped on average with 8.14 (SE = 0.83) females and 6.71 (SE = 0.18) other males, whereas females overlapped on average with 4.75 (SE = 0.64) males and 3.41 (SE = 0.47) other females. Based on half-weight association indices, overlap was > 5 times higher among males ($\bar{X}$ = 0.299; SE = 0.048) than among females ($\bar{X}$ = 0.057; SE = 0.015; $P < 0.0001$). The distribution of association index values also differed for males versus females (Fig. 2). The CV of our real-overlap matrices was greater than the mean CV of our randomly permuted matrices ($P < 0.0001$) for both females (2.192 versus 1.460) and males (0.694 versus 0.420), indicating both real matrices were nonrandom (Whitehead 2008). Five of 66 (7.5%) female dyads showed overlap greater than random expectations, whereas 5 of 21 (23.8%) male dyads showed overlap greater than random expectations ($P < 0.05$; Fig. 3).

Genetic relatedness and kin structure.—We collected 80 scats from 23 different ocelot latrines on Barro Colorado Island, and we genetically confirmed 68 (85%) as being from ocelots. From these 68 scats, we obtained complete 4-locus genotypes from 55 samples (81%), which consisted of 13 unique genotypes and 42 recaptures. The probability of 2 different individuals sharing the same genotype (probability of individual identity—Waits et al. 2001) from our 4 initial loci was 0.00031 among unrelated individuals ($P_{(ID)}$), and 0.038 among siblings ($P_{(ID)sibs}$). Six individuals were identified as male and 7 as female. Eight of 9 individuals detected in 2011 were detected again in 2012. We matched genotype data with photographic data from our latrine cameras for 8 individuals (4 males and 4 females). The 13 individuals were all successfully genotyped at all 11 loci, except for 2 individuals which were genotyped at 10 loci. Mean number of alleles per locus was 5 (range 3–6). None of the 11 loci deviated significantly from Hardy–Weinberg equilibrium (Supporting Information S1).

Mean R for the entire sampled population (n = 13) was −0.0832 (Var = 0.0422). There was no difference in mean relatedness between the sexes (female R = −0.0983, Var = 0.0203; male R = −0.0754, Var = 0.0372; P = 0.375). When both sexes were considered together, overlapping dyads were more related to one another (R = −0.0307, Var = 0.0399) than the population as a whole (R = −0.0832, Var = 0.0422; P = 0.022; Fig. 4A). Relatedness between overlapping male dyads (R = −0.1193, Var = 0.0321) was not different than relatedness between all male dyads (R = −0.0754, Var = 0.0772; P = 0.190; Fig. 4B). Overlapping female dyads were more related to one another (R = −0.0250, Var = 0.0135) than were all female dyads (R = −0.0983, Var = 0.0203; P = 0.085; Fig. 4C). Overlapping intersexual dyads (male-female) were more closely related (R = −0.0142, Var = 0.0469) than were all intersexual dyads (R = −0.0784, Var = 0.0548; P = 0.0257; Fig. 4D).

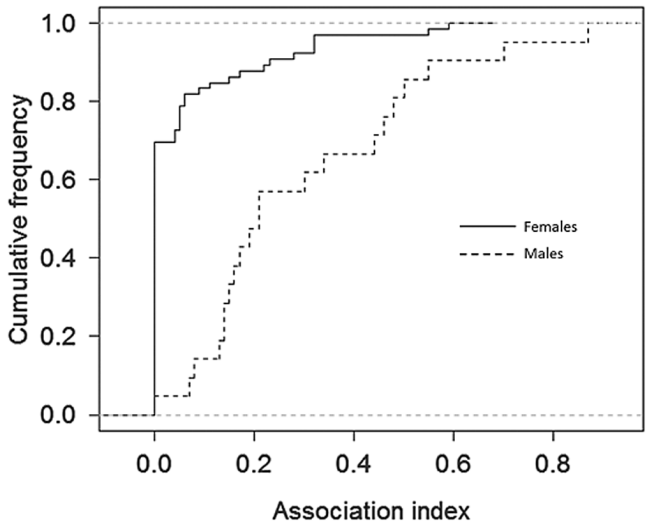

Fig. 2.—Cumulative frequency distributions of association index values among pairs of male versus female ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama. Half-weight association index values represent the strength of spatiotemporal overlap between same-sex dyads based on how often they were photographed at the same camera trap within the same 30-day interval.

Discussion

Kin selection theory predicts a positive relationship between space-use overlap and genetic relatedness among overlapping individuals of the same sex. We tested these relationships for a high-density population of ocelots, using a novel combination of camera trapping and noninvasive genotyping from fecal DNA. Both male and female ocelots overlapped with individuals of both the same and opposite sex. As predicted, female ocelots that overlapped in space were more related to each other than pairs of females in the population as a whole. For males no such relationship was found. These results are consistent with the hypothesis that kin selection influences spatial organization in female ocelots. Furthermore, our results contribute to emerging evidence that small felids are flexible in their social and spatial organization.

Spatiotemporal overlap.—Male ocelots overlapped with many different females during our study. Females also typically overlapped with several males (range = 1–7), potentially allowing females to exert mate choice. Mean strength of overlap was much greater among males than among females. Males overlapped with nearly all other males on the island to some extent, most males overlapped strongly with several other males (Fig. 3), and nearly a quarter of male-male dyads had

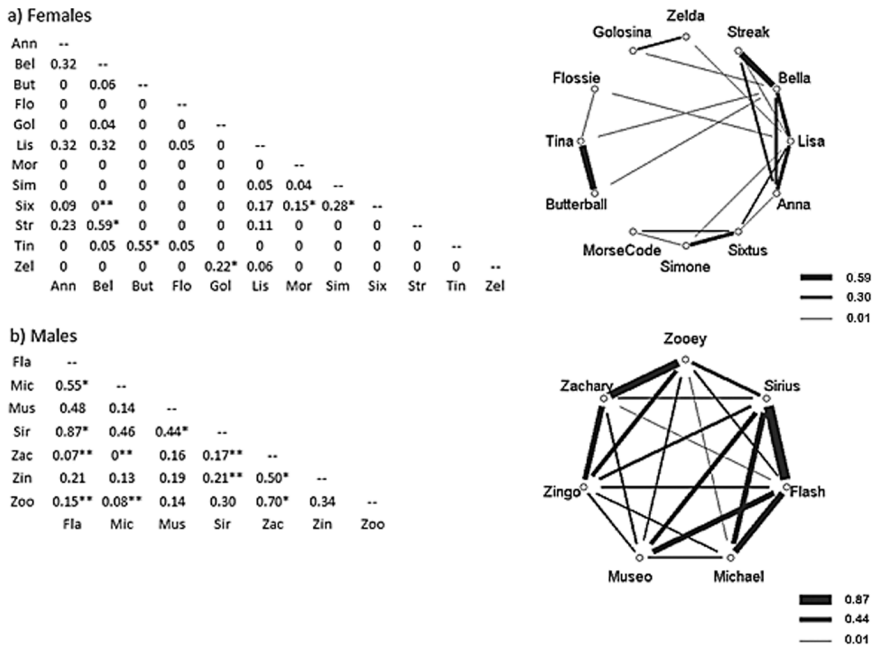

Fig. 3.—Half-weight association index values between pairs of a) female and b) male ocelots (*Leopardus pardalis*) from Barro Colorado Island, Panama, shown in both matrix and graphical format. Values and line weights represent the strength (on a scale of 0–1) of spatiotemporal overlap between pairs of individuals based on how often they were photographed at the same camera trap during the same 30-day period. Asterisks represent associations and double asterisks represent dissociations that differed from random expectations ($P < 0.05$).

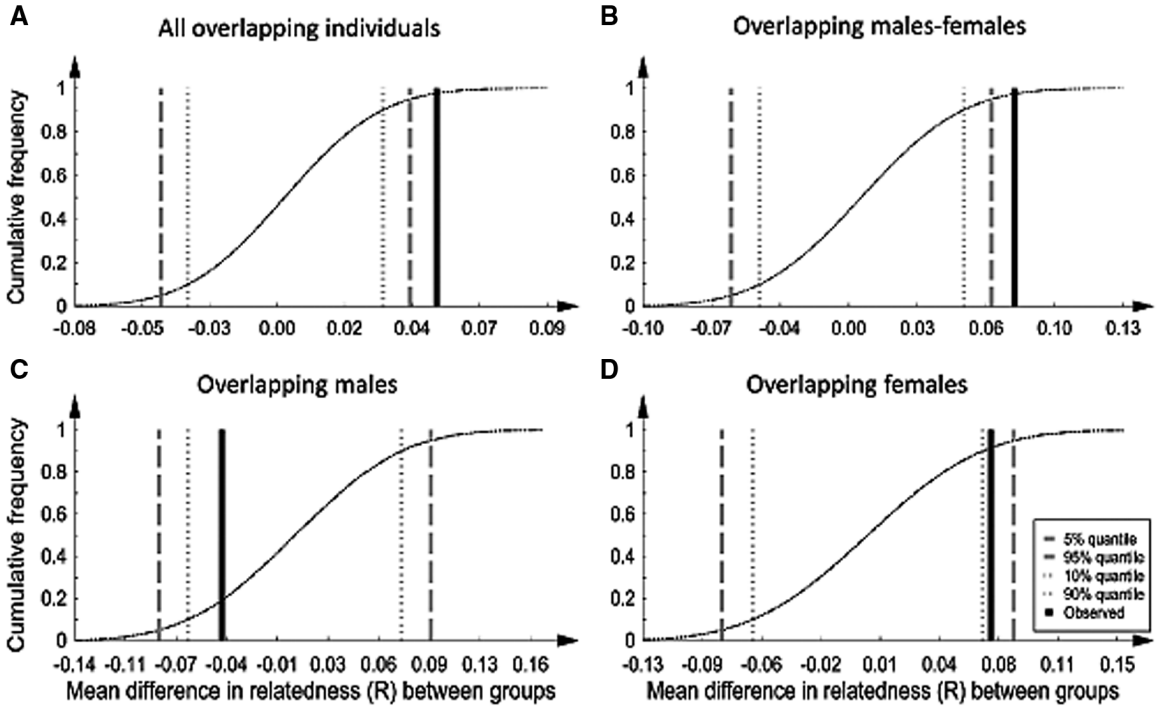

Fig. 4.—Relatedness of individual ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama, depending on sex and overlap of space use. Values shown are observed mean differences in relatedness between dyads of individual ocelots with overlapping space use (vertical bold lines) versus all dyads in the sampled population, along with the cumulative distribution of simulated differences from 1,000,000 randomly generated bootstrap replicates. Reference lines represent quantiles from the simulated distribution. A) All dyads, B) male-female dyads, C) male-male dyads, and D) female-female dyads.

stronger spatiotemporal association than expected by chance. All females overlapped with at least 2 other females during the study; however, the strength of this overlap was typically small, suggesting most females overlapped only in peripheral portions of their home ranges. Several female-female dyads, however, showed strong overlap in their use of space throughout the study (Fig. 3). The degree of intrasexual overlap was more extensive than most previous reports for ocelots (Sunquist

and Sunquist 2002), which supports our hypothesis that at high density it is costly for individuals to maintain territories and thus intrasexual overlap pervades.

The difference in mean strength of intrasexual overlap between males and females is likely the result of different strategies between the sexes in terms of maximizing fitness. For females, home range size should be determined by availability of nutritional resources for rearing young. For males, home range size is more likely to be determined by access to females for mating (Clutton-Brock and Harvey 1978; Sandell 1989). If population density and prey availability are high as in our study area (Terborgh 1992; and personal observations from camera trapping), females may contract their home range to minimize aggressive encounters with other females, as long as the home range is still large enough to contain sufficient resources for reproduction. For males however, decreasing home range size would also decrease the number of females with which they overlap, potentially decreasing fitness. Thus, the costs of overlapping and competing with other males could be less than the fitness benefits gained by overlapping with many females (Sandell 1989). This tradeoff may explain why males display a greater degree of overlap than females, but it does not explain why some females maintain strong overlap with other females. Philopatry could provide one possible explanation for instances of strong overlap among female dyads, whereby a daughter maintains a home range overlapping that of her mother. This behavior has been demonstrated in other felid species (Janečka et al. 2006; Goodrich et al. 2010). Unfortunately, we were not able to obtain complete genetic data from any of the female-female dyads with strong overlap to test this hypothesis directly.

Small felids exhibit substantial variation in their socio-spatial organization between species, ranging from exclusive home range defense in one or both sexes, to considerable home range overlap in one or both sexes (reviewed in Macdonald et al. 2010). In the genus *Leopardus*, margays (*Leopardus wiedii*) in Tamaulipas, Mexico displayed extensive home range overlap among males (Carvajal-Villarreal et al. 2012). In the Argentinian Pampas, both male and female Geoffroy's cats (*Leopardus geoffroyi*) displayed considerable intrasexual overlap (Manfredi et al. 2006), whereas in Chilean Patagonia, female Geoffroy's cats had overlapping home ranges but males did not (Johnson and Franklin 1991). Most inferences of spatial overlap in small felids, however, come from radiotelemetry studies that are based on small sample sizes, representing only a subset of individuals in the population because live capture of all individuals in a population is typically infeasible. As a result, it is likely that spatial overlap has often been underestimated in past studies (Sandell 1989; Johnson and Franklin 1991; Dillon and Kelly 2008). By using camera trapping, we were able to include most residents, if not the entire population in our analyses, giving us a more complete picture of true spatial overlap.

Most studies of ocelots have observed exclusive territories in one or both sexes (Tewes 1986; Ludlow and Sunquist 1987; Emmons 1988; Laack 1991). Contrarily, in broadleaf forest in Belize where ocelot density is more than 5 times lower than the density in our population, and where home ranges are large compared to most populations, Dillon and Kelly (2008) observed substantial intrasexual overlap in both sexes. Dillon and Kelly (2008) attributed this intrasexual overlap to the high cost of defending a large home range. In contrast, we observed intrasexual overlap in our population where home ranges are nearly an order of magnitude smaller than in Belize (1.5 km^2 for females and 3.5 km^2 for males—Moreno et al. 2012), but where density is extremely high (Rodgers et al. 2014). In better-studied large felid species such as pumas (*Puma concolor*), leopards (*Panthera pardus*), and tigers (*Panthera tigris*), degree of intrasexual overlap is highly flexible between populations (Goodrich et al. 2010; Macdonald et al. 2010). Recent evidence from our study and others suggests that social organization in small felids may be highly flexible within species as well.

Genetic relatedness and kin structure.—Overall, individuals in the sampled population were less related than would be expected by chance (mean $R < 0$). This result may indicate that the island population maintains gene flow with nearby mainland populations, or has in the recent past. As the distance between the island and mainland is < 0.5 km at its closest point, some dispersal to and from the mainland, although potentially costly, is not improbable. Alternatively, the roughly 100 years since the island was separated from the mainland may not have been long enough to cause inbreeding and loss of genetic diversity in the absence of gene flow.

Some of our hypotheses regarding relationships between spatial overlap and genetic relatedness were supported, and others were not. Contrary to our prediction, overlapping opposite-sex dyads were more related than were all opposite sex dyads. On average, however, overlapping male-female dyads were not closely related ($R < 0$) so mating between overlapping individuals would still be unlikely to cause inbreeding. As females overlapped with multiple males during the study, females could potentially avoid mating with close relatives to further prevent inbreeding (Pusey and Wolf 1996). Kin recognition occurs in many mammal species (Blaustein et al. 1987; Mateo 2003). Captive female cheetahs (*Acinonyx jubatus*) prefer the urine scent of distantly related potential mates over that of closely related potential mates (Mossotti 2010), and female feral cats (*Felis catus*) willfully avoid mating with close relatives (Ishida et al. 2001). Kin recognition could contribute to the lower than expected levels of inbreeding observed in our island population of ocelots.

Relatedness among overlapping males was not different than relatedness among all male-male dyads. Relatedness between overlapping females was higher than between all female-female dyads, which is consistent with our hypothesis that overlapping females may counter costs of sharing resources with gains through inclusive fitness. Nevertheless, mean relatedness values for all classes of overlapping individuals (male-female, male-male, female-female) were still lower than expected by chance ($R < 0$). Thus, on average, even overlapping females were not closely related. In terms of our hypotheses however, the important finding is that overlapping females were more closely related than the population as a whole, and some were relatives.

Thus overlapping female pairs may be gaining some net benefit from inclusive fitness due to their spatial organization.

We were able to obtain genetic data from just one-half of our population, and we obtained photo-genotype matches from only a subset of those. As a consequence, we could test if overlapping individuals were more closely related than were all genotyped individuals in the population, but we did not have a complete enough sample to test for a relationship between the strength of overlap and relatedness, which may have been more informative. Our results nevertheless indicate that our novel method of combining camera trapping with noninvasive genetics by photographing defecating individuals at latrine sites can be a useful tool for studies of latrine-using carnivores. Our inability to obtain photo-genotype matches from all individuals was mostly a consequence of not finding sufficient numbers of ocelot latrines distributed throughout our study area. One approach to overcome this limitation is the use of scat-detecting dogs (Kelly et al. 2012) to find most latrines in an area, and thus detect a larger proportion of the population. We also think our novel method of applying social network analysis to camera-trap data will be useful in future studies of the spatial ecology of elusive carnivores.

In summary, our results in combination with previous research demonstrate that ocelots are flexible in their social and spatial organization, like some other felid species. Although additional empirical research is needed to determine which ecological factors truly influence these differences between populations (Macdonald et al. 2010), population density and the dispersion of resources are likely to be important factors. Finally, we found a positive relationship between spatiotemporal overlap and genetic relatedness in females and among individuals of opposite sex, suggesting kin selection plays a role in structuring ocelot social and spatial organization.

Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Summary of 11 microsatellite loci used to estimate genetic relatedness. H_o is observed heterozygosity. H_e is expected heterozygosity under Hardy–Weinberg equilibrium (HWE). All loci were in HWE probability > 0.05.

Supporting Information S2.—PCR conditions.

Acknowledgments

We thank R. Kays and R. Moreno for sharing their knowledge of the Barro Colorado Island ocelot population. We also thank G. Smallwood for field assistance, N. Pawlikowski and J. Lyko for help with photo identification, and Y. Liefting for administration of the Smithsonian Tropical Research Institute (STRI) camera trap database. C. Kontos, Jr. helped to establish the ocelot photo identification procedure, and G. Willis provided financial support and years of mammal census fieldwork. K. Paige provided helpful comments on an earlier version of this manuscript. This work was funded by the Smithsonian Tropical Research Institute, American Society of Mammalogists, and University of Illinois Graduate College.

Literature Cited

Bejder, L., D. Fletcher, and S. Brager. 1998. A method for testing association patterns of social animals. Animal Behaviour 56:719–725.

Blaustein, A. R., M. Bekoff, and T. J. Daniels. 1987. Kin recognition in vertebrates (excluding Primates): empirical evidence. Pp. 287–331 in Kin recognition in animals (D. J. C. Fletcher and C. D. Michener, eds.). John Wiley & Sons, Chichester, New York.

Broquet, T., N. Menard, and E. Petit. 2007. Noninvasive population genetics: a review of sample source, diet, fragment length and microsatellite motif effects on amplification success and genotyping error rates. Conservation Genetics 8:249–260.

Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indexes. Animal Behaviour 35:1454–1469.

Carr, G. M., and D. W. Macdonald. 1986. The sociality of solitary foragers - a model based on resource dispersion. Animal Behaviour 34:1540–1549.

Carvajal-Villarreal, S., A. Caso, P. Downey, A. Moreno, M. E. Tewes, and L. I. Grassman. 2012. Spatial patterns of the margay (*Leopardus wiedii*; Felidae, Carnivora) at "El Cielo" Biosphere Reserve, Tamaulipas, Mexico. Mammalia 76:237–244.

Chaves, P. B., V. G. Graeff, M. B. Lion, L. R. Oliveira, and E. Eizirik. 2012. DNA barcoding meets molecular scatology: short mtDNA sequences for standardized species assignment of carnivore noninvasive samples. Molecular Ecology Resources 12:18–35.

Clutton-Brock, T. H., and P. H. Harvey. 1978. Mammals, resources and reproductive strategies. Nature 273:191–195.

Davis, B. W., et al. 2009. A high-resolution cat radiation hybrid and integrated FISH mapping resource for phylogenomic studies across Felidae. Genomics 93:299–304.

Davies, N. B., and A. I. Houston. 1984. Territory economics. Pp. 148–169 in Behavioural ecology, an evolutionary approach (J. R. Krebs and N. B. Davies, eds.). Blackwell, Oxford, United Kingdom.

Dillon, A., and M. J. Kelly. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. Journal of Zoology (London) 275:391–398.

Emmons, L. 1988. A field study of ocelots (*Felis pardalis*) in Peru. Revue d' Ecologie 43:133–157.

Goodrich, J. M., D. G. Miquelle, E. N. Smirnov, L. L. Kerley, H. B. Quigley, and M. G. Hornocker. 2010. Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. Journal of Mammalogy 91:737–748.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Hamilton, W. D. 1964. Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1–15.

Ishida, Y., T. Yahara, E. Kasuya, and A. Yamane. 2001. Female control of paternity during copulation: inbreeding avoidance in feral cats. Behaviour 138:235–250.

Janečka, J. E., T. L. Blankenship, D. H. Hirth, M. E. Tewes, C. W. Kilpatrick, and L. I. Grassman. 2006. Kinship and social

structure of bobcats (*Lynx rufus*) inferred from microsatellite and radio-telemetry data. Journal of Zoology (London) 269:494–501.

Janečka, J. E., et al. 2011. Reduced genetic diversity and isolation of remnant ocelot populations occupying a severely fragmented landscape in southern Texas. Animal Conservation 14:608–619.

Johnson, D. D. P., R. Kays, P. G. Blackwell, and D. W. Macdonald. 2002. Does the resource dispersion hypothesis explain group living? Trends in Ecology and Evolution 17:563–570.

Johnson, W. E., and W. L. Franklin. 1991. Feeding and spatial ecology of *Felis geoffroyi* in southern Patagonia. Journal of Mammalogy 72:815–820.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling for carnivores. Pp. 47–69 in Carnivore ecology and conservation: a handbook of techniques (L. P. R. A. Boitani, ed.). Oxford University Press, New York.

Kitchen, A. M., E. M. Gese, L. P. Waits, S. M. Karki, and E. R. Schauster. 2005. Genetic and spatial structure within a swift fox population. Journal of Animal Ecology 74:1173–1181.

Laack, L. L. 1991. Ecology of ocelots (*Felis pardalis*) in South Texas. Master's thesis, Texas A&M University, Kingsville.

Leigh, E. G., Jr. 1999. Tropical forest: a view from Barro Colorado Island. Oxford University Press, New York.

Ludlow, M. E., and F. Sunquist. 1987. Ecology and behaviour of ocelots in Venezuela. National Geographic Research 3:447–461.

Lührs, M. L., and P. M. Kappeler. 2013. Simultaneous GPS tracking reveals male associations in a solitary carnivore. Behavioral Ecology and Sociobiology 67:1731–1743.

Lynch, M., and K. Ritland. 1999. Estimation of pairwise relatedness with molecular markers. Genetics 152:1753–1766.

Macdonald, D. W. 1983. The ecology of carnivore social-behavior. Nature 301:379–384.

Macdonald, D. W., A. Mosser, and J. L. Gittleman. 2010. Felid society. Pp. 125–160 in Biology and conservation of wild felids (D. W. Macdonald and A. J. Loveridge, eds.). Oxford University Press, New York.

Manfredi, C., L. Soler, M. Lucherini, and E. B. Casanave. 2006. Home range and habitat use by Geoffroy's cat (*Oncifelis geoffroyi*) in a wet grassland in Argentina. Journal of Zoology (London) 268:381–387.

Mantel, N. 1967. Detection of disease clustering and a generalized regression approach. Cancer Research 27:209.

Mateo, J. M. 2003. Kin recognition in ground squirrels and other rodents. Journal of Mammalogy 84:1163–1181.

Menotti-Raymond, M., et al. 1999. A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). Genomics 57:9–23.

Moreno, R., and J. Giacalone. 2008. Ecological data obtained from latrine use by ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama. Tecnociencia 8:7–21.

Moreno, R., R. W. Kays, J. Giacalone-Willis, E. Aliaga-Rossel, R. Mares, and A. Bustamante. 2012. Home range and circadian activity of ocelots (*Leopardus pardalis*) in Barro Colorado Island, Panama. Mesoamericana 16:30–39.

Moreno, R. S., R. W. Kays, and R. Samudio. 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. Journal of Mammalogy 87:808–816.

Mossotti, R. H. 2010. Female reaction to male urine scents as potential indicator of mate choice in captive cheetahs (*Acinonyx jubatus*). M.S. thesis, Southern Illinois University, Carbondale.

Moyer, M. A., J. W. McCown, T. H. Eason, and M. K. Oli. 2006. Does genetic relatedness influence space use pattern? A test on Florida black bears. Journal of Mammalogy 87:255–261.

Murphy, W. J., S. Sun, Z. Q. Chen, J. Pecon-Slattery, and S. J. O'Brien. 1999. Extensive conservation of sex chromosome organization between cat and human revealed by parallel radiation hybrid mapping. Genome Research 9:1223–1230.

Nicholson, K. L., P. R. Krausman, A. Munguia-Vega, and M. Culver. 2011. Spatial and temporal interactions of sympatric mountain lions in Arizona. European Journal of Wildlife Research 57:1151–1163.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Pusey, A., and M. Wolf. 1996. Inbreeding avoidance in animals. Trends in Ecology and Evolution 11:201–206.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution 2:295–299.

Rodgers, T. W., J. Giacalone, E. J. Heske, J. E. Janeèka, C. A. Phillips, and R. L. Schooley. 2014. Comparison of noninvasive genetics and camera trapping for estimating population density of ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama. Tropical Conservation Science 7:690–705.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164–182 in Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Chapman & Hall, London, United Kingdom and Cornell University Press, New York.

Sunquist, M. E., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois.

Taberlet, P., and L. Fumagalli. 1996. Owl pellets as a source of DNA for genetic studies of small mammals. Molecular Ecology 5:301–305.

Taberlet, P., L. P. Waits, and G. Luikart. 1999. Noninvasive genetic sampling: look before you leap. Trends in Ecology and Evolution 14:323–327.

Terborgh, J. 1992. Maintenance of diversity in tropical forests. Biotropica 24:283–292.

Tewes, M. E. 1986. Ecological and behavioural correlates of ocelot spatial patterns. Ph.D. dissertation, University of Idaho, Moscow.

Trolle, M., and M. Kery. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. Journal of Mammalogy 84:607–614.

Wade, J. M., and F. J. Breden. 1987. Kin selection in complex groups: mating systems, migration, structure, and the evolution of social behavior. Pp. 3–26 in Mammalian dispersal patterns (D. B. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois.

Waits, L. P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10:249–256.

Wang, J. L. 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Molecular Ecology Resources 11:141–145.

Waser, P. M., and W. T. Jones. 1983. Natal philopatry among solitary mammals. Quarterly Review of Biology 58:355–390.

Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago, Illinois.

Whitehead, H. 2009. SOCPROG programs: analysing animal social structures. Behavioral Ecology and Sociobiology 63:765–778.

Submitted 27 January 2014. Accepted 24 July 2014.

Associate Editor was Bradley J. Swanson.