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Genetic relatedness and space use in two populations of striped hyenas (*Hyaena hyaena*)

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Surprising social complexity and variability have recently been documented in several mammalian species once believed to be strictly solitary, and variation in resource abundance may drive this variation in sociality. Wagner et al. (Wagner, A. P., S. Creel, L. G. Frank, and S. T. Kalinowski. 2007. Patterns of relatedness and parentage in an asocial, polyandrous striped hyena population. Molecular Ecology 16:4356–4369) reported unusual space-use patterns among female striped hyenas (*Hyaena hyaena*) in central Kenya, where pairwise relatedness among females increased with the geographic distance separating them. The authors suggested that this pattern, very rare among mammals, might reflect attempts by females to avoid competition with close relatives for scarce resources in areas of range overlap. Here, we compare those data to new data, documenting genetic relatedness and space use in a previously unstudied wild population of striped hyenas in southern Kenya. We tested hypotheses suggesting that resource abundance and population density affect patterns of genetic relatedness and geographic distance in this species. Our results suggest that higher per capita prey density results in relaxed competition for food, and greater social tolerance among female striped hyenas. An hypothesis suggesting lower population density in the southern population was not supported. Relaxed resource competition may also lead to female–female cooperation in the southern population; we documented for the first time behavioral evidence of den sharing by adult female striped hyenas. Our data indicate that different populations of this little-studied species exhibit behavioral plasticity, in this case, markedly different space-use patterns and patterns of spatial relatedness under different ecological conditions.

Key words: carrion feeding, hyenas, population genetics, relatedness, space use

Although most mammalian carnivores are solitary (Bekoff et al. 1984; Gittleman 1989; Sandell 1989; Prange et al. 2011), the study of spatial organization in carnivores has focused mainly on gregarious species. However, some investigators have found evidence that variation in resource distribution can significantly influence mammalian spatial organization even in solitary species (Wehtje and Gompper 2011; Quaglietta et al. 2014; Holekamp and Sawdy 2019), as suggested earlier by Eisenberg (1966) and Carr and MacDonald (1986). Although most carnivores consume some carrion in their diets (Houston 1979), species specialized for carrion feeding might be expected to have unusually little range overlap with conspecifics, as their food resources are rare, patchily distributed, ephemeral, slowly replenishing, and unpredictable in occurrence (Deygout et al. 2010; Jones et al. 2015). Here, we inquire whether the spatial organization and population density of one carrion specialist, the striped hyena (*Hyaena hyaena*), differs between populations characterized by different levels of resource abundance.

Previous studies suggested a high degree of plasticity in the behavior of striped hyenas, particularly in their ability to live in a variety of habitats and to forage on foods ranging from fruits and invertebrates to livestock and human remains (Ilani 1975; Kruuk 1976; Macdonald 1978; Horwitz and Smith 1988; Leakey et al. 1999; Wagner 2006; Alam and Khan 2015). Variation in home range size has also been reported across the species' range, with home ranges of males tending to be larger than those of females, but with the magnitude of this sex difference varying among populations (Table 1; Kruuk 1976; Mills 1978b; Wagner et al. 2008; Singh et al. 2010). Mills (1978a, 1982, 1989) argued that home range size of the brown hyena (*Parahyaena brunnea*), another carrion feeder and the striped hyena's closest extant relative (Koepfli et al. 2006), is most likely determined by food availability. This may also be true for striped hyenas, particularly given that the diets of these two species appear to be highly similar (Kruuk 1976; Mills 1978b, 1989; Mills and Hofer 1998; Wagner 2006).

One of four extant species in the family Hyaenidae, striped hyenas are widely distributed across northern and eastern Africa, the Middle East, and western Asia (Kruuk 1976; Mills and Hofer 1998; Abi-Said and Abi-Said 2007; Holekamp and Kolowski 2009; Wagner 2013). Striped hyenas are nocturnal scavengers that feed mainly on carrion that tends to be rare and widely scattered throughout their habitat. Though they are primarily scavengers, striped hyenas also hunt opportunistically for small prey such as hares and gazelle fawns, and they may also attack livestock (Rosevear 1974; Kruuk 1976; Skinner and Ilani 1979; Leakey et al. 1999; Kuhn 2005; Wagner 2006). Striped hyenas are also known to take advantage of carrion made available via depredation of large prey animals by sympatric large carnivores. Striped hyenas typically spend many hours each day traveling solitarily, presumably searching for food (Macdonald 1978; Leakey et al. 1999; Wagner 2006). When resting, they are most often found alone, but may also be found in pairs or groups of up to four individuals in some areas (Kruuk 1976; Wagner et al. 2008). They have been observed provisioning cubs at dens, and caching food in and near their dens, in eastern Africa (Kruuk 1976; Wagner 2006), Israel (van Aarde et al. 1988), and India (Davidar 1985, 1990; Alam 2011; Alam and Khan 2015).

Table 1.—Reported mean home range size estimates (in km^2) for striped hyenas (*Hyaena hyaena*) from previous studies, and the present study. Sex differences are listed when reported. Estimates were based on sample sizes of individuals given in parentheses (*n*). All means (where $n > 1$) are reported ± the *SEM*. All data for the present study were collected in the Shompole population from February 2007 to February 2009, using VHF collars and behavioral observations, with the exception of three individuals fitted with GPS collars.

Population	Overall mean home range size (in km^2)	Male mean	Female mean
Serengeti, Tanzania (Kruuk 1976)	60 ($n = 2$)	72 ($n = 1$)	44 ($n = 1$)
Negev Desert, Israel (van Aarde et al. 1988)	60.9 ($n = 1$)		60.9 ($n = 1$)
Laikipia, Kenya (Wagner et al. 2008)	68.9 ± 7.8 ($n = 10$)	76.0 ± 13.8 ($n = 4$)	64.2 ± 9.8 ($n = 6$)
Shompole, Kenya (present study)	33.77 ± 7.17 ($n = 10$)	50.45 ± 19.73 ($n = 3$)	26.62 ± 5.07 ($n = 7$)

Wagner et al. (2007) reported an unusual spatial grouping pattern among striped hyenas inhabiting the Laikipia region of central Kenya (Fig. 1). They presented the first molecular data documenting relatedness among striped hyenas, and reported that average pairwise values among females increased with geographic distance. This finding was unexpected because dispersal behavior in most mammals, including hyaenid species other than striped hyenas (Mills 1989; Smale et al. 1997; Holekamp and Smale 1998; Honer et al. 2007), is male-biased, such that males generally disperse farther and more frequently than do females (e.g., Greenwood 1980; Dobson 1982; Shields 1982). Male-biased dispersal in mammals typically results in distributions of relatives that differ by sex, with female kin occurring in closer proximity to one another than to their male relatives (Greenwood 1980; Sherman 1981; Chepko-Sade and Halpin 1987; Waser and Elliott 1991; Smale et al. 1997; Gompper et al. 1998). The observation by Wagner et al. (2007) suggested that, in contrast to the typical mammalian pattern, female striped hyenas in the Laikipia population might disperse preferentially to areas far from their natal ranges. Wagner et al. (2007) suggested that this highly unusual pattern might reflect attempts by females to avoid competing with close relatives for scarce resources in areas of range overlap.

The unusual finding by Wagner et al. (2007) of a positive correlation between genetic relatedness among females and degree of spatial separation raises several important questions about the factors influencing spatial distributions of kin in this

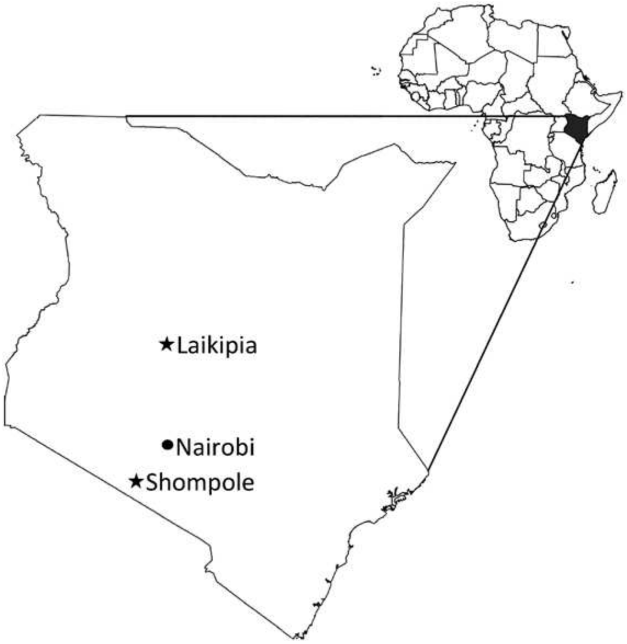

Fig. 1.—Study areas of both the Laikipia (LK) and Shompole (SH) populations of striped hyenas (*Hyaena hyaena*) shown in relation to Nairobi, the capital of Kenya. Data were obtained for the LK population from Wagner et al. (2007) and collected from the SH population from February 2007 to February 2009.

species. For example, it is not clear whether the pattern described by Wagner et al. (2007) is general to striped hyenas everywhere, or simply reflected conditions specific to the Laikipia study area. The latter hypothesis predicts that, in areas with higher resource concentrations or lower population densities of striped hyenas than those found in Laikipia, we should observe the typical female mammalian pattern of decreasing relatedness with increasing geographic distance, such that more-closely related females live in closer proximity to one another than do more-distantly related female pairs.

Comparative data on distinct populations of conspecifics in contrasting resource environments can enhance our understanding of mammalian dispersal and social strategies. Here, we present data documenting genetic relatedness and space use collected from a previously unstudied wild population of striped hyenas in the southern Rift Valley of Kenya, near Shompole. We use these data to explore the relationship between space-use patterns and relatedness in the Shompole population, and compare our results to those reported from Laikipia by Wagner et al. (2007). To our knowledge, the Laikipia and Shompole populations of striped hyenas are the only ones for which both genetic and spatial data are currently available, along with concurrent data documenting resource availability. Additionally, we were able to repeatedly observe multiple known Shompole individuals during focal follows, and collect behavioral data from them. Finally, we use demographic, telemetry, and prey transect data to examine predictions of hypotheses suggesting that relationships between genetic relatedness and spatial distance among individuals differ between the Shompole and Laikipia populations due to differential food abundance or hyena population density in the two areas.

Materials and Methods

We compared the spatial distribution pattern of striped hyenas in our Shompole (SH) study population with that previously described by Wagner et al. (2007) for striped hyenas occupying the Laikipia Plateau in the central highlands of Kenya. All data from the Laikipia (LK) population studied by Wagner et al. (2007) were available to us, but smaller sample sizes in the SH population made it impossible to implement exactly the same analytical methods as those utilized by Wagner et al. (2007). Therefore, we reanalyzed the data collected by Wagner et al. (2007) using methods that allowed us to directly compare the SH and LK populations. Analyzing both populations with the same methods enabled us to ascertain whether space-use patterns differed significantly between these two populations and whether space use was associated with spatial genetic structure at an individual level.

Study populations and radiotelemetry.—Our SH study site lies approximately 300 km south of the LK population in Kenya, East Africa (Fig. 1). These two populations differ with respect to many ecological variables, including elevation, rainfall, and abundance of food resources utilized by striped hyenas. The SH study site is located at the base of the Nguruman Escarpment in the Great Rift Valley at about 900 m above sea level, whereas the LK study site is located on the equator in central Kenya, and varies in elevation from 1,500 to 2,600 m above sea level. SH has lower average annual rainfall than LK (317.5 ± 63.5 mm versus 464 ± 37 mm [± *SE*], respectively), and higher average temperatures (ranging from an average low of 24.2°C to an average high of 37.7°C in SH, compared to a range of 16–26°C in LK—Wagner 2006; this study). Average prey densities were consistently higher in SH than LK, both with respect to densities of native ungulates (average monthly density of the native ungulate species occurring in both areas: SH: 28.16 ungulates/km^2; LK: 9.94 ungulates/km^2) and livestock (average monthly density of cattle, sheep, and goats: SH: 74.9 individuals/km^2; LK: 5.1 individuals/km^2—Wagner 2006; Schuette 2012; Schuette et al. 2016). We assume that carrion availability varies directly with abundance of living prey, as shown previously for East Africa by Sinclair (1979) and Sinclair and Arcese (1995).

SH population data were collected on the Olkiramatian and Shompole Maasai Group Ranches in the southern Rift Valley of Kenya from February 2007 to February 2009. Animals were caught in pre-set soft-catch foot-hold traps baited with carrion, and anesthetized using either Telazol (dose: 6.5 mg/kg body weight) or a combination of Ketamine HCl (dose: 3.6 mg/kg) and medetomidine HCl (dose: 0.06 mg/kg). We administered the sedative in a lightweight plastic dart fired from a CO_2-powered rifle. We collected blood and tissue for DNA extraction from all anesthetized hyenas in SH, as well as morphological measurements and body mass data (data not reported here). All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00) and met guidelines approved by the American Society of Mammalogists (Sikes et al. 2016). We fit a total of nine striped hyenas (six females and three males) in the SH population with VHF radiocollars (Telonics, Inc., Mesa, Arizona.; or SirTrack Ltd, Havelock North, New Zealand), and an additional three individuals (two males and one female) were fitted with global positioning system (GPS) collars that also had VHF capabilities (Savannah Tracking Ltd, Nairobi, Kenya). From these GPS collars, geographic fixes were downloaded automatically, approximately every 20 min for 21 and 169 days from the two males, respectively, and for 26 days from the female. All collared animals were adults, with the exception of F108, a SH female fitted with a VHF radiocollar, who was a den-dependent juvenile when first collared in 2007, but was fully adult by the end of the study.

Behavior and location sampling.—Uniquely in the SH population of striped hyenas, we were able to follow focal individuals and collect behavioral data. Striped hyenas typically move very little during the day, but can travel quite far while foraging at night (Kruuk 1976). In an effort to collect data during the hyenas' period of peak activity at SH, we recorded location data from 1830–0630 h using focal animal follows (FAF). Individuals were located using their VHF transmitters and radioantennas mounted on the roof of our vehicle. Once located, spotlight-habituated individuals (n = 14) were followed from a minimum distance of 100 m, so as to minimize interference with their behavior. Non-habituated individuals (n = 5) were often followed at distances exceeding 200 m in closed habitats, and at maximum sight distance in open areas. Focal animals without tracking transmitters (n = 7) were followed opportunistically. All were animals observed on multiple previous occasions, both by human observers and in camera-trap photos, and identified using known stripe patterns and other distinguishing marks (i.e., ear damage).

The GPS coordinates of each focal animal were recorded every 10 min during every FAF. Each FAF continued until we were no longer able to follow the animal due to rough terrain or other impediments. If a FAF was abandoned, a new FAF was begun on a different individual if one could be located before dawn. During any FAF, other radiocollar frequencies (n = 11) were constantly monitored, and we recorded the ID and location of any other hyenas detected via telemetry or seen near the focal individual. Behavioral data at dens were opportunistically recorded during FAF data collection.

Spatial distances and home range size estimation.—Our analyses focused on potential spatial overlap among individual hyena home ranges rather than intensity of area use, as we lacked sufficient data from a large enough sample of animals to reliably calculate utilization distributions. Our analysis makes no assumptions about interactions between individuals within overlapping areas. In an effort to maximize data, we included seasonal shifts in home ranges during the study period by assessing the total area used by an individual over the entire study period. To do so, we calculated home range sizes as minimum convex polygons derived from all sampled locations using the "mcp" function in the adehabitatHR package in R version 3.5.0 (R Core Development Team 2015) for every individual in both the LK and the SH populations for which we had ≥ 20 locations. We determined the geographic center of each home range using the "gCentroid" function in the rgeos package. Any home range size calculations completed in the current analysis for the LK population were used exclusively to assess extent of spatial overlap, as described above. All analyses involving calculations of explicit measures of home range size for the LK population used the previous calculations performed by Wagner et al. (2007).

Within each population, we calculated two spatial measurements for each possible dyad of individuals alive concurrently: 1) the pairwise distance (in km) between the geographic centers of their calculated home ranges, and 2) the area of home range overlap, calculated as the mean percent overlap of one animal's home range with the home range of the other. The percent of home range overlap was calculated separately from the perspective of each individual in a dyad, and then the mean percent of home range overlap between these two calculations for the dyad was used in all analyses. Only one individual died during our study, an adult female found dead during the first month of the study period; she was removed from all spatial analysis. Overlap area between home ranges was calculated for each dyad in both LK and SH study areas using the "gIntersection" function from the rgeos package in R. Total study area size (480 km^2) and hyena density for LK were obtained from Wagner (2006). The study area size at SH (320 km^2) was defined as the total number of square kilometers in which we had spatial data from striped hyenas that we sampled regularly. Hyena density in SH was calculated as part of this study by dividing the total number of individuals alive concurrently in the SH population by the total study area size (km^2). Based on data from an extensive grid of camera traps in SH throughout our study period (Schuette et al. 2013b), we are confident that we identified all striped hyenas present in the study area.

Microsatellite genotyping, relatedness, and parentage.—DNA was obtained from 20 individuals from the SH population (11 females, nine males). Ten microsatellite loci previously developed for use in spotted hyenas (*Crocuta crocuta*) were successfully amplified and genotyped in all samples from the SH population using conditions described previously (Libants et al. 2000; Wilhelm et al. 2003; Wagner et al. 2007) and in Supplemental Data SD1. Genotypic data for eight microsatellite loci from a total of 57 striped hyenas of known sex from the LK population (25 females, 32 males) were obtained from Wagner et al. (2007) for purposes of comparison with the SH population data. Six of the loci genotyped were the same between the populations, but one locus (Ccroc06) was monomorphic (i.e., uninformative) in the SH population, and therefore not used in our analysis. We calculated all relatedness estimates used in analyses with the remaining five loci genotyped in both populations, and we also calculated relatedness in each population separately using all loci available for each (n = 9 for SH and n = 8 for LK). However, because our relatedness estimates using different numbers of loci did not differ significantly within populations, and because these relatedness estimates were significantly correlated within both populations (Supplemental Data SD2), all results reported here were based on the relatedness estimate using all available loci in each population (n = 9 for SH and n = 8 for LK). Differences between relatedness estimates, and statistical tests for these differences, are reported for both populations in Supplemental Data SD2.

Pairwise relatedness estimates (r), number of microsatellite alleles per locus, and heterozygosity were calculated for both populations using the program ML-RELATE (Kalinowski and Taper 2006; Kalinowski et al. 2006). We tested for Hardy–Weinberg equilibrium and the presence of null alleles at each locus using 10,000 randomizations in ML-RELATE. For specific patterns of relationship, we used ML-RELATE to calculate the full range of pedigree relationships available for all dyads (unrelated [UR], half-sib [HS], full-sib [FS], and parent–offspring [PO]), and identified the relationship with the highest likelihood for each dyad (ML(R)). The results from this analysis were validated with behavioral observations whenever possible.

Comparison of genetic–spatial distance relationships between populations.—We evaluated correlations between PW genetic relatedness and each of our two spatial distance measurements. We did this for all possible dyads concurrently alive, and also for dyads separated by sex class (i.e., male–female, male–male, and female–female) in each population by computing Mantel's r statistic (r) between genetic relatedness (r) and each spatial measurement for all dyads for both populations, using

10,000 permutations. These analyses were performed using the "vegan" package in R version 3.5.0 (R Core Development Team 2015). Differences between populations in other metrics (i.e., home range (HR) size) were assessed using two-group Mann–Whitney *U*-tests, but we used dependent two-group Wilcoxon Signed Rank tests for metrics assessing dyads, where the assumption of sample independence was not met (i.e., pairwise distance between home range center and pairwise percent home range overlap). Statistical differences between measures of relatedness were determined with unpaired two-tailed Student's *t*-tests. Means are reported ± *SE*. We used nonparametric statistical tests because of small sample sizes and data that failed to meet assumptions of normality needed for parametric tests. All corresponding *P*-values were adjusted to compensate for the false discovery rate (FDR[q]—Benjamini et al. 2006).

RESULTS

Hyena density and home range size estimation.—Although average striped hyena density was very low in both study areas, it was twice as high in SH (0.06 hyenas/km^2) as in LK (0.03 hyenas/km^2—Wagner 2006).

We compared home range size estimates for the SH population to previously reported estimates of striped hyena home range size in Table 1. Of the 12 adult hyenas fitted with radiocollars in the SH population (nine animals with VHF collars and three with GPS collars), 10 (seven females and three males) had a minimum of 20 locations per individual. All locations available for each of these individuals that had a minimum of 20 locations were used to calculate home range size estimates. All 10 SH hyenas were in the population concurrently throughout the entire period of data collection.

Overall mean home range size was significantly smaller in the SH population than that observed in LK (Table 1; W = 87, $P = 0. 004$), as were the home ranges of females alone (W = 40, $P = 0.005$). Home ranges of males also tended to be larger in LK than those in SH, although this difference was not statistically significant (W = 8, $P = 0.629$). In both SH and LK populations, mean home range size was slightly larger for males than for females (Table 1; SH: W = 6, $P = 0.383$; LK: W = 10; $P = 0.762$), but this sex difference was not statistically significant.

Intercentroid distance and percent home range overlap.—A total of 20 individuals (nine females and 11 males) in the LK population had a minimum of 20 locations, and all 20 LK hyenas overlapped in time and space with one another for at least 3 months, and up to 3.2 years. The mean distance between home range centers (intercentroid distance) calculated for dyads was significantly shorter in SH than in LK, and this was true for all sex-specific dyads except for male–male dyads (Table 2; male–male: W = 39; $P = 0.138$; female–female: W = 113; $P < 0.0001$; male–female: W = 468; $P < 0.0001$; all dyads: W = 1,726; $P < 0.0001$). Furthermore, the mean PW percent of home range overlap within all dyads was significantly higher in SH than LK (Table 2; W = 5,532.5; $P = 0.0001$). Of specific interest, within female–female dyads, the mean pairwise percent overlap between female home ranges was three times higher in SH than in LK (W = 507; $P = 0.013$), and mean distance between home range centers of females was almost three times less in SH than LK (W = 113; $P < 0.0001$). Home ranges of females in SH also overlapped significantly more with those of males observed in male–female dyads in LK (W = 1,341; $P = 0.015$). There was no difference in mean pairwise percent overlap between populations in male–male dyads (W = 93; $P = 0.535$). In SH, the mean pairwise percent overlap was highest in female–female dyads (0.17 ± 0.06), and lowest in male–male dyads (0.08 ± 0.08),

Table 2.—Mean pairwise distances (in km) within striped hyena (*Hyaena hyaena*) dyads for which we estimated home range areas in two populations. Mean pairwise distance between home range centers for each dyad, mean pairwise percent overlap of the home ranges of both members of each dyad, and the average pairwise relatedness (*r*; ML-RELATE—Kalinowski et al. 2006) between dyad members are given. All mean measurements are given ± *SEM*. Sample sizes are given as number of individuals (n_i) and as number of dyads (n_d) for all measures. Sample sizes for pairwise relatedness for the overall population are given in parentheses. Data were obtained for the Laikipia population from Wagner et al. (2007), and collected from the Shompole population from February 2007 to February 2009.

	n		Mean pairwise distance between home range centers (km)	Mean % pairwise overlap (proportion of home range; km^2)	Average pairwise relatedness (*r*)
Shompole					
Total population	n_i	10	6.83 ± 1.04	0.19 ± 0.03	0.101 ± 0.01 ($n = 20$)
	n_d	45			
Male–male dyads	n_i	3	8.39 ± 2.64	0.08 ± 0.08	0.11 ± 0.07
	n_d	3			
Male–female dyads	n_i	10	6.67 ± 1.04	0.22 ± 0.07	0.117 ± 0.03
	n_d	21			
Female–female dyads	n_i	7	6.75 ± 1.08	0.17 ± 0.06	0.115 ± 0.05
	n_d	21			
Laikipia					
Total population	n_i	20	18.59 ± 0.89	0.1 ± 0.02	0.103 ± 0.004 ($n = 57$)
	n_d	189			
Male–male dyads	n_i	11	18.85 ± 1.66	0.08 ± 0.03	0.14 ± 0.03
	n_d	54			
Male–female dyads	n_i	20	18.13 ± 1.28	0.12 ± 0.03	0.1 ± 0.01
	n_d	99			
Female–female dyads	n_i	9	19.43 ± 1.89	0.06 ± 0.03	0.105 ± 0.03
	n_d	36			

which contrasts with the pattern in LK, where the highest mean pairwise percent overlap was within male–female dyads (0.12 ± 0.03) and the lowest within female–female dyads (0.06 ± 0.03).

Relatedness estimates and patterns of relationship.—Average pairwise relatedness (*r*) estimates did not significantly differ between the entire SH and LK populations ($t_{227.5} = 0.16$; $P > 0.1$), nor between sex-specific dyads between populations (Table 2; Supplementary Data SD2).

Den attendance and parentage in Shompole.—Behavioral data were opportunistically recorded in the SH population at 30 dens on 125 nights between August 2007 and May 2009, for a total of 187.9 h. We observed 15 different individuals (four adult females, two adult males, and nine juveniles) at these dens. We were able to reliably obtain genotypes for five of the nine juveniles, and for all six adults. Details on pairwise relatedness, most likely relationships, and concurrent den attendance within dyads are given in Supplementary Data SD3.

Multiple hyenas were observed concurrently at a single den during 48% of our observations (60 of 125 nights), and the same dyads were observed repeatedly at the same den up to 19 different times. Genotyping allowed us to calculate pairwise relatedness values for 18 of the 24 SH dyads observed concurrently at dens (Supplementary Data SD3). Our data did not permit us to determine how often members of these dyads were together away from dens. For all categories of these 18 dyads (i.e., female–female, male–female, and male–male), the average pairwise relatedness was higher than the overall population measure ($r = 0.261 \pm 0.05$ versus $r = 0.101 \pm 0.01$, respectively). Most of these dyads ($n = 11$ of 18) were composed of one adult and one juvenile, and the average pairwise relatedness for all categories of adult-juvenile pairs observed concurrently at dens was $r = 0.301 \pm 0.06$. The only two adult females observed concurrently at a den were a known mother–daughter pair (F104 and F105; $r = 0.628$). The remaining adult-adult dyads ($n = 4$) were composed of one male and one female each, and had an average pairwise relatedness value of $r = 0.073 \pm 0.145$, which was the lowest average pairwise relatedness of any category of dyads observed together at dens.

Adult hyenas of both sexes ($n = 1$ male, $n = 3$ females) were observed provisioning at dens on 18 occasions on 15 different nights (Supplementary Data SD3). The average pairwise relatedness between dyads involved in provisioning interactions was $r = 0.304 \pm 0.083$. For all of these observations, the provisioning adult was either the predicted parent of at least one of the juveniles observed at the den, or a half-sibling of the observed juvenile.

The adult male (M114) who provisioned cubs was observed carrying unidentified food scraps to the den on two separate occasions (in May and August of 2008), while two cubs (M112 and M113) were known to reside there. These two juveniles are predicted in our analysis to be half-siblings, and behavioral observations of nursing support the conclusion that they are littermate offspring of female F104. Adult male M114 was determined to be the likely father of only one of these juveniles (M113). M114 was observed on multiple occasions at dens with three different adult females, including F104, the mother of this litter (Supplementary Data SD3). M114 was also observed at this den on other occasions in the presence of one or both of these cubs.

Correlations between relatedness and spatial measures.—As pairwise relatedness increased between females in the LK population, so too did their spatial separation, confirming the trend reported by Wagner et al. (2007) of a positive correlation between distance and relatedness between females (Fig. 2; Table 3: Mantel's r = 0.249; $P = 0.252$, $n = 36$ dyads). However, the opposite trend was seen among SH female–female dyads, such that distance decreased between home range centers (intercentroid distance) with increasing relatedness (Fig. 2; Table 3; Mantel's r = −0.544; $P = 1$, $n = 21$ dyads). No significant correlations between intercentroid distance and average pairwise relatedness were found for any other dyads in either population (Table 3).

When we tested for correlations between genetic pairwise relatedness and mean pairwise percent of home range overlap, we found a more typical mammalian pattern among females in the LK population (Fig. 3) than that shown in Fig. 2. That is, as the relatedness between two females increased in LK, the mean pairwise percent overlap between their home ranges also tended to increase slightly (Table 3; Mantel's r = 0.199; $P = 0.35$). This same pattern was also seen among female–female dyads in the SH population (Fig. 3; Table 3; Mantel's r = 0.948; $P = 0.028$), but with a significantly stronger correlation found between these two measures in SH than in LK (Fig. 3; Table 3; Mantel's r = 0.199; $P = 0.139$). Although this pattern was more marked for all dyads in SH than in LK, no significant correlations between mean pairwise percent home range overlap and average pairwise relatedness were found for any other dyad type in either population (Table 3).

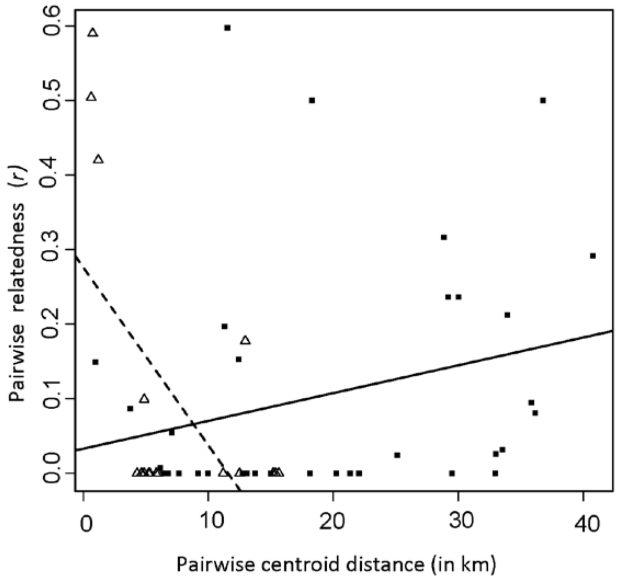

Fig. 2.—Pairwise genetic relatedness (*r*) in female–female dyads of striped hyenas (*Hyaena hyaena*), as a function of spatial distances between individuals' home range centers (km) in the Laikipia (LK) population (Wagner et al. 2007) and the Shompole (SH) population, with a line of best fit for each population. The SH population is noted by open triangles (Δ) and a dashed line. The LK population is noted by dark squares (■) and a solid line. Data were obtained for the LK population from Wagner et al. (2007) and collected from the SH population from February 2007 to February 2009.

Table 3.—Mantel's r statistic (r) and associated one-tailed *P*-values testing for correlation between pairwise relatedness and spatial measures for striped hyenas in two populations. Separate tests were run for each dyad category, including all dyads, male–female dyads only (MF), male–male dyads only (MM), and female–female dyads only (FF). Separate tests were run for our two spatial distance measurements (mean pairwise home range [HR] overlap in km^2 and intercentroid distance) using estimates of genetic relatedness obtained from ML-RELATE, based on all available loci for each population: All *P*-values are corrected for the false discovery rate; significant *P*-values are indicated in bold. Data were obtained for the Laikipia (LK) population from Wagner et al. (2007), and collected from the Shompole (SH) population from February 2007 to February 2009.

Population	Comparison	Dyads considered	Number of valid dyads	Mantel's r	*P*- value	FDR corrected *P*-value
LK	Average proportion home range overlap (km^2)	All	190	0.117	0.061	0.252
		FF	36	0.199	0.136	0.350
		MF	99	0.068	0.175	0.350
		MM	55	0.209	0.084	0.270
	Centroid distance	All	190	0.037	0.308	0.474
		FF	36	0.249	0.063	0.252
		MF	99	0.032	0.326	0.474
		MM	55	-0.069	0.694	0.926
SH	Average proportion home range overlap (km^2)	All	45	*0.555*	*0.0002*	*0.003*
		FF	21	*0.948*	*0.004*	*0.028*
		MF	21	0.104	0.243	0.433
		MM	3	0.993	1.000	1.000
	Centroid distance	All	45	-0.353	1.000	1.000
		FF	21	-0.544	0.996	1.000
		MF	21	-0.176	0.878	1.000
		MM	3	0.956	0.167	0.350

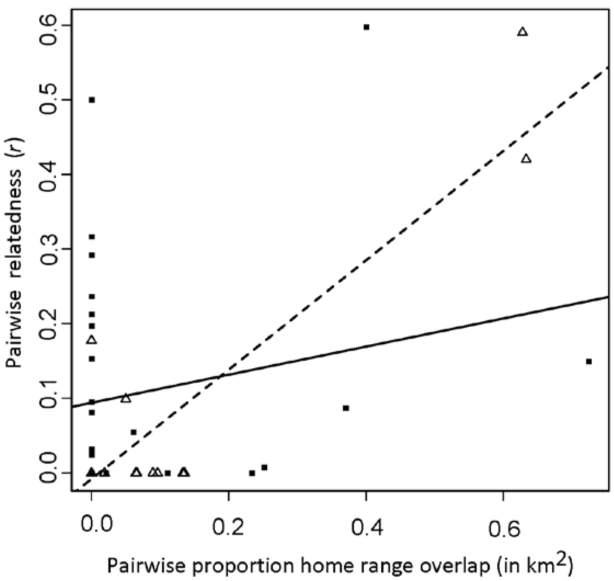

Fig. 3.—Pairwise genetic relatedness (*r*) in female–female dyads of striped hyenas (*Hyaena hyaena*), as a function of the average pairwise percent home range overlap (in km^2) in the Laikipia (LK) population (Wagner et al. 2007) and the Shompole (SH) population, with a line of best fit for each population. The SH population is noted by open triangles (Δ) and a dashed line. The LK population is noted by dark squares (■) and a solid line. Data were obtained for the LK population from Wagner et al. (2007) and collected from the SH population from February 2007 to February 2009.

In SH, one adult male's (M114) home range overlapped substantially with that of four adult females (Fig. 4A). The only example in LK showing a similar degree of male–female home range overlap among adults involved the home ranges of three different males overlapping the home ranges of each of two different adult females (Fig. 4B). Whereas the highest average pairwise home range overlap observed for a single SH male–female dyad (M114 and F105) was similar to the highest observed in a LK male–female dyad (M26 and F48; Fig. 4; 71.685% versus 87.833%, respectively), the relatedness within these dyads differed considerably (r = 0 in SH versus r = 0.2311 in LK). Additionally, the home range of LK male M10, also overlapped substantially with that of another, highly related, adult male (LK male M11; Fig. 4A; average PW overlap = 82.897%; r = 0.674). The highest pairwise home range overlap within a male–male dyad in the SH population was markedly lower (24.46 %), and occurred between two unrelated males (M103 and M114; r = 0; not pictured). The two SH adults whose home ranges overlapped the most (F104 and F105 in Fig. 4A; 81.95 % average pairwise overlap) were a mother and her adult daughter (r = 0.628), whereas the highest pairwise overlap in home range area in LK was the male M26–female F48 dyad described above (average pairwise home range overlap = 87.83 %; r = 0.231). The LK female–female dyad with the highest average pairwise overlap (72.5%; F09 and F48 in Fig. 4B) had a much lower relatedness estimate than the SH female–female dyad described above of r = 0.149. The overall average pairwise relatedness among all individuals illustrated in Figs. 4A and 4B was slightly lower in SH (r = 0.119) than that calculated for the LK individuals shown (r = 0.201). In summary, home range overlap at SH was lower between related males than at LK, and a considerably higher degree of home range overlap between related females was observed at SH than at LK (Table 2). Our home range overlap data show marked differences in space-use patterns between the SH and LK populations of striped hyenas, suggesting that different ecological forces govern group dynamics in these populations.

Discussion

Striped hyenas demonstrated behavioral plasticity in space use in several ways. Even though we used slightly different

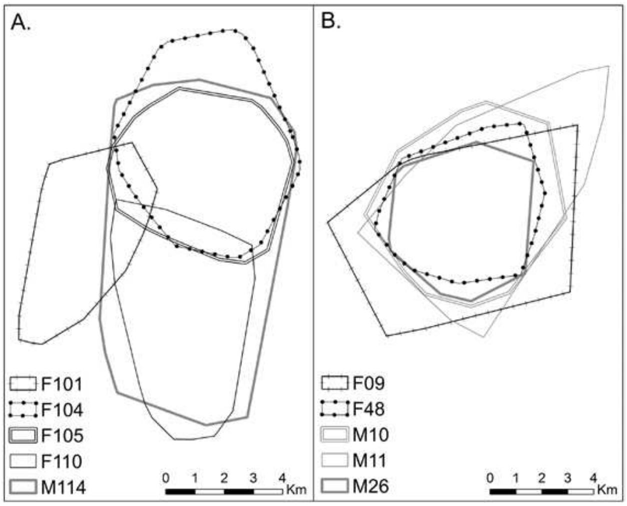

Fig. 4.—Home ranges shown for four adult striped hyena (*Hyaena hyaena*) females (F) and one adult male (M114) in the Shompole (SH) population (A), and for two adult females (F) and three adult males (M) in the Laikipia (LK) population (B). Individual home ranges are indicated by the style of line shown in each figure legend. Females are indicated by black lines, males are indicated by gray lines. Scale bars (in km) for both figures are given at the bottom and reflect the larger home ranges in LK versus SH. Data were obtained for the LK population from Wagner et al. (2007) and collected from the SH population from February 2007 to February 2009.

analytical techniques than those utilized by Wagner et al. (2007), we confirmed the patterns in relationships between relatedness and geographic distance reported previously in the LK population by those researchers. Although our methods for calculating home ranges in both study areas differed slightly from those used by Wagner et al. (2007, 2008) in LK alone, we were able to document marked differences between these two populations. That is, our data showed that individuals in SH were found significantly closer together than in LK, and that, on average, individual home ranges overlapped in SH considerably more than they did in LK. These populations also differed noticeably with respect to space-use patterns among the sexes. For example, one SH male was found to share space with more females than was ever observed in LK (Fig. 4). Further, whereas several home ranges of LK males overlapped considerably with those of other males (up to 83%), this degree of overlap was not seen among the home ranges of SH males, for which the maximum home range overlap was only 24% (Fig. 4A). We found contrasting patterns between the populations with regard to female–female spatial dynamics as well; females in SH were found in closer proximity to relatives than were females in LK, and home ranges of females in SH overlapped significantly more with those of other females than was observed in the LK population (Table 2; Figs. 3 and 4A and 4B). Specifically, SH females were found almost three times closer to one another than were LK females, and the percentage overlap between home range areas of SH females was almost three times that seen in LK females (Table 2; Fig. 4A and B).

Our two study areas differ with respect to food abundance, weather, and human occupation. Native ungulate and livestock densities are higher in SH than in LK, and the weather in SH is hotter and dryer than that in LK. LK is located on a privately held livestock ranch and wilderness reserve, but SH is inhabited by Maasai pastoralists who move seasonally with their livestock, occupying the same area as the SH hyena population during approximately only 6 months of the year (Schuette et al. 2013a). Wagner et al. (2007) hypothesized that food abundance was the most important variable shaping the spatial distribution of female striped hyenas, and our data support this hypothesis in both populations. Limited food is often proposed as the primary determinant of spacing among solitary animals (e.g., rodents—Ostfeld 1985, 1990; Schradin and Pillay 2005; primates—Kappeler 1997; carnivores—Gittleman and Harvey 1982), and our data are consistent with this idea. Specifically, theory predicts that female mammals optimize their fitness by improving their access to food resources, whereas males optimize their fitness by improving access to females (e.g., Emlen and Oring 1977; Andersson and Iwasa 1996; Bercovitch 1997). Here, the greater abundance of available food in SH appeared to permit the higher observed hyena population density and smaller home ranges in the SH population than those observed in the LK population.

We hypothesize that high prey density in SH has favored female striped hyenas with small home ranges that overlap with those of multiple adults of both sexes, whereas SH males are favored who occupy larger home ranges to maximize access to females (Fig. 4B). Our relatedness data showing that M114 likely only sired one of two littermates suggest that female striped hyenas mate with multiple males. Multiple paternity is also seen in other hyaenids as well (Engh et al. 2001; East et al. 2003).

Higher resource concentration, but not lower population density, predicted the observed space-use patterns seen here among female striped hyenas in SH, which was the typical mammalian pattern of decreasing relatedness with increasing geographic distance. Striped hyena density was twice as high in SH as LK, but the higher prey density in SH may nevertheless relax competition over food resources such that the costs of competing with kin are smaller than the benefits females might receive by cooperating with kin. Our data suggest that the more relaxed resource competition in SH has increased tolerance among these females for home range overlap with those of other individuals of both sexes, as the mean pairwise percent overlap was significantly greater in SH than LK for both male–female dyads and female–female dyads. Relaxed competition for food may also have led to female–female cooperation, such as the den sharing and provisioning of young we observed in the SH population. All of the unrelated dyads observed concurrently at SH dens were either composed of two adults, or one provisioning adult with a juvenile littermate of this adult's offspring. This suggests that adults may even provision non-relatives, if they have offspring within the same litter. Both these forms of cooperation (den sharing and provisioning) are commonly observed in brown hyenas, the striped hyena's sister species (Koepfli et al. 2006). Female striped hyenas in the LK population may maintain larger home ranges than those in SH in order to acquire sufficient food, and our data suggest that LK females are less tolerant than SH females of HR overlap with other individuals of both sexes, presumably due to more intense resource competition. This hypothesis is consistent with the notion that females in LK also disperse to sites farther away from their natal areas than do females in SH to reduce competition with their female kin. As a result, female–female dyads within the LK population display a general trend of increasing relatedness with increasing distance between home range centers (Fig. 2). In general, dispersal by females is favored in mammals when resource competition among closely related animals is intense in the natal area (reviewed by Clutton-Brock and Lukas 2012). The greater prey density in SH suggests that sufficient food is available to this population to support a higher density of striped hyenas than in LK.

Although striped hyenas are often referred to as asocial or solitary, our data suggest that the sociality of these animals is in fact more complex and variable than generally assumed. Our data provide evidence that two discrete populations of the same species, separated by only approximately 300 km, can exhibit markedly different space-use patterns and relatedness structures when ecologies differ between populations; apparently striped hyenas can alter their space-use patterns as resource availability and population density change. Striped hyenas have been historically under-studied relative to other medium- and large-bodied carnivores, including other members of the family Hyaenidae (Wagner 2013). Although short-term studies of striped hyena movements have been conducted in Tanzania (Kruuk 1976), the Middle East (Lewis et al. 1968; Ilani 1975; Macdonald 1978; Kerbis-Peterhans and Horwitz 1992; Kuhn 2005; Abi-Said and Abi-Said 2007), and India (Alam 2011), most information on space-use in this species has come mainly from a single population, the LK population analyzed here (Wagner et al. 2007). Previous studies have shown intraspecific variation in home range size in other carnivore species (McLoughlin et al. 2000; Herfindal et al. 2005). Studies such as ours highlight the need for population-specific data, and caution against extrapolation across multiple populations with varying ecologies. The short-term nature of ours and other studies of striped hyenas also highlight our limited ability to understand space-use dynamics in the absence of historical and larger-scale community data, particularly for mammals with such enormous species ranges and such remarkable ecological plasticity as striped hyenas. Most large carnivores are under threat, solitary, and difficult to study; as they evade ever growing human populations, they may continue to become more challenging to observe (Gittleman et al. 2001; Boydston et al. 2003). A camera-trap study by Schuette et al. (2013b) suggested that both striped hyenas and lions in the SH study area shift their movements seasonally in response to movements of local pastoralists. These seasonal movements were encompassed by our home range estimates. Understanding how threatened species are altering their behaviors in response to changing landscapes is critical for their effective conservation and management.

Striped hyenas are currently listed by the IUCN as a near-threatened species (Abi-Said and Dloniak 2015), particularly due to their increasing overlap with human populations; humans currently represent the greatest source of mortality for this species (Mills and Hofer 1998; Ziaie 2008; Tourani et al. 2012). The hyenas' habitat is undergoing fragmentation, sometimes stranding them in marginal habitats characterized by low resource availability (Mills and Hofer 1998). Our study highlights the need for more research on the behavioral ecology and population genetics of this and other species that are putatively solitary, as recent research continues to reveal surprising social complexity and variability in many of these animals.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online

Supplementary Data SD1.—Number of alleles observed, and the observed (H_O) and expected heterozygosities (H_E) of each locus used for relatedness analyses in two populations of striped hyenas (*Hyaena hyaena*). The locus Ccroc06 was removed from analyses of the Shompole population due to lack of variation and is noted here with an asterisk (*). The frequency of null alleles at three loci in the Laikipia population is given by p_n. No null alleles were detected at any loci genotyped in the Shompole population. Data were obtained for the Laikipia population from Wagner et al. (2007), and collected from the Shompole population from February 2007 to February 2009. Both populations are located in Kenya, East Africa.

Supplementary Data SD2.—Results of tests for differences between relatedness (*r*) estimates obtained using different number of loci. Mean population estimates of pairwise relatedness (*r*) given for the Shompole (SH) and Laikipia (LK) populations (Avg *r*), based on all loci possible for each population: nine for SH; eight for LK, and based only on common loci genotyped in both populations ($n = 5$ loci). Sample size (*n*) given as number of individuals considered. *SD* and *SEM* of *r* are also given. Student's *t*-test results are given for comparisons of population average relatedness (*r*) estimates obtained using the different number of loci; Mantel's test results (r) are given for tests of correlation between relatedness (*r*) estimates for all individuals from both populations using different number of loci. All measures obtained using ML-RELATE (Kalinowski et al. 2006).

Supplementary Data SD3.—Matrix of individual striped hyenas (*Hyaena hyaena*)observed concurrently at dens in Shompole, Kenya, collected from August of 2007 to May of 2009. Individuals are listed by ID number and denoted as female (F) or male (M). Juveniles are indicated by a plus sign (+); all other observed individuals were adults. Juveniles not assigned ID numbers are labeled as Unidentified Juveniles (UnIDJuv) 1 through 4. Pairwise relatedness (*r*) is indicated in italics for pairs that were observed concurrently at any one den where genetic data were available. Number of times each pair was seen together at a den (when this value was > 0) is given in parentheses, followed by the relationship most consistent with genotypic data as determined by MLRelate [PO = parent–offspring; FS = full siblings; HS = half-siblings; U = unrelated). Relatedness values marked with an asterisk (*) indicate pairs where den provisioning was observed (i.e., the adult of the indicated pair was observed carrying food towards the den while the juvenile offspring of the indicated pair was also present).

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