

Patterns of relatedness and parentage in an asocial, polyandrous striped hyena population

AARON P. WAGNER,* SCOTT CREEL,† LAURENCE G. FRANK‡ and STEVEN T. KALINOWSKI†

*Department of Zoology, Michigan State University, East Lansing, MI 48824, USA, †Department of Ecology, Montana State University, Bozeman, MT 59717, USA, ‡Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

Abstract

We investigated patterns of relatedness and reproduction in a population of striped hyenas in which individuals are behaviourally solitary but form polyandrous spatial groups consisting of one adult female and multiple adult males. Group-mate males were often close relatives, but were unrelated or distantly related in some cases, indicating that male coalitions are not strictly a result of philopatry or dispersal with cohorts of relatives. Most male–female pairs within spatial groups were unrelated or only distantly related. Considering patterns of relatedness between groups, relatedness was significantly *higher* among adult males living in non-neighbouring ranges than among neighbouring males. Mean relatedness among male–female dyads was highest for group-mates, but relatedness among non-neighbouring males and females was also significantly higher than among dyads of opposite-sex neighbours. Female–female relatedness also increased significantly with increasing geographic separation. These unusual and unexpected patterns may reflect selection to settle in a nonadjacent manner to reduce inbreeding and/or competition among relatives for resources (both sexes), or mates (males). Finally, resident males fathered the majority of the resident female's cubs, but extra-group paternity was likely in 31% of the cases examined, and multiple paternity was likely in half of the sampled litters.

Keywords: dispersal, *Hyaena hyaena*, maternity, paternity, polyandry, reproductive skew

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Introduction

For carnivores (and other taxa), the dispersion and renewal of resources (primarily food) is expected to influence spacing among females, while male space-use strategies should respond to the distribution of females to maximize mating opportunities (Jarman 1974). Cooperative establishment and defence of exclusive territories by multiple males are predicted (outside of monogamous systems) only if it provides for the simultaneous defence of multiple females (Macdonald 1983; Johnson *et al.* 2002) which, in turn, provides a fitness benefit exceeding the costs of increased competition for mating opportunities among group-mates. Support for this model is extensive. In many species of social carnivores, multimale coalitions defend the range of a group of cooperatively living females (e.g. palm-civets, *Nandinia binotata*, Waser *et al.* 1994; lions, *Panthera leo*, Packer *et al.* 1991; spotted

hyenas, *Crocuta crocuta*, Frank 1986; banded Mungos *Mungos mungo* and dwarf *Helogale parvula* mongooses, Creel & Creel 1991; Creel 1996). Male coalitions also facilitate access to multiple females in several less gregarious species. In cheetahs (*Acinonyx jubatus*), groups of males maintain ranges in areas used by several females (Caro & Collins 1987). In kinkajous (*Potos flavus*), pairs of males share a range with a single female, but the larger male ranges also overlap with those of neighbouring females (Kays & Gittleman 2001). Coalitions of male slender mongooses (*Galerella sanguinea*) share ranges large enough to fully encompass those of several solitary females (Waser *et al.* 1994).

In these and other species where cooperative male grouping has been detected, one clear benefit of multimale coalition formation is access to multiple breeding females. In contrast, in the only well-studied population, striped hyenas *Hyaena hyaena* live in stable, polyandrous spatial groups containing up to three adult males and a single reproductively mature female (Wagner 2006; Wagner *et al.* in press). Within spatial groups, male and female ranges

Correspondence: Aaron P Wagner, Fax: 603-457-0304; E-mail: apwagner@msu.edu

are highly congruent and equivalently sized. Despite using essentially identical ranges, group-living *Hyaena* are behaviourally solitary. Foraging and feeding is strictly solitary and levels of direct interaction are low in all other behavioural contexts. This strictly solitary lifestyle distinguishes *Hyaena* from species with fission–fusion societies in which individuals are often solitary but also congregate in groups while feeding or resting (e.g. kinkajous, Kays & Gittleman 2001; spider monkeys, *Ateles geoffroyi*, and chimpanzees, *Pan troglodytes*, Chapman *et al.* 1995; orangutans, *Pongo pygmaeus*, van Schaik 1999; spotted hyenas, Frank 1986), and from other demographically polyandrous species (e.g. saddle-back tamarins, *Saguinus fuscicollis*, Goldizen 1987; moustached tamarins, *Saguinus mystax*, Heymann 1996). Superficially, the space-use system of the striped hyena appears most similar to that in some coalition-forming carnivores, particularly proto-social carnivores (i.e. kinkajous, cheetahs, slender mongooses). However, the combination of equal size male and female home ranges (vs. slender mongooses), congruent male and female ranges (vs. cheetahs), and behavioural solitude (vs. kinkajous) distinguishes them even from these species. This social system is apparently unique among carnivores and primates, and has the potential to clarify the selection pressures that operate in primitively social species.

Although the social system observed in *Hyaena* has not been described for other carnivores or other mammals, multimale grouping in this species can still be explained by applying the root logic of existing models of group formation. Specifically, coalition formation may reflect male attempts to optimize trade-offs between the number of females (or female ranges) defended and the effectiveness of defence in the face of an unusual combination of constraints imposed by aseasonal breeding and a diet that favours large female territories and solitary foraging and feeding (Wagner *et al.* in press). In essence, if conditions dictate that ineffective lone-male defence is the only alternative, males may be forced to adopt a cooperative defence strategy. If this explanation is correct, we would expect several patterns:

- 1 Effective defence of resident females should be demonstrated by group-living males, who should father the majority of cubs born into the group.
- 2 Paternity should be shared equally among unrelated resident males, although reproductive success among related males may not be distributed evenly (Packer *et al.* 1991; Creel & Waser 1994).

Here we present genetic data from *Hyaena* and evaluate these basic predictions. We also address several questions related to patterns of genetic dispersion in *Hyaena* that naturally arise in light of their unusual social system. We address four such questions:

- 1 What patterns of dispersal account for these spatial group structures?
- 2 Does group formation reflect a lack of dispersal or codispersal with relatives?
- 3 What are the sex-specific patterns of genetic relatedness within and between spatial groups?
- 4 Is the polyandrous spatial organization reflected in a polyandrous mating system?

Methods

Field methods

Our analyses are based on genetic data collected as part of a 4-year field study of striped hyena ecology. Details of the study site and basic field methods are described in Wagner (2006) and Wagner *et al.* (in press). Briefly, this work was conducted on Loisaba, a private livestock ranch and wilderness reserve, and portions of nine neighbouring properties in Laikipia District, Kenya (Fig. 1). Within Loisaba, we caught striped hyenas using soft-catch foot-hold traps in 240, 192, 432, and 1865 trap-nights in each of the respective calendar years of the study. In the first 3 years of the study, we primarily set traps opportunistically in areas where hyenas were known to occur. In the final year, we applied a spatially systematic trapping approach in which traps were set in a pattern radiating outward from the centre of the Loisaba study area, attempting to sample all adult residents on Loisaba. Occasionally, neighbouring ranchers caught hyenas in their own cage traps, which we then collared and sampled as described below. The Laikipia Predator Project also caught and processed hyenas on other properties in traps set for lions or spotted hyenas. Consequently, striped hyenas were caught and processed throughout Laikipia (Fig. 1).

Using a blowpipe or dart gun, we anaesthetized trapped animals with Telazol (Zoletil) at a dose of approximately 2.5 mg/kg, or with a combination of ketamine HCl (3.6 mg/kg) and medetomidine HCl (0.06 mg/kg). We assigned each animal to one of four age classes: cub (< 6 months), juvenile (6 mos to 1 year), young adult (1–3 years), and adult (> 3 years). We fit all adult hyenas caught within Loisaba with VHF radio collars. For all hyenas, we collected tissue samples from the ear and drew blood into evacuated tubes. Post-collection, we froze all samples, transported them on dry ice and stored them in a –40 °C freezer until DNA extraction.

Throughout Laikipia, we collected samples from 59 individuals (cubs: females $n = 2$, males $n = 4$; juveniles: females $n = 1$, males $n = 0$; young adults: females $n = 10$, males $n = 7$; adults: females $n = 14$, males $n = 21$). Despite more than a fourfold increase in trapping effort, we caught no previously unknown adults on Loisaba in the final study year, suggesting that the entire population was identified.

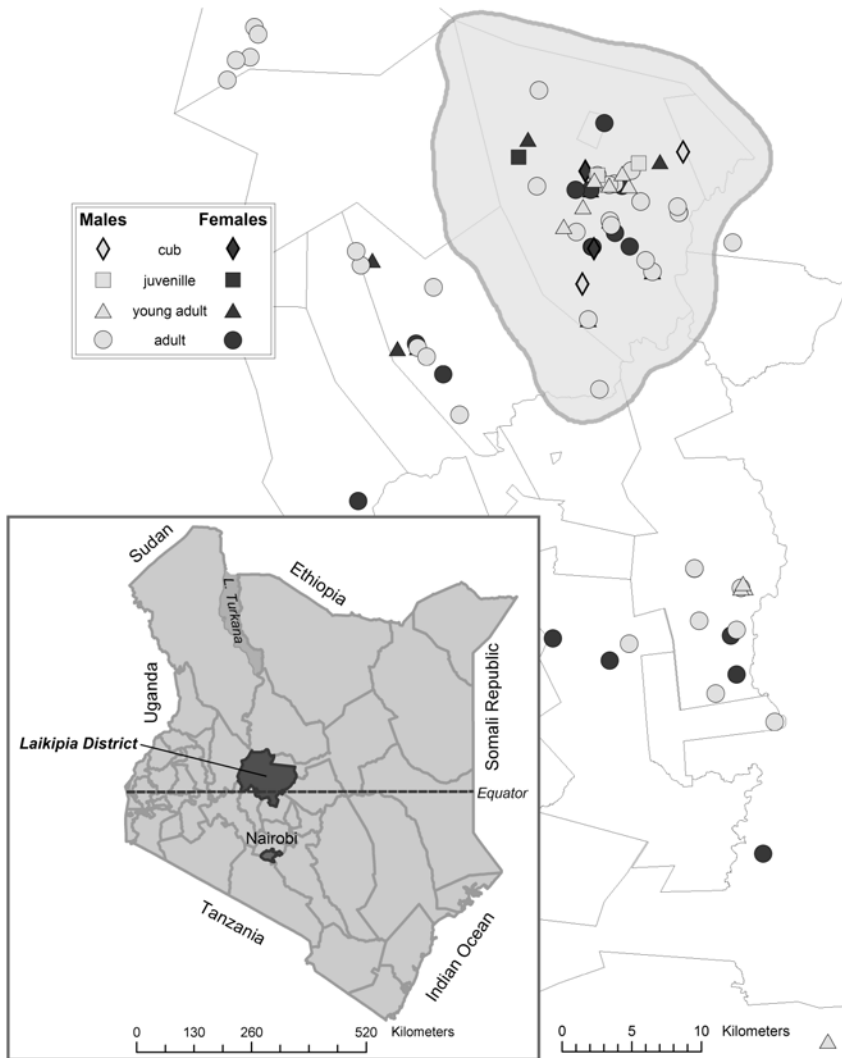


Fig. 1 Locations of captures overlaid on a property map of central Laikipia District and an inset map of Laikipia's location within Kenya. Area shaded and outlined in the main map indicates the core Loisaba study area. Point styles and shading indicate the age class and sex, respectively, of each hyena captured. Points represent all capture events, including recaptures.

In subsequent parentage analyses, we identified mothers for all of the subadult hyenas (i.e. all cubs, juveniles, and young adults) caught on Loisaba, and identified fathers for all but one (see Results). These lines of evidence also indicate that we sampled the majority of adults in the Loisaba population.

Whereas trapping was the primary tool used for sample collection, we used radio-tracking as the primary tool for collecting data on space use and patterns of association among individuals. The radio-tracking data are the focus of Wagner *et al.* (in press). Although some overlap cannot be avoided, we do not analyse the telemetry data in detail here; our primary focus is on analysis of genetic data and its relationship to the patterns of space used described in Wagner *et al.* (in press). Space-use patterns among

adults were largely stable over the course of the study (see Wagner 2006), with only two adults shifting from the spatial group in which they were initially caught.

Genetic analyses

For all hyenas sampled, we used polymerase chain reaction (PCR) to amplify DNA extracted from tissue or blood samples. We evaluated primers for 23 microsatellite loci (all previously developed for spotted hyenas) for use in striped hyenas (Ccr11–17, Libants *et al.* 2000; Ccroc01–10, Wilhelm *et al.* 2003; ccr01, ccr04–06, ccrA3, ccrA5, Funk and Engh unpublished). Eight of these primers (ccr04–06, Ccroc01 & 05–06, ccrA3, ccrA5) performed well and were used for genotyping (Table 1).

Table 1 The number of alleles observed and the observed (H_O) and expected (H_E) heterozygosities of each locus used for relatedness and relationship evaluation. The frequency of null alleles at the three loci where they were detected is given by p_n

	Ccr04	Ccr05	Ccr06	Ccroc01	Ccroc05	Ccroc06	ccrA3	ccrA5
No. of alleles	7	6	4	3	7	2	4	5
H_O	0.70	0.64	0.51	0.61	0.83	0.15	0.34	0.32
H_E	0.76	0.78	0.44	0.60	0.81	0.14	0.64	0.67
p_n		0.074					0.18	0.21
False exclusion probability		0.047					0.061	0.067

Each 15- μ L PCR contained 10–50 ng of template DNA, 1 \times Gold PCR Buffer (Applied Biosystems), 1.5 mm MgCl₂, 1.0 mm dNTPs, 200 ng BSA, 8.5 pmol 5'-end forward labelled primer, 8.5 pmol reverse primer (Integrated DNA Technologies and Applied Biosystems), 0.15 U of AmpliTaq Gold DNA polymerase (Applied Biosystems), and water to fill 15- μ L reaction volume. The thermal profile we used was a variation of Wilhelm *et al.*'s (2003) profile 67–55, consisting of a touchdown cycle (94 °C for 30 s, X °C for 45 s, 72 °C for 45 s, where X = 67–58 °C decreasing by 3 °C each step). Each touchdown annealing temperature was cycled twice, yielding a total of 10 cycles. After these touchdown cycles, the PCR amplification continued with 50 cycles of 94 °C for 30 s, 55 °C for 45 s and 72 °C for 45 s, followed by final extension at 72 °C for 30 min, and a hold step at 4 °C. PCR products were combined or separately visualized on a 3100-Avant Genetic Analyser (Applied Biosystems). The amount of PCR product loaded for visualization varied, depending upon whether PCR products were combined or visualized separately. Genotypes were assigned using GENEMAPPER software (version 3.7, Applied Biosystems).

For each locus, we used ML-RELATE (Kalinowski *et al.* 2006) to test for the presence of null alleles, as indicated by a deficiency of heterozygotes relative to Hardy–Weinberg expectations (Guo & Thompson 1992; Rousset & Raymond 1995). Null alleles were detected at three loci (ccr05, ccrA3, and ccrA5; see Table 1) and their frequency was estimated within ML-RELATE using a maximum-likelihood method (Kalinowski & Taper 2006). We then applied a correction for the presence of these null alleles (Wagner *et al.* 2006) in our calculations of relatedness (r) and the probability of relationships. This method assumes that any homozygote observed at a locus having null alleles could be either a true homozygote or a heterozygote with one null and one non-null allele. For each dyad considered, the probability of the observed pair of genotypes is then calculated using the partial probabilities of all possible combinations of true genotypes that could produce the genotypes observed. In general, this correction for null alleles improves the accuracy of relatedness and relationship estimation. In particular, it eliminates the problem of falsely excluding

parents when a null allele causes an apparent mismatch between truly matching genotypes. For pairwise estimates of relatedness, ML-RELATE uses a maximum-likelihood approach and calculates Wright's (1922) coefficient of relatedness (r), so the degree of relatedness between individuals is on an absolute scale (0–1), not a relative scale as with other programs (e.g. KINSHIP, Queller & Goodnight 1989). For specific patterns of relationship (R), we evaluated the full range of relationships available in ML-RELATE – unrelated (UR), half-sib (HS), full-sib (FS), and parent–offspring (PO) – and identified the relationship with the highest likelihood [ML(R)].

The performance of the method underlying ML-RELATE is evaluated in Wagner *et al.* (2006). However, use of ML-RELATE and the applied corrections for the occurrence of null alleles will be new to almost all readers and our choice of this methodology deserves a brief explanation. In addition to seeking more accurate estimates of relatedness, we used ML-RELATE as one tool to minimize Type II errors. A 1% scoring error rate, which can be accounted for in other genetic analysis programmes, could be expected to cause 9–10 errant allelic assignments in our data set (calculated as 8 loci*59 individuals genotyped*2 alleles per individual*.01). In contrast, we could expect 34 null alleles (or errors) in our data (calculated as the sum across all loci of $1-H_O$ *59 individuals typed*2 alleles per individual*the null allele frequency). In parentage analysis, the probability of falsely excluding a candidate parent due to a null allele at a single locus is given by H_O*p_n , where p_n is the frequency of the null allele at that locus (Wagner *et al.* 2006). If no correction is applied, the total probability of false exclusion due to a null allele at any locus is the sum of these partial probabilities. In our data, the total probability of falsely excluding a candidate parent due to a genotyping mismatch attributable to a null allele at any of the three loci where null alleles were detected was 0.175 (Table 1). Null alleles are a common source of genotyping error, but they are often ignored (Dakin & Avise 2004). Because readers may not appreciate the impact that null alleles can have in interpreting genetic data, we have highlighted those areas in our results where the impact of null alleles is most apparent.

Patterns of relatedness across geographic and social distances

We determined the spatial and 'social' distance between pairs of individual adult hyenas in two ways. First, we calculated the central balancing point (harmonic mean, HM) of the range of each individual in ArcView 3.2a (ESRI). We then calculated the distance (km) between every combination of two harmonic means (HM distance) as a continuous measure of the geographical separation between every pair of adults. Second, we categorized every possible pair of adults as to whether they lived in the same spatial group, lived in adjacent spatial groups, or lived in nonadjacent groups. We employed this 'social distance' approach to consider the possibility that pairs of contiguous neighbours could have substantial variation in the HM distance that separated their range centres. In both cases, we considered distances for all possible pairwise comparisons and pairwise comparisons separated by sex class (i.e. all pairs, male–male, male–female, and female–female dyads). We then compared the degree of relatedness between each pair of adults to the distance between them measured categorically (same, adjacent, nonadjacent) or continuously (HM distance).

For statistical analyses involving patterns of relatedness across HM and social distances, different dyads with one individual in common cannot be considered independent. Pairwise observations are also repeated measures nested within dyads, not individuals, so we could not employ the common method of including individual identity as a random effect to avoid pseudoreplication. A frequently employed alternative procedure is to construct matrixes of pairwise genetic and geographical distances and test for correlations between the two using Mantel tests (Mantel 1967; Manly 1997). For our data, 'valid' spatial distance measurements could not be assigned to some dyads because not all individuals were present or alive at the same time. To address these concerns, we used partial Mantel tests (Manly 1997; Anderson & Legendre 1999) to exclude any effect of temporal separation.

Partial Mantel tests evaluate the correlation between two matrixes, *A* and *B*, while controlling for the effect of a third matrix, *C* (Smouse *et al.* 1986; Manly 1997; Anderson & Legendre 1999; Bonnet & Van de Peer 2002; Reynolds & Houle 2002). In our analyses, all partial Mantel tests were conducted using the software *ZT* (Bonnet & Van de Peer 2002), applying the method developed by Anderson & Legendre (1999). This approach is based on permutations of a matrix of the residuals taken from a simple linear regression of the values in matrix *A* over the values contained in matrix *C*. This procedure is more appropriate for large sample sizes than those based on permutations of the rows and columns of raw values in matrix *A* (e.g. Smouse *et al.* 1986) (Legendre 2000). In each of our tests, we gener-

ated 10,000 randomized permutations of the residual matrix. The *P* value associated with each test represents the proportion of simulations for which the associated correlation coefficient was greater than or equal to the observed Mantel correlation statistic ($r_{A,B,C}$).

For all pair-types considered together, for male–male dyads, for female–female dyads, and for male–female dyads, we used the partial Mantel approach to test for significant correlations between HM distance (matrix *A*) and relatedness (matrix *B*), while controlling for the effects of any dyads not of interest (matrix *C*). In every test, all three matrixes contained all possible dyads. However, we used matrix *C* to distinguish valid dyads (i.e. those dyads for which the individuals lived at the same time and which represented the pair-type of interest) from invalid dyads (i.e. either the wrong pair-type or individuals in the dyad did not live at the same time) by assigning a value of 1 to all cells corresponding to the former and 0 to all cells for the latter. This approach allowed us to correct for the effect of time alone or the combined effects of time and pair-type(s), as appropriate for each test.

Maternity and paternity

Because the Loisaba population was more completely sampled than the broader Laikipia population, we only evaluated parentage for subadults (cubs, juveniles, and young adults) sampled on Loisaba (where all resident and most neighbouring adults were known), although all adults sampled from throughout Laikipia were initially included in the parental candidate pool. To evaluate maternity (and paternity, below) for each of the 14 subadults caught on Loisaba, we determined the likelihood of the parent–offspring relationship [L(PO)] for every possible adult female–subadult dyad in which the adult female lived within three territories of the location at which the offspring was captured. Of those, we considered only females for which L(PO) was greater than zero to be viable maternal candidates. We further evaluated the L(PO) for every viable maternal candidate against the highest L(PO) among all viable candidates. Finally, we compared maternal assignments with our best guess of maternity based on field observations. We considered the ability to assign maternity (and paternity) for each offspring as a test our success in sampling all resident adults on Loisaba.

We assigned paternity in much the same way as maternity. However, since there were more males in any area than females, there were more paternal candidates. Our approach was deliberately designed to minimize false exclusions and, in many cases, our method did not allow for definitive exclusion of all but one paternal candidate. Rather, the confidence of a paternal assignment is indicated by the degree of support for the top candidate relative to the others, as measured by likelihood ratios. This is

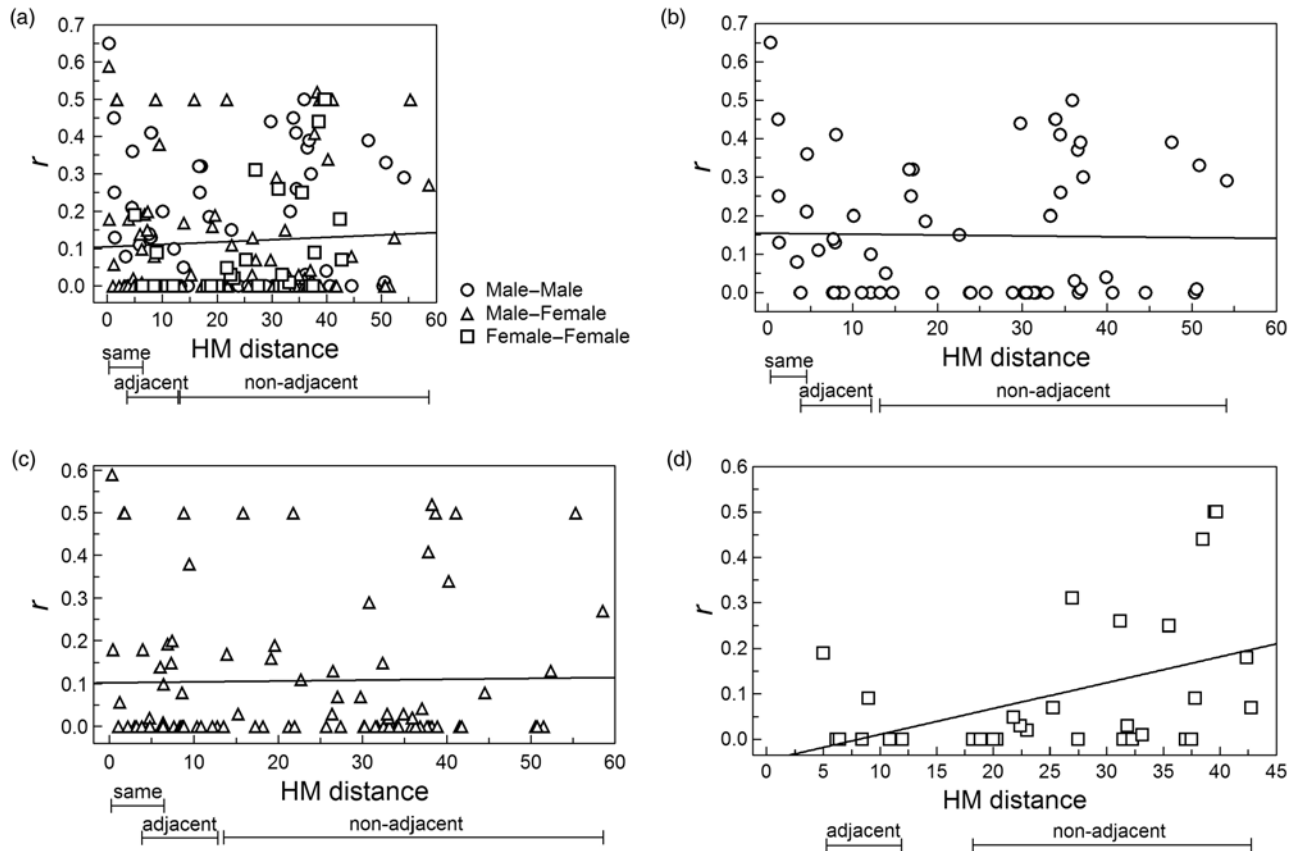


Fig. 2 Spatial distance (km) between the central harmonic mean of individual ranges [harmonic mean (HM) distance] compared to the degree of genetic relatedness (r) between individuals for (A) all pairwise comparisons for the entire adult population, (B) male-male dyads only, (C) male-female dyads only, and (D) female-female pairs. Horizontal bars beneath each plot indicate the range of HM distances observed within each categorical descriptor of distance (i.e. social distance; Fig. 3). Fitted least-squares regression lines are included within each plot.

analogous to the commonly employed Δ score given in programs like CERVUS (Marshall *et al.* 1998). Finally, we evaluated if the genotype of each paternal candidate was compatible with the genotype(s) of the maternal candidate(s).

Because we considered the likelihoods of all viable dyads and not just the adult-cub dyad with the highest L(PO), our criteria for assigning maternity and paternity were conservative in the sense of not excluding potential parents when the evidence, based solely on L(PO), was equivocal. That is, the likelihood of the parent-offspring relationship represented only a portion of the comparative data we considered (e.g. genetic consistency of the maternal and paternal candidates, consistent assignment of mothers to litter-mates). We applied this approach to minimize both Type II false exclusion errors (beyond what was accomplished by considering null alleles) and Type I false assignment errors due to incomplete consideration of the available data. Our distance criterion was also intended to allow all potential fathers into consideration.

Although we never detected any extra-territorial foray that crossed even one full range, we considered all adults living within three ranges of natal ranges as viable parental candidates.

Results

Patterns of relatedness across geographic and social distances

Using HM distances for pairs of individuals present at the same time, we detected no significant correlation between distance and relatedness for all adult dyads (disregarding sex), for male-male dyads, or for male-female dyads (Fig. 2A-C, Table 2). However, relatedness between females was positively (Fig. 2D) and significantly (at $\alpha = 0.05$) correlated with HM distance (Table 2). That is, among females living at the same time, those living farther apart were more closely related than those living close together.

Table 2 The Mantel statistic (Mantel $r_{A,B,C}$) and associated one-tailed P value from partial Mantel tests of the correlation between distance and relatedness. Separate partial Mantel tests were evaluated for each possible type of dyad across the full range of harmonic mean (HM) distances, the full range of social distances, and across every combination of two social distance measurements. The number of valid dyads (dyads for which the individuals were present at the same time and which correspond to the pair-type being evaluated) is indicated for each test. Adult females do not live in groups with other adult females. Significant correlations (at $\alpha = 0.05$) between distance and relatedness are indicated by P values in bold.

	Dyads considered	No. of valid dyads	Mantel $r_{A,B,C}$	P value
HM distances	All	181	0.029	0.289
	Male	60	-0.013	0.419
	Female	31	0.207	0.046
	Male-female	90	0.038	0.231
All social distances	All	181	-0.042	0.185
	Male	60	-0.104	0.103
	Female	31	0.130	0.136
	Male-female	90	-0.096	0.029
Same – adjacent	All	63	-0.083	0.053
	Male	20	-0.073	0.160
	Female	0	N/A	N/A
	Male-female	36	-0.091	0.037
Same – nonadjacent	All	140	0.005	0.489
	Male	47	-0.005	0.448
	Female	0	N/A	N/A
	Male-female	69	-0.076	0.063
Adjacent – nonadjacent	All	159	-0.103	0.017
	Male	53	-0.171	0.022
	Female	31	0.130	0.136
	Male-female	75	-0.098	0.024

Considering 'social distance' (i.e. living in the same, adjacent, or nonadjacent groups), again restricted to pairs of individuals present at the same time, mean relatedness for adult male-male and male-female dyads was highest for those living in the same group and lowest for those living in adjacent groups (Fig. 3; mean r values for male-male dyads: same = 0.30, adjacent = 0.08, nonadjacent = 0.14; for male-female dyads: same = 0.14, adjacent = 0.08, nonadjacent = 0.11). Adult female striped hyenas do not share ranges but, as it was for males and mixed-sex dyads, mean relatedness for adult females living in adjacent groups was lower than for those living in nonadjacent groups (mean r : adjacent = 0.04, nonadjacent = 0.12).

Relatedness and social distance were significantly correlated for male-female dyads across all social distances combined and for the comparison of same-group to adjacent-group social distances (Table 2). A significant correlation was also detected for all adult dyads (disregarding sex) across same and adjacent social distances. Note that

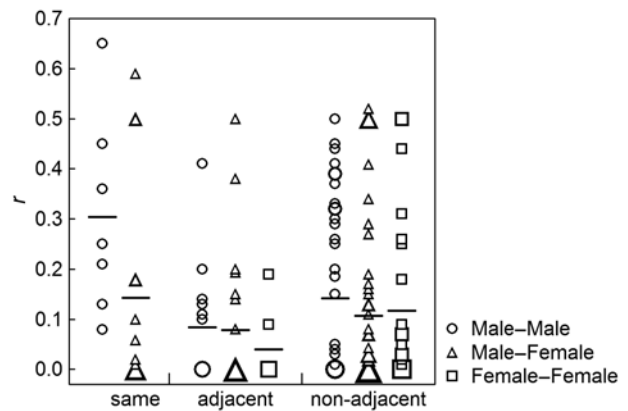


Fig. 3 Pairwise genetic relatedness (r) of individuals relative to social distances for male-male, female-female, and male-female dyads. Horizontal lines indicate the mean degree of relatedness within each distance and dyad-type category. Size of each point in the plot reflects the number of observations with that r value (minimum count = 1, maximum = 7). No two females lived in the same group.

when spatial and genetic distances are correlated (Bonnet & Van de Peer 2002), the sign of the Mantel r -statistic indicates only whether a small difference between points in one matrix is correlated with a small (+) or large (-) difference in the other (Reynolds & Houle 2002). That is, the direction of the relationship between genetic and social distances is shown in Fig. 3, but cannot be inferred from Table 2. Given spatial patterns of relatedness in other species, we were surprised to find higher levels of relatedness between individuals living in nonadjacent groups than between those living adjacent to one another (Fig. 3). This unusual pattern was significant for most pair-types: relatedness was significantly correlated with social distance across adjacent and nonadjacent social distances for male-male dyads, male-female dyads, and for all dyads considered together (Table 2).

Maternity and paternity

The pattern of maternity and paternity most in agreement with the data is summarized in Fig. 4. For all but two of the young hyenas evaluated (f15, m34), maternity was assigned to a single adult female (Table 3). In all cases, the maternal candidate thought to be the mother based on field observations was also the most likely mother based on genetic data. Viewed another way, the offspring was found in the area used by the most likely mother in all cases, so behavioural and genetic assessments of maternity aligned fairly well. In three cases (f41, f49, m30), PO was not the most likely relationship for the assigned mother-offspring dyad, but the most likely relationship was less than one-and-a-half times the likelihood of PO. In one of those three cases (m30), two litter-mates (m31 and m32)

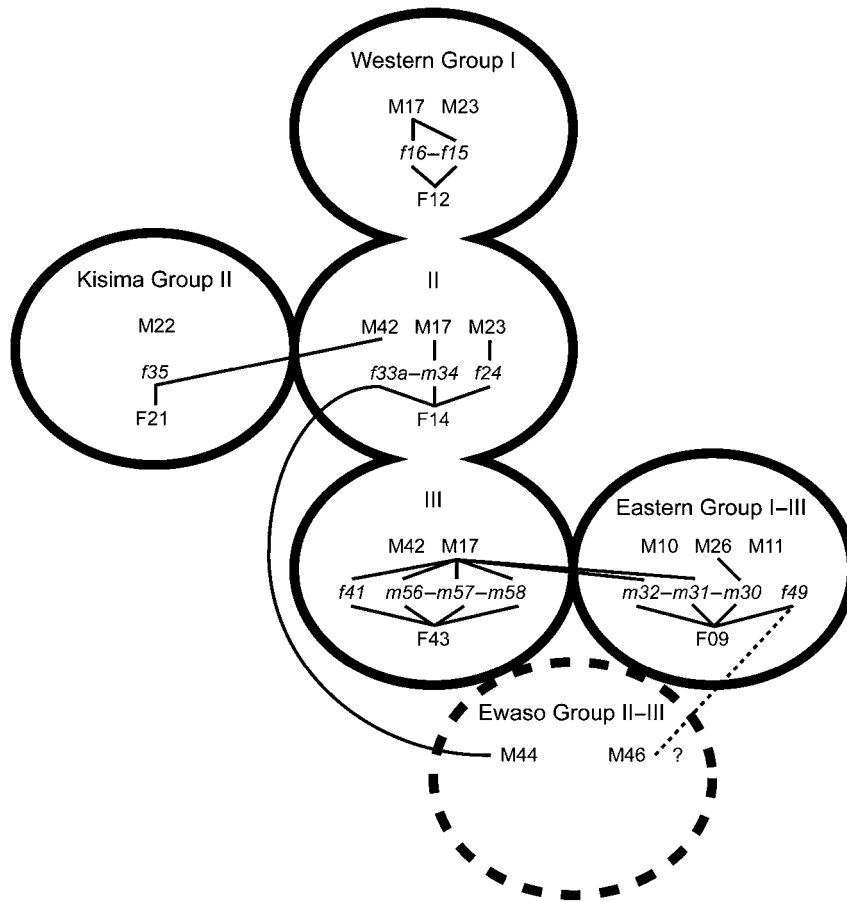


Fig. 4 Simplified representation of the compositions and orientations of the four spatial groups from which parents were identified for the sampled subadults. Resident adults are indicated by capital, block letters. Resident subadults are indicated by lower-case, italics. The dashed outline for the Ewaso Group indicates that this group was less well studied and the full group membership was not known. Lines between adults and subadults indicate paternity and maternity (Tables 3 and 4). Dashes between subadults indicate littermates. A dotted line is drawn between M46 and f49 to indicate that that paternal assignment would be incompatible with the maternal assignment. Note that there are only four spatial groups represented here – group membership in the Western Group changed three times during the study. Roman numerals differentiate group membership at each of these stages and indicate contemporary residents across spatial groups. As depicted, the Ewaso and Eastern Groups were physically adjacent to each other and the Western Group was adjacent to all of the groups shown.

Offspring	Maternal candidate	<i>r</i>	ML(R)	ML(R)/L(PO)	Best guess	Same?	No. of territories apart
f15	F12	0.50	PO	1.00	F12	Yes	0
f16	F12	0.50	PO	1.00	F12	Yes	0
f24	F14	0.59	PO	1.00	F14	Yes	0
f35	F21	0.60	PO	1.00	F21	Yes	0
f41	F43	0.70	FS	1.21	F43	Yes	0
f49	F09	0.28	HS	1.23	F09/F43	Yes	0
m30	F09	0.61	FS	1.26	F09	Yes	0
m31	F09	0.50	PO	1.00	F09	Yes	0
m32	F09	0.50	PO	1.00	F09	Yes	0
f33a	F14	0.52	PO	1.00	F14	Yes	0
m34	F14	0.50	PO	1.00	F14	Yes	0
m56	F43	0.59	PO	1.00	F43	Yes	0
m57	F43	0.59	PO	1.00	F43	Yes	0
m58	F43	0.59	PO	1.00	F43	Yes	0

Table 3 Offspring, the possible mothers for each offspring, the degree of relatedness (*r*) for the parent-offspring pair, the relationship most consistent with the genotypes [ML(R), maximum-likelihood relationship], the ratio of the most likely relationship to the likelihood of a parent-offspring relationship [ML(R)/L(PO)], the best guess of maternity based on field observations (Best guess), and the social distance (measured in number of territories) between the offspring and maternal candidate. Outline around offspring ids indicate probable same-litter siblings. In two cases (f15, f34) two females were viable maternal candidates. The most likely (highest likelihood) mother is listed above the less likely maternal candidate

had the same mother identified, both with PO most likely. The mother for m30 and m31 could only be identified by application of the correction for the presence of null alleles.

Paternity was assigned to a sampled adult male for all of the offspring evaluated (Table 4). Up to six males were viable candidates for paternity, but because we found consistent maternal assignment within litters of cubs, we

Table 4 Offspring, the possible fathers for each offspring, the degree of relatedness (r) for the parent–offspring pair, the relationship most consistent with the genotypes [(ML(R)], the ratio of the most likely relationship to the likelihood of a parent–offspring relationship, the best guess of paternity based on field observations, and the social distance between the offspring and paternal candidate. Outlines indicate probable same-litter siblings. The last column indicates whether the paternal candidate was genetically consistent with the maternal candidate identified in Table 3 (Y, Yes; N, No). Without the application of the correction for null alleles, several viable candidate males, those indicated by Y (null), would have been identified as genetically inconsistent with the maternal candidate. For f15 and m34, the consistency of the paternal candidate is only indicated for the most likely maternal candidate (no paternal candidates were genetically consistent with the less likely maternal candidate for either offspring)

Offspring	Paternal candidate	r	ML(R)	ML(R)/L(PO)	L(PO) _{best} /L(PO) _x	Best guess	Same?	No. of territories apart	Consistent with maternal candidate?
f15	M17	0.50	PO	1.00	1.00	M17	Yes	0	Y
	M23	0.50	PO	1.00	1.68			1	Y
	M26	0.26	HS	1.27	4.71			1	N
	M44	0.41	PO	1.00	29.37			1	N
f16	M17	0.50	PO	1.00	1.00	M17	Yes	0	Y
	M23	0.50	PO	1.00	3.19			1	Y
f24	M44	0.50	PO	1.00	1.00	M23	No	1	Y
	M36	0.50	PO	1.00	2.27			1	N
f35	M42	0.50	PO	1.00	1.00	M22	No	1	Y
	M39	0.26	HS	1.21	7.32			1	Y (null)
	M46	0.27	HS	1.25	9.49			2	N
	M36	0.50	PO	1.00	70.11			1	N
	M22	0.27	HS	1.19	119.10			0	Y (null)
	M37	0.00	UR	2.41	572.49			1	Y (null)
	M17	0.50	PO	1.00	1.00	M17/M42	Yes	0	Y
f41	M46	0.27	HS	1.19	1.00	M10/M11/M26/M42	No	1	N
f49	M26	0.51	PO	1.00	1.00	M10/M11/M26	Yes	0	Y
m30	M46	0.42	PO	1.00	1.80			1	Y (null)
	M11	0.37	HS	1.03	18.92			0	Y (null)
	M10	0.33	HS	1.26	55.15			0	Y (null)
	M17	0.41	PO	1.00	1.00	M10/M26/M11	No	1	Y (null)
m31	M10	0.46	PO	1.00	1.60			0	Y (null)
	M46	0.50	PO	1.00	1.00	M10/M26/M11	No	1	N
m32	M26	0.50	PO	1.00	3.25			0	N
	M17	0.50	PO	1.00	19.30			1	Y (null)
	M10	0.30	HS	1.35	333.62			0	Y (null)
f33a	M42	0.50	PO	1.00	1.00	M17	No	0	N
	M44	0.50	PO	1.00	19.89			0	Y
m34	M17	0.50	PO	1.00	1.00	M17	Yes	0	Y
	M23	0.50	PO	1.00	3.35			0	Y
m56	M17	0.50	PO	1.00	1.00	M17/M42	Yes	0	Y
m57	M17	0.50	PO	1.00	1.00	M17/M42	Yes	0	Y
m58	M17	0.50	PO	1.00	1.00	M17/M42	Yes	0	Y

also considered genetic inconsistency with maternal assignments in excluding paternal candidates. This criterion resolved paternity unambiguously in most cases, but in some cases, there remained multiple genetically consistent ways in which paternity could be assigned to the cubs of a litter. Overall, 63% (13 of 22) of candidate males genetically consistent with the maternal assignment lived within the natal group. Among the subset of males with the highest likelihood (literally, the most likely) of paternity for each offspring that were also genetically consistent with the maternal assignment, 69% (9 of 13) lived within the natal group. In all cases, PO was the most likely relationship

for most likely fathers. Thus the pattern of paternity indicated by the set of 13 most likely fathers (Fig. 4) is consistent with the broader ‘average’ picture of approximately one-third of paternities being extra-territorial.

Discussion

Paternity

Group-living males fathered the majority (69%) of the resident female’s offspring (Table 4, Fig. 4). This supports the interpretation of coalition formation as a strategy to

Table 5 Pairwise relatedness of adults in the spatial groups for which parents were identified (Fig. 4). Parts I, II and III are for different time periods. For each time period, only females with offspring are included here (see Fig. 4). Italicized male IDs indicate fathers. Bold IDs indicate males that fathered cubs born in the same spatial group. Shaded IDs indicate males that fathered cubs in a neighbouring group. Shaded cells identify relatedness (r) values for all dyads that include breeding females. Bold and italicized r values indicate relatedness for parental dyads. Dashed cell outlines identify sets of r -values for members of a single spatial group

		Western			Eastern		
I		F12	<i>M17</i>	M23	M10	M11	M26
Western	F12	—					
	<i>M17</i>	0	—				
	M23	0	0.62	—			
Eastern	M10	0	0.42	0.45	—		
	M11	0	0	0.53	0.66	—	
	M26	0	0.12	0.49	0.2	0.36	—

		Kisima		Western				Eastern			Ewaso	
II		F21	M22	F14	<i>M17</i>	M23	<i>M42</i>	M10	M11	M26	<i>M44</i>	M46
Kisima	F21	—										
	M22	0	—									
Western	F14	0.17	0	—								
	<i>M17</i>	0	0	0.01	—							
	M23	0	0	0	0.62	—						
	<i>M42</i>	0.19	0.17	0.1	0.08	0	—					
Eastern	M10	0	0	0	0.42	0.45	0	—				
	M11	0	0.22	0	0	0.53	0	0.66	—			
	M26	0	0	0	0.12	0.49	0	0.2	0.36	—		
Ewaso	<i>M44</i>	0.5	0	0.16	0	0	0.01	0	0	0.05	—	
	M46	0	0.06	0	0	0	0	0	0	0.63	0.13	—

		Western			Eastern				Ewaso	
III		F43	<i>M17</i>	M42	F09	M10	M11	<i>M26</i>	M44	M46
Western	F43	—								
	<i>M17</i>	0.18	—							
	M42	0	0.08	—						
Eastern	F09	0	0	0	—					
	M10	0	0.42	0	0	—				
	M11	0.08	0	0	0.03	0.66	—			
	<i>M26</i>	0.14	0.12	0	0.59	0.2	0.36	—		
Ewaso	M44	0	0	0.01	0	0	0	0.05	—	
	M46	0	0	0	0.44	0	0	0.63	0.13	—

defend mating opportunities. Although coalition-forming males did not fully eliminate extra-territorial paternities, we hypothesize that increased odds of paternity for residents presumably outweighs the costs of competition for breeding opportunities among group-mates. Our data are not sufficient to directly measure these costs and benefits. However, it may be telling that some paired-male coalitions included only distantly related males, whereas male trios included at least two close relatives (see Table 5) — if the defensive benefits of having more than one group-mate are eclipsed by competition with group-mates for

mating opportunities, larger groups would be unstable unless they include relatives who could realize inclusive fitness benefits (see below), as has been shown for male lions (Packer *et al.* 1991).

Extra-territorial paternity is known also for kinkajous (Kays *et al.* 2000), saddle-back tamarins (Terborgh & Goldizen 1985), European badgers, *Meles meles* (Woodroffe *et al.* 1995), and the red fox, *Vulpes vulpes* (Baker *et al.* 2004), and are likely in moustached tamarins (Huck *et al.* 2005). In the closely related aardwolf *Proteles cristatus*, females overtly copulate more with neighbouring males than with resident

males (Richardson 1987). The same is also true of the Ethiopian wolf *Canis simensis*, where extra-group copulations may be an adaptive strategy to avoid inbreeding (Sillero-Zubiri *et al.* 1996). This explanation seems unlikely for striped hyenas, however, because male–female dyads within groups were typically unrelated or distantly related (although relatedness of females to their male neighbours was often still lower) (Fig. 3).

Multiple paternity was possible in three of four litters (Table 4), and probable in two (Fig. 4). Although the frequency with which it occurs varies, multiple paternity of litters is common in other carnivores (Gompper & Wayne 1996), including lions (Packer *et al.* 1991), dwarf mongooses (Creel & Waser 1994; Keane *et al.* 1994), Ethiopian wolves (Sillero-Zubiri *et al.* 1996), European badgers (da Silva *et al.* 1994), African wild dogs *Lycaon pictus* (Girman *et al.* 1997), grey wolves *Canis lupus* (Lehman *et al.* 1992) and red foxes (Baker *et al.* 2004). Multiple paternity within litters is also reported for a diverse range of mating and social systems, including those with polyandrous mating systems similar to striped hyenas (grey mouse lemurs, *Microcebus murinus*, Eberle & Kappeler 2004; moustached tamarins, Huck *et al.* 2005; banner-tailed kangaroo rats, *Dipodomys spectabilis*, Winters & Waser 2003). In *Hyaena*, the observed incidents of extra-group paternities (which include cases of multiple paternity) and the lack of cases of intragroup multiple paternity (male group-mates only shared paternity in one case) (Table 4, Fig. 4), suggest that the mating system may be promiscuous. However, this conclusion is dependent on data from only four litters, and group membership remains the best overall predictor of paternity.

Reproductive success

Reproductive success among unrelated group-living males is expected to be more evenly distributed than reproductive success among related males. Because relatives can accrue the benefits of indirect fitness, they are always more exploitable than nonrelatives (Hamilton 1963; Vehrencamp 1983; Creel & Waser 1991). If reproductive success among unrelated males is skewed because one male is able to dominate his group-mates, coalitions may be unstable. However, nonmating males could still accrue benefits by remaining for some time with unrelated males because group-living could provide a relatively safe haven compared to roaming, and subordinate males could wait for opportunities to inherit territories or capitalize on vacancies in neighbouring territories. These ‘make-the-best-of-a-bad-lot’ and ‘group augmentation’ strategies are well established for subordinates in many cooperatively breeding species (Brown 1987; Stacey & Koenig 1990; Koenig & Dickinson 2004), including some carnivores (Creel & Waser 1994; Waser 1996; Clutton-Brock *et al.* 2002). Our data is not adequate to quantify these fitness effects, but the presence

of both related and unrelated pairs of males sharing the same range suggest that a mixture of direct and indirect effects may be important in maintaining male coalitions.

Our data allow limited scope for evaluating reproductive skew among group-living *Hyaena* males — our trapping on Loisaba was designed to collect samples from all adults, not subadults, and there are only six cases of intragroup paternity to consider (two singletons, two full litters, and two partial litters; Fig. 4). Within this limited framework, however, paternity was not distributed evenly. Specifically, M17 bred more successfully with females in his own group than the other (related and unrelated) males in the group (Fig. 4, Table 5). Biases in male reproductive success are also common among more social carnivores, proto-social carnivores (including kinkajous, Kays *et al.* 2000), and callitrichin primates (e.g. moustached tamarins, Huck *et al.* 2005). However, lifetime reproductive success, which we could not measure in this study, may be more evenly distributed among group-living males than short-term reproductive success (as demonstrated in dwarf mongooses, Creel 1998).

Relatedness within spatial groups and among parents

Male coalitions included both closely related and distantly related males (Fig. 3), a pattern also reported for coalitions in other proto-social carnivores (cheetahs, Caro 1994; kinkajous: Kays *et al.* 2000; slender mongooses, Waser *et al.* 1994), polyandrous callitrichin primates (saddle-back tamarins, Goldizen *et al.* 1996), and social carnivores (lions, Packer *et al.* 1991). Within male coalitions, mean relatedness (r) was high (0.3), falling between that of noninbred half-sibs (0.25) and full-sibs/parent–offspring (0.5). This level of relatedness is similar to that in groups of highly social, cooperatively breeding carnivores (e.g. dwarf mongooses: Creel & Waser 1994; lions: Packer *et al.* 1991) as well as other hyenids (brown hyenas *Parahyaena brunnea* and spotted hyenas: Mills 1989). Within groups, male and female *Hyaena* were often only distantly related (Fig. 3), adding weight to the interpretation of spatial groups as breeding groups.

Relatedness of breeding females to their male mates was fairly low (Table 5), averaging 0.16. This is marginally higher than mean within-group male–female relatedness. However, for the six dyads other than F09–M26 (which were closely related), mean r was only 0.09. With the exception of F09, we did not find breeding females living in a group with close male relatives. Consequently, it may be that the mechanism of spatial group formation (e.g. dispersal), rather than mate choice per se, plays a significant role in preventing inbreeding within a group. Considering that mean relatedness among male–female dyads was lowest for neighbours (Fig. 3) and that we did not detect any mating forays extending beyond a neighbouring range (Tables 4 and 5), the same may be true of extra-territorial matings.

Relatedness across distances

Relatives generally live closer together than nonrelatives, and levels of relatedness are expected to decline with increasing distance (e.g. Gompper *et al.* 1998; Spong *et al.* 2002; Van Horn *et al.* 2004). Counter to this expectation, mean relatedness among neighbouring *Hyaena* males was significantly lower than relatedness among males living in nonadjacent ranges (Fig. 3, Table 2). Male–female relatedness was also significantly lower for neighbours than for non-neighbours. Patterns across geographic (HM) distances were also surprising. Relatedness among female *Hyaena* increased significantly across HM distances, and remained unchanged for male–male and male–female dyads (Fig. 2, Table 2).

Although our examinations of geographical and social distances both yielded results different from expectations, the two measures did not generate identical pictures of patterns of relatedness. However, the relationship between geographic and social isolation can be complex, particularly at fine scales. For example, the shape of individual territories can result in a segment of a given length (distance) drawn from one harmonic mean to cross less than one territory if projected in one direction, but more than one territory if projected in another direction. This variable relationship between HM distance and social isolation was demonstrated in this population by HM distances between some same group members (e.g. F09 and M11, M42 and M17) being the same as the distance to individuals living in adjacent groups (e.g. F09 and M42) (Fig. 5). Consequently, a categorical measure of social proximity (Fig. 3) could

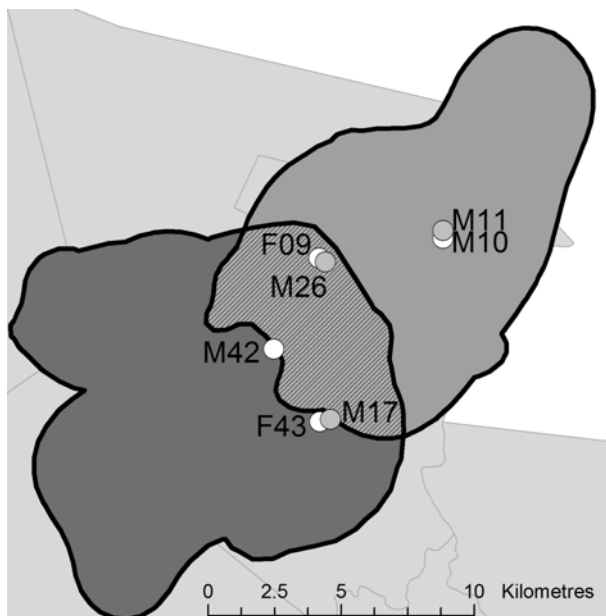


Fig. 5 Group ranges (i.e. the combined ranges of residents) for two spatial groups. Points and labels indicate the harmonic mean of space-use areas for each individual adult within each spatial group.

conceivably be more sensitive than a continuous measure (Fig. 2) and better reflect biologically important patterns, even though categorization of continuous data typically reduces power. This may explain the detection of significant patterns across HM distances but not across social distances for females (where $n = 5$ for adjacent dyads) and the lack of a detectably significant difference between the males dyads in the same group (where $n = 7$) vs. adjacent groups.

The low level of relatedness among neighbours relative to non-neighbours is a surprising pattern. Spatial patterns of relatedness can reflect dispersal strategies to minimize the potential for inbreeding (Pusey 1987) and, given the occurrences of extra-group copulations, the observed low levels of relatedness among male–female neighbours seems to fit expectations under this model. However, this model cannot explain low levels of relatedness among same-sex neighbours. Alternatively, patterns of relatedness across social distances may reflect dispersal strategies to minimize competition for resources (Macdonald 1983). Accordingly, the observed patterns for *Hyaena* may indicate reinforcing selection to settle in a nonadjacent manner to reduce competition with relatives for food (both sexes), or mates (males). Although natal dispersal to nonadjacent ranges could be the main mechanism underlying the observed genetic patterns, secondary dispersal could also be involved. Secondary dispersal due to the death of a mate, eviction by new immigrants, to avoid inbreeding, or to increase mate access is reported for male dwarf mongooses, lions, and spotted hyenas (Waser 1996). In this *Hyaena* population, M11 secondarily dispersed to a range adjacent to the one he shared with a close relative (M10, who remained on the original range). If secondary and/or tertiary dispersal, in combination with coalition fission, is common, it could lead to a pattern of spatial separation between relatives like that observed for *Hyaena* (as in diffusion models of dispersal).

Conclusion

Overall, the picture of striped hyena social organization is familiar in many ways and surprising in others. They are behaviourally solitary, have a polyandrous system of space use, and a polyandrous or promiscuous mating system. Although the polyandrous spatial system is not perfectly reflected in the mating system, differences in the size and form of feeding, foraging, breeding, and/or spatial groups are common among mammals. Fundamentally, *Hyaena* spatial groups can be considered breeding groups because all offspring can be assigned to the female of the natal group, and the majority of offspring are sired by males within the natal group. Reproductive success was not evenly distributed among unrelated group-mates. Relatedness within *Hyaena* spatial groups was similar to levels in highly

social carnivores such as dwarf mongooses and lions. However, relatedness between some pairs of group-mates (including male–male dyads) was low and it is unlikely that male coalitions simply represent cohorts of codispersers or natal family groups. These and other patterns of relatedness and reproduction in *Hyaena* are shared with many of the more social carnivores, proto-social carnivores, and primates. In contrast, the patterns of relatedness across spatial groups in *Hyaena* (i.e. lower levels of relatedness among neighbours than among non-neighbours) are atypical and more difficult to resolve. For now, prior models of social evolution in carnivores suggest that these patterns probably reflect dispersal strategies that reduce inbreeding and/or reduce resource competition among relatives when conditions do not permit cooperative group formation.

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AP Wagner is an evolutionary ecologist whose research focuses on the links between social evolution, sexual development, endocrinology, and genetics, as well as on carnivore conservation outside of protected lands and human impacts on carnivore behavior. S Creel is a behavioral ecologist whose research generally focuses on interactions between behavior, endocrinology, population ecology, and conservation. His recent work has focused on the factors that limit African wild dogs, and on predator-prey interactions between wolves and elk. LG Frank's research focuses on conservation of large carnivores in Africa and human-carnivore conflict. ST Kalinowski is a conservation geneticist. Much of his research seeks to make genetic data more useful for answering ecological questions.
