

**Linking social structure to fine-scale genetic structure and genetic variance in
fitness in spotted hyenas**

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18 **Abstract**

19 Many animal populations are structured by social relationships that influence dispersal, mating,
20 and the spatial distribution of individuals. Theory predicts that social structure can affect gene
21 flow and population genetic structure, as well as the distribution of genetic variance in fitness.
22 However, these processes have never been examined together in natural populations. Using
23 nearly 30 years of behavioural, life-history, and genomic data from spotted hyenas (*Crocuta*
24 *crocuta*) in Tanzania's Ngorongoro Crater, we investigated whether social structure, dispersal,
25 genetic structure, and genetic variation in fitness covary in a spatially continuous population.
26 Genome-wide analyses revealed modest genetic differentiation among social groups (called
27 clans), despite genetic variation being distributed fairly continuously across the population.
28 Genetic differentiation between clans decreased with increasing male dispersal, consistent with
29 dispersal facilitating gene flow. Individuals with greater ancestry from outside the Crater had
30 higher lifetime reproductive success and longer lifespans, suggesting that immigration
31 introduced genetic variation associated with higher fitness. Finally, additive genetic variance in
32 fitness differed among some clans, but not consistently across the population. Together, our
33 findings suggest that social structure can shape fine-scale genetic structure and the genetic
34 basis of fitness, although these patterns are evident in some social groups rather than others.
35 More broadly, our study highlights the value of integrating social, behavioural, genomic, and
36 quantitative genetic data to understand the interplay between social structure and
37 microevolution in wild populations.

38 **Keywords:** microevolution, dispersal, sociality, genetic variance, fitness, gene flow

39

40 ***Introduction***

41 Social behaviours have evolved across a wide range of animal species and give rise to diverse
42 forms of social structure, from transient pairwise associations to stable family groups and
43 multilevel cooperative societies (1,2). These social structures are defined by differentiated social
44 relationships which contribute to the non-random distribution of individuals across space.
45 Accordingly, theory and empirical work across behavioural ecology, social evolution, and
46 population genetics have long recognised that social structure can influence dispersal, gene
47 flow, and population genetic structure (3–5). However, social structure may also be associated
48 with how genetic variation underlying individual fitness is distributed within populations, which
49 predicts a populations potential response to selection under quantitative genetic theory (6,7).
50 Understanding these links would help bridge behavioural ecology with population and
51 quantitative genetics and clarify how social structure relates to microevolutionary processes in
52 the wild.

53 Social structure emerges from individual and group-level behaviours such as mating,
54 grouping, and dispersal (8), and these behaviours collectively influence how genetic variation is
55 distributed within populations. Social interactions and dispersal are highly interdependent and
56 are jointly shaped by kinship, sex, and ecological context (4,9,10). For instance, dispersal
57 decisions are often coordinated among social partners, frequently kin, and are further
58 influenced by mate choice (11–14). As a result, social structure and dispersal behaviour can
59 influence the rate and direction of gene flow, generating fine-scale genetic structure even in
60 continuous populations (3,15). Links between dispersal, social structure, and genetic
61 differentiation have been demonstrated across diverse taxa (8,16–22) but social structure and
62 dispersal may also be associated with genetic variation in fitness. Dispersal among social groups

can introduce alleles that alter the distribution of breeding values for fitness and the genetic variance available to selection within recipient groups (6,7,21,67). These associations may be particularly important when spatial variation in ecological selection pressures aligns with the distribution of social groups. Although additive genetic variance in fitness has been estimated in natural populations (7), few studies integrate quantitative genetics with behavioural and demographic data to examine how dispersal-mediated gene flow relates to the distribution of genetic variation for fitness. To our knowledge, no study has tested whether dispersal among social groups is associated with variation in breeding values for fitness or additive genetic variance in fitness among groups. Investigating these processes together within the same population would allow us to examine whether patterns of social organisation and dispersal associated with genetic structure among groups are also reflected in how genetic variation for fitness is distributed among those groups.

We address this integrative gap by leveraging an exceptionally rich dataset from a population of spotted hyenas (*Crocuta crocuta*) living in Tanzania's Ngorongoro Crater. Spotted hyenas provide a valuable system for examining how social structure and dispersal behaviour are associated with patterns of genetic structure and quantitative genetic variation under natural conditions because their societies generate clear, biologically interpretable axes of social structure (20,23–26). Their multilevel fission–fusion social groups (called clans), stable female-dominated dominance hierarchies, low rates of extra-group mating, and pronounced reproductive skew create social environments in which individuals experience different opportunities for mating, competition, and kin interactions (20,27–30). Moreover, male-biased dispersal between clans is often coordinated among kin and based on female availability (14,29,31), which may result in structured patterns of gene flow.

The Ngorongoro Crater population is one of the best-characterised wild mammal systems, with nearly three decades of continuous behavioural monitoring, detailed demographic records for more than 3,200 individuals, a nine-generation genetic pedigree, and genome-wide SNP data from 1,181 animals. Previous work in this population has estimated additive genetic variance in fitness (7), providing evidence for contemporary adaptive evolution and creating an opportunity to examine how social and demographic structure coincide with population- and quantitative-genetic variation. The population is structured into eight resident social groups (called clans) whose territories vary along key ecological axes such as group size (e.g., min = 22, max = 90 individuals in June 2024), habitat type, territory size, exposure to pastoralism and sex ratio (Figure 1, (32)). These differences create social subunits that may differ in the distribution of genetic variation and in ecological conditions experienced by individuals.

We addressed four specific questions: (1) is genetic variation structured among clans? (2) are patterns of dispersal associated with observed genetic structure? (3) does clan ancestry predict individual fitness, and (4) does additive genetic variance in fitness vary among clans? By addressing these questions, we integrate dispersal, genetic ancestry, fitness and quantitative genetic variation to examine whether socially defined population structure corresponds to heterogeneity in the distribution of genetic variation underpinning fitness.

Methods

Study population and data collection

We used data collected as part of a long-term individual-based study of a population of spotted hyenas occupying the floor of the Ngorongoro Crater in Tanzania (approx. 250 km², 3°11' S, 35°34' E). The population is part of the wider hyena metapopulation of the Greater Serengeti-

Mara ecosystem (29) and has been continuously monitored on five to seven days a week as part of a long-term individual-based study since April 1996. All hyenas in the population are individually identified by their spot pattern and colouration of their coat, as well as other uniquely identifiable features (e.g., scars and ear notches, described in (29,31)). Demographic, life-history and behavioural data are collected by observing hyenas from a vehicle that they are well habituated to from birth (31,33). DNA is isolated from tissue, faecal, skin or hair samples which are collected opportunistically.

Births and deaths are rarely observed in the wild, but are estimated using a combination of resighting data during surveys, behavioural observations and morphology (explained in (29,32)). Social ranks of all individuals are determined via established rules of maternal inheritance and social support, and are verified via behavioural interaction data (33,34). Males were considered to have chosen a breeding clan when they displayed sexual behaviour towards the females of either their natal clan (a philopatric male) or another clan (a disperser) and engaged in social interactions with members of that clan for at least 3 months (29,33). The majority of males (>90%) dispersed to a breeding clan once and remained there for their entire adult life. However, a small number of males had multiple dispersal events throughout their lifetime, where they may disperse to a new clan later in life after spending some time living and reproducing in the clan to which they dispersed first (29). For these males, their adult clan was identified as the clan in which they spent the majority of their adult life. Parentage is identified via a combination of observations of nursing and genetic parentage assignment, which is reconstructed using nine polymorphic microsatellite loci in CERVUS 3.0 (28,35). In this study, we used records collected between April 1996 and February 2025. The full pedigree used in this study contained 3,239 individuals sampled across a maximum depth of nine generations, which included 2,985 born in one of the eight Crater clans. 1,843 individuals had both parents

identified, 940 with a known mother only, and 4 with a known father only. Amongst the remaining 452 hyenas with no known ancestors, 134 were alive at the start of the study (“founders”).

Field data collection and transport was permitted by the Vice President's office of the United Republic of Tanzania (Ref. No. BA 78/130/01/42), the Tanzania Wildlife Research Institute (TAWIRI), the Tanzania Commission for Science and Technology (COSTECH; Permit No. 2021-380-NA-1990), and the Ngorongoro Conservation Area Authority (NCAA). All study procedures were performed in compliance with the ethical regulations of these institutions and the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research Berlin (No. 2020-06-02).

Genotyping-by-sequencing

A detailed description of the methodological approach we used to generate the genotype-by-sequencing dataset is provided in (36). Briefly, library construction followed the 3RADseq protocol (37) using the restriction enzymes *EcoRI*, *XbaI*, and *NheI* and incorporating a modification to remove PCR duplicates (38), which enabled sequencing approximately 23,500 loci (380 - 460 bp). Barcoded samples were pooled prior to fragment size selection (range to 480-640 bp) using the Blue Pippin (Sage Science) with a 1.5% cassette. The product was split into two aliquots and each was subjected to a single-cycle PCR to incorporate the iTru5-8N primer, followed by an indexing PCR. A low coverage sequencing run (approximately 2,000 reads per individual) was conducted to screen samples for endogenous DNA content and, based on the proportion of reads assigned to each individual, new volumes of the digestion/ligation product were calculated and re-pooled for a second library preparation to ensure equal representation across individuals (described in detail in (36)). Final libraries were sequenced on an Illumina NovaSeq S4 platform using 150 bp paired-end reads targeting $\geq 30\times$ coverage per individual.

Reads were then trimmed of their adapters using Cutadapt (39) before being demultiplexed using Flexbar (40). PCR duplicates were removed using a custom Python script. We then concatenated the two replicates of each library and merged forward and reverse reads using PEAR v0.9.11 (maximum assembled sequence length of 270 bp (41)). Unmerged reads were trimmed to a maximum length of 130 bp and a minimum quality score of 30 using Trimmomatic (42). An *in silico* digestion was performed to filter out undigested or chimeric sequences and we only retained reads with correct sequences at both ends (using a custom Python script).

Reads were mapped to the *C. crocuta* genome (accession number GCA_008692635.1) using Bowtie2 with default parameters and the options “-no-mixed” and “-no-discordant”. Mitogenome and sex scaffolds identified with RADsex (43) were excluded using Samtools (44). SNP calling was performed using Stacks reference-based pipeline v2.61 (45,46) and loci were retained if genotyped in $\geq 60\%$ of individuals. Individuals with $>2.5\text{M}$ reads were subsampled to normalize coverage ($\sim 60\times$). In total, 1,187 spotted hyenas were genotyped at a total of 69,816 SNP markers. For all downstream analyses, we further filtered genotypes to include genotype calls that had a read depth of at least 10 and no more than 110 before filtering the SNPs to remove SNP loci that had a minor allele frequency of less than 1% or a genotype missing rate of more than 30%. We also removed sequences for six individuals that had a genotyping rate of less than 50%. The final dataset used in all downstream analyses therefore consisted of 1,181 individuals and 27,219 unlinked SNPs.

Is genetic variation structured among clans?

Genetic diversity was estimated for each clan using mean observed heterozygosity (H_o) and expected heterozygosity (H_e) across loci. H_o was calculated at each locus as the proportion of individuals that were heterozygous, while H_e was calculated as $1 - (p^2 + q^2)$ where p and q are the

frequency of allele p and q at each locus. We report unbiased expected heterozygosity (uHe) to account for sample size, which was calculated as $He \times [2 \times nInd / (2 \times nInd - 1)]$, where $nInd$ is the number of individuals with non-missing genotypes. F_{IS} was calculated for each locus as $1 - (Ho/uHe)$, and we report mean F_{IS} across loci. Standard deviations reported in Table 1 describe variation among loci in measures of genetic diversity. Differences in Ho between pairs of clans were tested by repeatedly resampling loci with replacement to generate sampling distributions of pairwise differences in Ho and assessed whether the observed difference was different from zero. We report results using the more stringent $\alpha = 0.01$ threshold to account for multiple pairwise comparisons. All heterozygosity and F_{IS} estimates were calculated using the *dartR* R package (47).

To characterise genetic substructure and differentiation, we conducted genomic principal component analysis (PCA), calculated pairwise F_{ST} between clans, and conducted isolation-by-distance analyses. Genomic PCA was used to describe patterns in genetic variation through the population, and was run in the *ADEGENET* package in R (48), retaining all of the principal components as per (49).

Genetic differentiation between clans was estimated as pairwise F_{ST} using the *StAMPP* R package (50), which quantifies the proportion of genetic variation attributable to differences in allele frequencies among populations. Individuals were assigned to their natal clan, and all individuals and clans were retained when calculating F_{ST} , including individuals born to non-Crater clans that had dispersed into a Crater clan. For each pair of clans, uncertainty in the estimated F_{ST} was assessed by bootstrapping loci with replacement, generating a distribution of F_{ST} estimates and corresponding 95% confidence intervals. Pairwise F_{ST} was considered significantly greater than zero when the bootstrap distribution exceeded zero. To identify

differences in F_{ST} between pairs of clan comparisons, we calculated the difference between their F_{ST} estimates for each bootstrap replicate and generated 99.9% confidence intervals for these differences. Pairs were considered to have significantly different F_{ST} values when the 99.9% confidence interval for the difference did not include zero, using the stricter threshold to account for multiple comparisons.

Isolation-by-distance among individuals was assessed using a Mantel test in the *vegan* R package (51), testing the correlation between geographic distance and Nei's genetic distance (52). Significance was assessed using 1,000 permutations. Nei's genetic distance between individuals was calculated using the *StAMPP* R package (50). Geographic distance between individuals was estimated as the distance in metres between the centroids of individuals' home ranges, which were calculated as 95% minimum convex polygons (MCPs) using GPS coordinates collected at individuals' sightings (53). Centroids of MCPs were calculated using geometric unary operations via the *sf* R package (53,54). Individuals with less than five sightings were removed to ensure precision in estimation of home ranges.

Isolation-by-distance among clans was assessed using a Mantel test comparing pairwise genetic differentiation, expressed as $F_{ST}/(1 - F_{ST})$, with the logarithm of geographic distance between clan centroids. Geographic distance between clans was estimated as the distance in metres between the centroid of clans' territories (Figure 1). Clans and territories have remained very stable across time: the territory boundaries have remained largely the same across time and there have been no instances of clan replacement or formation during the study period (Figure 1 (55,56)). Clan territories were estimated as utilisation distributions (UD) via the kernel density methods in the *adehabitatHR* R package (57) using sightings of resident individuals of each clan. UDs for each clan were estimated with a smoothing parameter of 440 metres, which was

identified as the maximum value used when optimised per clan and when assuming a bivariate normal distribution of geographic coordinates. We decided to use a single smoothing parameter for all clans, rather than different parameters for each clan via the *href* option to standardise the estimation of clan territories across the population. Centroids per clan territory and geographic distance between all centroids were then identified as described above for individuals. While distance between territory centroids is a simplified estimate of spatial separation, our aim was to assess the effect of broad spatial proximity among clans rather than model dispersal pathways explicitly. We therefore considered centroid distance an appropriate first-order measure of geographic separation (34). Although alternative measures could incorporate landscape features, we do not consider water bodies or other geographical features within the Crater to constitute substantial barriers to hyena movement, as hyenas readily cross water and these areas are greatly reduced during the dry season. Significance was assessed using 1,000 permutations.

Are patterns of dispersal associated with observed genetic structure?

Dispersal rates between pairs of clans were estimated as the proportion of males that dispersed from one clan to another clan, relative to the total number of dispersing males from the first clan. This generated an asymmetric matrix that estimated the probability of dispersal between clans and where the diagonal element of the matrix describes the proportion of adult males that are philopatric and reproduce in their natal clan. We tested whether the probability of dispersal between pairs of clans was predicted by geographic proximity between clans using multiple regression quadratic assignment procedure (MRQAP) with dispersal as the response and geographic distance as the predictor. MRQAP is an extension of the mantel test (a statistical procedure commonly used to identify correlations between matrices) which allows the user to

248 estimate the effects of predictor matrices while controlling for other matrices. We ran MRQAP
249 using the *asnipe* R package (58) and we used the double semi-partialling method (DSP) to assess
250 significance, which permutes ($N = 1,000$ randomisations) the matrix of residuals from the
251 ordinary least regression of the dependent matrix on the independent matrices to estimate error
252 and calculate the effects.

253 To test whether pairwise F_{ST} between clans was greater than expected under random
254 dispersal among clans, we ran a null model to generate pairwise F_{ST} between clans that would
255 be expected if males dispersed at random. This model randomly permuted adult clan
256 membership between males, thereby randomly distributing them through the population and
257 simulating random dispersal. This permutation model was run a total of 1,000 times, calculating
258 pairwise F_{ST} between clans in each permutation to generate an expected range of pairwise F_{ST}
259 under random male dispersal. We then identified whether observed pairwise F_{ST} between clans
260 were greater than expected if the confidence intervals of observed F_{ST} (estimated from the
261 bootstraps explained above) did not overlap with the 95th percentile of the distribution of the F_{ST}
262 generated in the null model. This model was run in R using custom scripts and the *StAMPP* R
263 package to calculate F_{ST} for each iteration of the permutation model.

264 Next, to test if the probability of dispersal between clans predicted pairwise F_{ST} , we ran a
265 multiple regression quadratic assignment procedure (MRQAP) with F_{ST} as the response matrix
266 and dispersal as the predictor matrix. We further included geographic distance as an additional
267 predictor matrix to control for any effect of geographic distance on F_{ST} . We calculated confidence
268 intervals of effect sizes for each MRQAP by propagating the bootstrapped estimates of F_{ST}
269 through and re-running the MRQAP for each bootstrap permutation. However, we used the
270 double semi-partialling method (DSP) described above to assess significance using the mean
271 estimate of F_{ST} as this method has been found to be robust against statistical violations of

autocorrelation, confounder effect sizes and skewness in the data (59). This method permutes (N = 1,000 randomisations) the matrix of residuals from the ordinary least regression of the dependent matrix on the independent matrices to estimate error and calculate the effects. These analyses were conducted using the 8 Crater clans. Non-Crater clans were excluded because their estimated rate of dispersal and home range are likely to be inaccurate due to lower monitoring effort.

Analyses of clan ancestry–fitness relationships and among-clan variation in additive genetic variance in fitness

Data selection

We used two measures associated with realised lifetime fitness: lifetime reproductive success (LRS), defined as the total number of offspring produced by an individual, and lifespan, defined as age at death in years. LRS was calculated using the pedigree described above, and lifespan was estimated from birth and death dates as described above. We analysed both measures because they capture overlapping aspects of life-history and lifetime fitness (60,61). Specifically, LRS includes both survival and reproductive output, whereas lifespan captures survival but does not quantify reproductive success (62). Although LRS and lifespan were strongly positively correlated ($r = 0.78$), analysing both allowed us to assess whether our inferences were consistent across measures of fitness. In addition, LRS can be a challenging variable to model with appropriate statistical distribution (7), and Lifespan therefore provides a complementary and comparatively straightforward measure to model.

To ensure that we had observations across the complete lifespans of individuals, we included individuals who were born after 1996 (the beginning of the study period) and had died

by February 2025. To ensure measures of fitness were accurate for each cohort in the dataset, we removed individuals born after 2015 because 90% of individual hyenas die before 10 years of age (last observation date in analyses = February 2025). Most individuals were of known sex; however, sex was unknown for 204 individuals, normally because they died before reaching an age where sex could be determined. Rather than remove these individuals, we randomly assigned a sex to them as removing them would have systematically biased our distribution of fitness estimates as they were mostly juveniles. Retaining them also allowed us to maximise the statistical power in the models described below. The estimated effect of sex on relative LRS or lifespan from models that randomly assigned 204 individuals a sex (as described) was very similar to models that were fitted to a dataset without these 204 individuals (LRS: without N = 204 individuals $\beta_{\text{SEX}}^{\text{MALE}} = -0.814$ (-1.134 - -0.547), random assignment of sex $\beta_{\text{SEX}}^{\text{MALE}} = -0.814$ (-1.114 - -0.519); Lifespan: without N = 204 individuals $\beta_{\text{SEX}}^{\text{MALE}} = -0.228$ (-0.372 - -0.068), random assignment of sex $\beta_{\text{SEX}}^{\text{MALE}} = -0.248$ (-0.406 - -0.104)). As such, we determined that the random assignment of sex did not have a significant impact on the estimated effect of sex, but removing them would have both selectively removed individuals with low fitness and appreciably reduced our statistical power. Analyses described below therefore included N = 1,635 Crater-born individuals for which mothers and social ranks at birth were known together with the population pedigree of 3,239 individuals of known natal clans.

Statistical models

To test whether ancestry from social groups was associated with (a) differences in fitness and (b) differences in additive genetic variance in fitness (V_A), we used genetic group animal models (17,63–65). Animal models are linear mixed-effects models that incorporate relatedness information as a covariance matrix to estimate additive genetic variance, i.e., the variance of

additive genetic values for a response variable (66,67). Genetic group animal models further allow the distribution of the genetic values to differ according to genetic substructures (so-called “genetic groups”) in the population. In our case, each genetic group corresponded to one of the clans, in addition to a group lumping together non-Crater (immigrant) individuals. Pedigree-based genetic group animal models assume that founder individuals are unrelated both within and among genetic groups (17,68). We acknowledge that this assumption is unlikely to be fully met in our study system because clans are connected by low levels of dispersal and are therefore not completely reproductively isolated. As is typical of genetic group models applied to natural populations, the fitted groups should therefore be interpreted as pedigree-defined ancestry partitions rather than completely isolated demes (64,69). Moreover, any resulting shared ancestry among founder groups would be expected to reduce, rather than inflate, genetic differences among groups, making inference of group-specific effects conservative.

LRS and lifespan were analysed relative to the global population mean fitness (i.e., individual fitness divided by the overall mean fitness across the dataset) using a Gaussian distribution. This scaling placed fitness measures on a comparable scale and improved fitting of these relatively complex models while retaining variation in fitness across cohorts and sexes. We did not standardize fitness separately within cohort or sex because these effects were modelled directly through fixed and random effects in the animal models (see below). Correlations between mean fitness and additive genetic variance among clans were low for both fitness measures ($r^2(V_A^{LRS} \text{ and mean LRS}) = -0.42$, $r^2(V_A^{Lifespan} \text{ and mean lifespan}) = 0.27$) (see also results), suggesting that mean–variance relationships after relativisation were weak.

For each response variable, we fitted two models. The first estimated a single V_A for the whole population and tested for the effect of ancestry on fitness, and the second estimated clan-

specific estimates of V_A . Fixed effects included individual inbreeding coefficient (F , estimated from the pedigree), sex, clan size at birth, social rank at birth and the proportion of genetic ancestry from each clan (17,65)). Ancestry proportions were calculated using the full pedigree using the *nadiv* R package (70) following methodology and code provided in (17,64). Random effects included maternal identity, cohort (i.e., year of birth), birth clan and adult clan. Cohort effects were fit to account for temporal variation in environments. Birth clan was included to account for effects of the developmental environment on both juvenile and adult fitness in hyenas (28,71). Adult clan was included to account for environmental conditions experienced after dispersal or during adulthood. The models that estimated homogeneous variances were therefore:

$$w_i = \mu + \beta_1 F_i + \beta_2 \text{sex}_i + \beta_3 \text{socialrank}_i + \beta_4 \text{clansize}_i + \beta_5 (\text{sex}_i \times \text{socialrank}_i) + \beta_6 qA_i + \beta_7 qE_i + \beta_8 qF_i + \beta_9 qL_i + \beta_{10} qM_i + \beta_{11} qN_i + \beta_{12} qT_i + \beta_{13} qS_i + m_j + cb_l + cd_k + y_z + a_i + \varepsilon_i$$

(Equation 1)

where w_i is the estimate of fitness (w) for individual i , μ is the population mean, $\beta_{1,...,13}$ are the fixed effects explained above, where q denotes the expected ancestry proportion for individual i from each Crater clan (A = Airstrip, F = Forest, T = Triangle, E = Engitati, L = Lemala, S = Shamba, M = Munge, N = Ngoitokitok), m is the maternal effect for mother j , cb is the clan of birth effect for clan l , cd is the adult clan effect for clan k , y is the cohort effect for cohort z , a is the genetic breeding value (i.e., the effect of individual i 's genome relative to μ), where breeding values are distributed as $(a_1, ..., a_n) \sim N(0, V_A A)$ with additive genetic variance V_A and genetic relatedness matrix A (estimated via the population pedigree), and ε is the residual term.

Because ancestry proportions sum to one, one genetic group must be used as the reference level, analogous to fitting a categorical fixed effect (64,65). We used non-Crater

ancestry as the reference group. Although the analysed dataset did not include individuals born outside the Crater, some individuals possessed ancestry from outside the Crater and ancestry proportions were therefore estimated using the full pedigree. To ensure that ancestry effects were not confounded with inbreeding, we tested for collinearity between inbreeding coefficient and non-Crater ancestry. These variables were only weakly correlated ($r^2 = 0.11$). In standard animal models, breeding values (a_i) describe deviations from the mean of a single genetically homogeneous population and therefore have a mean of zero. The genetic group model in Equation 1 relaxes this assumption by allowing clans to differ in mean breeding value. Accordingly, coefficients $\beta_6 - \beta_{13}$ represent the deviation of each groups mean breeding value from the reference groups mean breeding value, while additive genetic variance remains homogeneous across clans.

To allow the additive genetic variances to differ among clans, we fitted a second model that partitioned individuals' genetic breeding values (a_i) into clan specific contributions. Following methods explained in (64), we estimated partial genetic breeding values (a_{ij}) for each group (clan), where a_{ij} represents the contribution to the breeding value of individual i from group j . These partial genetic breeding values are estimated for all groups ($j=1,...,r$) and are distributed as $(a_{1j},...,a_{nj}) \sim N(0, V_{A_j} A_j)$, where V_{A_j} is the additive genetic variance in group j and A_j is a group-specific relatedness matrix. Clan-specific relatedness matrices were specified following (64) such that relatedness between individuals was scaled according to ancestry proportions to estimate pairwise relatedness at genetic variants inherited from specific clans. Although methods exist to construct these matrices using genomic estimates of realised ancestry (63), we used a pedigree-based approach following (64) to maximise sample size (the full pedigree contains 3,239 individuals, whereas the genomic dataset contains 1,181 individuals).

To account for environmental differences that could generate among-clan differences in phenotypic variance, we additionally fitted heterogeneous residual variances among natal clans in the heterogeneous V_A models. Heterogeneous residual variances were not fitted in the homogeneous V_A models because our objective was to compare estimates obtained under homogeneous versus heterogeneous variance structures, including non-genetic sources of variance heterogeneity.

To assess statistical support for among-clan differences in V_A , we did not rely on standard model-selection criteria such as DIC because these can be unreliable, especially for highly structured mixed effects models (72). Instead, following (64,73), we calculated posterior distributions of pairwise differences in (V_A) among clans by subtracting posterior samples of clan-specific estimates. We considered there to be statistical support for a difference when the 95% credible interval of the posterior difference distribution (defined by the 5% and 95% quantiles) did not include zero, indicating that more than 95% of the posterior probability supported a non-zero difference between clans.

All models described above were fitted in a Bayesian framework using *MCMCglmm* package in R (74). We used the default weakly informative parameter expanded priors set to $F_{1,1}$ distribution setting the scale to 1,000 for random effects, the default Inverse-Wishart prior for residual variance and non-informative priors for fixed effects. We re-ran models with a larger scale on the prior for the random effect variance (set instead at 10,000) to check our priors did not strongly affect the parameter estimates. Variance estimates did not vary between models run with different priors (See Table S2). Models were run for 60,000 iterations, with a 10,000 burn-in period and a thinning interval of 10. This was sufficient in all cases to achieve effective sample sizes of at least 1,000 for all parameters and low autocorrelation. Model convergence was assessed using effective sample sizes and visual inspection of trace plots.

410 **Results**

411 *Is genetic variation structured among clans?*

412 Mean observed heterozygosity within clans ranged from 0.259 to 0.264 (Table 1). Mean unbiased
413 expected heterozygosity within clans ranged from 0.250 to 0.266. Although heterozygosity
414 differed significantly between most pairs of clans, the magnitude of these differences was very
415 small (a difference of approximately 0.001). Lemala and Munge clans did not differ significantly
416 in observed heterozygosity, nor did Engitati, Ngoitokitok and Triangle clans. Mean F_{IS} values
417 ranged from -0.040 to 0.017 across clans (Table 1). Negative F_{IS} values indicate that observed
418 heterozygosity exceeded unbiased expected heterozygosity, whereas positive values indicate
419 lower observed than expected heterozygosity. Although some clans showed evidence of a
420 departure from zero, the magnitude of the deviation of F_{IS} estimates from zero was small (Table
421 1). We did not detect any differences among clans in F_{IS} .

422 Genomic PCA revealed that genetic variation was distributed continuously through the
423 population. The first two axes (PC1 and PC2) of the PCA each explained a relatively low
424 proportion (2%) of the genetic variation in the population, and individuals generally sat
425 continuously across both of these axes. However, individuals that were born into the same clan
426 clustered together across PC1 and PC2 (Figure 2A). This suggests that individuals born into the
427 same clan were more genetically similar to each other than to individuals from other clans.
428 Individuals born into the same clan also clustered together across a continuum of genetic
429 variation in the third and fourth PCA axes (Figure S1), further suggesting that individuals that were
430 from the same clan were more similar to each other than to individuals from other clans.

Pairwise F_{ST} between clans varied between 0.013 and 0.043 and were all significantly different from 0.001 (Figure 2B). Most F_{ST} estimates were also significantly different from each other, but two pairs of F_{ST} values (Airstrip - Munge / Engitati - Lemala, and Munge - Forest / Lemala - Shamba) were not significantly different from each other.

We found evidence for isolation-by-distance among individuals born into the Crater, whereby individuals that lived further apart from each other were less genetically similar than those living closer (Mantel $r = 0.230$, $p = 0.001$, Figure 2C). However, we did not find evidence for isolation-by-distance among clans (Mantel $r = 0.167$, $p = 0.211$, Figure 2D)

Are patterns of dispersal associated with observed genetic structure?

Median dispersal among clans was 10% (standard deviation of dispersal between clans = 10%, 95% quantiles = 2 – 27%) (Figure 3A). Dispersal rates were often asymmetric in that the exchange of males between clans via dispersal was rarely reciprocal (Figure 3A). Geographic distance partly explained the probability of male dispersal, but the relationship was quite weak, with dispersal probability decreasing by approximately 0.02 for every 1 km increase in distance between clans (MRQAP: $\beta = -1.98 \times 10^{-5}$, $p = 0.006$, Figure S4), suggesting that other factors contributed to heterogeneous rates of male dispersal between clans.

There were multiple lines of evidence to suggest that genetic differentiation between clans was linked to rates of male dispersal between clans. First, for all pairs of clans, observed F_{ST} was larger than that expected under a null model that simulated random male dispersal (Figure 3B). Second, dispersal rates between clans were negatively correlated with pairwise F_{ST} between clans (MRQAP: mean β [95% bootstrapped CI's] = -0.036 [-0.037; -0.035], $p = 0.017$, Figure 3B). This remained true after controlling for the effect of geographic distance, which did not have an effect on F_{ST} in isolation-by-distance analyses (see above) or when fitted in a model

together with dispersal rates (MRQAP: mean β [95% bootstrapped CI's] = -2.15×10^{-7} [-2.22×10^{-7} ; -2.13×10^{-7}], $p = 0.750$, Figure 2D). Finally, we found that when males were assigned to their adult clans (i.e., the clan that they disperse into), F_{ST} between clans were lower than when assigned to their natal clan, although they were still all significantly different from 0.001 (Figure S2).

Does clan ancestry predict individual fitness?

Among the 1,635 individuals included in analyses, the number with non-zero genetic ancestry from each clan ranged from 105 (Shamba) to 1,318 (non-Crater). Counts were calculated independently for each clan and are therefore not mutually exclusive, as individuals have ancestry from multiple clans. The counts represent the number of analysed individuals with at least some genetic ancestry from each clan: Lemala (722), Munge (877), Shamba (105), Triangle (117), Ngoitokitok (346), Engitati (413), Forest (256), Airstrip (840), and non-Crater (1,318).

Individuals with a greater proportion of immigrant genetic ancestry had higher LRS and longer lifespans (Table 2, Figure 4). This pattern was reflected in negative regression coefficients for the proportion of genetic ancestry from Crater clans (Table 2), indicating lower expected fitness relative to individuals with greater immigrant ancestry, which served as the reference category (see Methods). Thus, higher Crater ancestry was associated with lower fitness relative to higher immigrant ancestry. Beyond this contrast, the relative contributions of individual Crater clans did not significantly affect LRS or lifespan (Table 2).

Does additive genetic variance in fitness vary among clans?

At a population level, we found substantial V_A in both lifetime reproductive success (LRS) and lifespan, with posterior distributions clearly distinct from zero (Table 2, Figure 4). These

estimates were broadly consistent with previous estimates from this population (7), although our estimates had narrower credible intervals. Clan-specific estimates of V_A were associated with greater uncertainty due to reduced sample sizes within clans (Table 3, Figure 5). Nevertheless, some pairwise comparisons provided evidence of heterogeneity in V_A among clans, defined as comparisons for which the posterior distribution of the difference excluded zero. For LRS, six of 36 pairwise comparisons met this criterion (Figure S6), with Lemala showing lower V_A than Ngoitokitok, Forest, Airstrip, and non-Crater, and Ngoitokitok showing higher V_A than Triangle and Munge (Figure 5A). For lifespan, 11 of 36 comparisons met this criterion (Figure S7). Lemala had the lowest estimated V_A , with lower values than Forest, Triangle, Ngoitokitok, Airstrip, and Shamba. Non-Crater and Munge also had lower V_A than Ngoitokitok, Triangle, and Forest (Figure 5B).

Prior-posterior comparisons indicated that estimates of V_A for LRS were weakly informed by the data for Lemala, with limited prior-to-posterior contraction, and to a lesser extent for Munge, Engitati, and Triangle (Figure S8). In contrast, estimates for other clans for LRS and for all clans for lifespan showed substantial contraction, indicating greater information from the data. Re-fitting models with a substantially broader prior on random-effect variances (scale = 10,000) yielded highly similar estimates of V_A (Table S2), suggesting limited sensitivity to prior specification. Despite weak support for the Lemala V_A (LRS), lifespan estimates were consistently well supported across clans and prior specifications. Relative differences among clans were also broadly consistent between fitness measures, including lower V_A in Lemala, and estimates showed no apparent relationship with clan sample size for either trait. Overall, these results suggest that among-clan differences in V_A are reasonably robust to prior specification, although the Lemala LRS estimate remains comparatively uncertain.

Residual variance (which reflects the remaining phenotypic variance not explained by parameters in the model) for LRS varied substantially between clans. The Lemala clan, which had the lowest V_A , had the lowest residual variance in LRS, whereas Engitati and Airstrip clans had the largest residual variance in LRS (Table 3, Figure S5). Residual variance for lifespan did not differ much between clans, although it was marginally smaller for Engitati clan and marginally larger for Lemala clan (Table 3, Figure S5).

Fixed effect estimates suggest that males had lower mean LRS than females (Table 2), reflecting the slightly lower rate of paternities assigned in the pedigree than maternities in the selected dataset. Individuals born into a higher social rank had higher fitness, both living longer and having more offspring overall (Table 2), which is a well-established phenomenon in spotted hyenas (27,29,75). We did not find that the effect of social rank was different between the sexes (Table 2). We also found a negative relationship between the inbreeding coefficient, F , and both fitness measures, corroborating evidence for inbreeding depression found in previous work (76) (Table 2). There was evidence for a negative relationship with natal clan size for both fitness measures (Table 2), providing evidence for an effect of density in early life on fitness (77). The fixed effect estimates were similar in models that fit either homogeneous or heterogeneous variances, and results of the latter can be found in Table S1. Variance estimates for all other random effects (i.e., not V_A) were fairly small (Table 3). There was very low variance in fitness associated with natal clan (Table 3), suggesting very little difference in the phenotypic means in fitness between clans.

Discussion

Social structures in wild animals emerge from interactions between ecological and evolutionary processes (78), but may also impact gene flow, genetic drift, and the distribution of genetic

variation within populations (2,3,5,15). Using nearly 30 years of behavioural, life-history, and fitness data alongside a new genome-wide SNP dataset, we examined associations between social structure, fine-scale genetic structure, and quantitative genetic variation in a wild population of spotted hyenas. We found modest genetic differentiation among clans associated with heterogeneous dispersal patterns, and greater immigrant ancestry was associated with increased fitness. Additive genetic variance in fitness also showed some evidence of heterogeneity among clans, although differences were concentrated in specific pairwise comparisons rather than reflecting a consistent pattern across groups.

While theory and empirical studies show that social structure can shape population genetic structure across species (5,11,19,79), testing the underlying mechanisms remains challenging because dispersal is difficult to quantify. In our study, genetic variation was distributed continuously across the population, yet social groups within the 250 km² Ngorongoro Crater exhibited modest but statistically significant genetic differentiation. Dispersal between clans was negatively associated with genetic differentiation, consistent with dispersal facilitating gene flow. This genetic structure may reflect the kinship structure of hyena social groups (25,80) and reproductive skew in both sexes (27,28,30,81), which can increase genetic similarity among clan members. The tendency for male relatives to disperse to the same clan (14) may further limit genetic mixing and contribute to genetic differentiation among clans (82). Interestingly, geographic distance weakly predicted dispersal rates, suggesting that local variation in clan density, sex ratio, and kin structure may play a greater role in shaping dispersal dynamics (14,29).

Dispersal can influence the distribution of additive genetic variance in fitness by introducing genetic variation into recipient groups (69). However, we found no association

between Crater clan ancestry and breeding values for fitness, consistent with evidence that dispersal between Crater clans confers no fitness advantage over philopatry (29). In contrast, ancestry from immigrants originating outside the Crater, some from as far as 150 km away (83), was associated with higher fitness, as reported in other animal populations (84). This is reflected in breeding and ancestry patterns: only 9% of breeding males immigrated from outside the Crater, yet approximately 80% of individuals carried some outside-Crater ancestry, compared with an average of 44% with ancestry from Crater clans. In group-living species such as hyenas, where mating is often biased towards members of the same social group (85), immigration may reduce inbreeding by introducing genetic variation into kin-biased groups (86,87). Although the positive association between immigrant ancestry and fitness is consistent with this hypothesis, our data cannot distinguish reduced inbreeding from preferential mating with immigrants. The association also provides evidence against selection against immigration, which would predict lower fitness with increasing immigrant ancestry (88). Together, these findings suggest that immigration from outside the Crater contributes to genetic variation associated with fitness in the population (69).

Most wild populations are subdivided to some extent, resulting in population genetic structure and heterogeneous gene flow (15). Because mating opportunities and ecological selection pressures can vary among locations, this structure may influence the distribution of genetic variation for fitness within populations (5,18,89–91). We found statistical support for differences in V_A for fitness in six of 36 pairwise comparisons for LRS and 11 of 36 for lifespan. These differences were concentrated in comparisons involving Lemala clan rather than being widespread across clans. Thus, genetic variation in fitness appears heterogeneous among some groups within a genetically connected population, but does not indicate widespread

differentiation across clans. Substantial uncertainty around clan-specific estimates also means that some underlying differences may remain unresolved.

Heterogeneity in V_A may affect the capacity of social groups to respond to selection (6,92). Even in populations connected by gene flow, selection pressures may vary among groups, with gene flow either facilitating or constraining local adaptation depending on the balance between migration and selection (16,93–97). These principles, well established in studies of local adaptation and adaptive divergence (16,98), may also apply to socially structured populations, where groups may function as partially differentiated demes within a connected population (3,98). Critically, our analyses do not establish differences in realised evolutionary change among clans or imply that clans are independently evolving. Rather, they suggest that genetic variance underlying fitness may vary among social groups, potentially creating heterogeneity in their capacity to respond to selection.

The repeated observation of the Lemala clan having lower V_A than several other clans provides an illustrative example of how socio-demography may be associated with V_A . Lemala has the lowest additive genetic variance in fitness, the lowest male-to-female sex ratio, the highest proportion of philopatric males, and the most stable social hierarchy. It also exhibits some of the strongest female reproductive skew, with a few individuals contributing disproportionately to the next generation (30). These characteristics could reduce genetic variance for fitness by limiting mate pools and increasing relatedness, although our analyses cannot establish whether they explain observed differences in V_A .

Our analyses were not designed to identify the causal mechanisms underlying any differences in additive genetic variation. Social structure itself emerges from ecological and

evolutionary processes, and environmental heterogeneity, reproductive skew, historical demography, social behaviour, and finer-scale social processes could all contribute jointly to the observed patterns. Indirect genetic effects (IGEs), whereby the genotypes of social partners influence an individual's phenotype and fitness, provide one mechanism through which social interactions could alter both the expression and evolutionary consequences of genetic variation in socially structured populations (99,100). In particular, IGEs could contribute to variation in fitness within and among clans as a result of repeated interactions within relatively stable social environments. However, distinguishing among these mechanisms while simultaneously estimating clan-specific additive genetic variances would require statistical power beyond what our data can currently support. Nevertheless, the inclusion of natal-clan and adult-clan random effects, together with clan-specific residual variances, may account for broad-scale differences in shared environmental and social conditions among clans. More broadly, the combination of higher fitness associated with immigrant ancestry and heterogeneity in additive genetic variance among certain clans raises questions about how gene flow interacts with local demographic, social, and selective processes in socially structured populations. Addressing these questions will require future work that explicitly links dispersal decisions, social interactions, selection, and realised evolutionary change through time.

Our study integrates behavioural, genomic, pedigree, and fitness data to provide a rare empirical examination of the relationship between social organisation, dispersal, genetic structure, and quantitative genetic variation in a wild population. We cannot yet quantify how population structure or clan-level variation in genetic variance for fitness correspond to realised evolutionary change, which fitness-related traits are under selection, or whether these processes operate consistently across clans. Nonetheless, our findings suggest that social organisation,

dispersal, genetic structure, and quantitative genetic variation can covary at fine spatial scales within a connected population. Together, these findings suggest that socially structured populations can exhibit fine-scale heterogeneity not only in genetic ancestry and connectivity, but also in the distribution of genetic variation for fitness. This highlights the value of integrating social structure into studies of dispersal, population genetic structure, and quantitative genetic variation in wild populations.

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637 **Author contributions:**

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639 Investigation: KS, OPH, LSA, ED; Formal analysis: KS, LSA; Methodology: KS, LSA, JLP, KA;
640 Software: KS, LSA; Validation: KS, OPH, ED, JLP, KA; Visualisation: KS; Supervision: LEBK; Project
641 administration: KS, LEBK; Funding acquisition: LEBK, OPH; Writing – original draft: KS; Writing –
642 review and editing: all

643 **Competing interest statement**

644 The authors have declared that no competing interests exist.

645 **Data and code availability**

646 The raw sequencing data are deposited in the Genbank with the NCBI BioProject accession no.
647 PRJNA951614. Code used for bioinformatic analyses of genetic data can be found at:
648 [https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-](https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-/blob/main/scripts/filterPCRDups/filterPCRDups_CM.py)
649 [/blob/main/scripts/filterPCRDups/filterPCRDups_CM.py](https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-/blob/main/scripts/digestion/checkRestrictionSites.py) and
650 [https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-](https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-/blob/main/scripts/digestion/checkRestrictionSites.py)
651 [/blob/main/scripts/digestion/checkRestrictionSites.py](https://github.com/kashastrickland/HyenaGroups)). R code and data needed to reproduce
652 analyses and results, including all tables and figures, can be found at
653 <https://github.com/kashastrickland/HyenaGroups>. This includes shape files which were used to
654 create the map in Figure 1, which were created manually.

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Figures

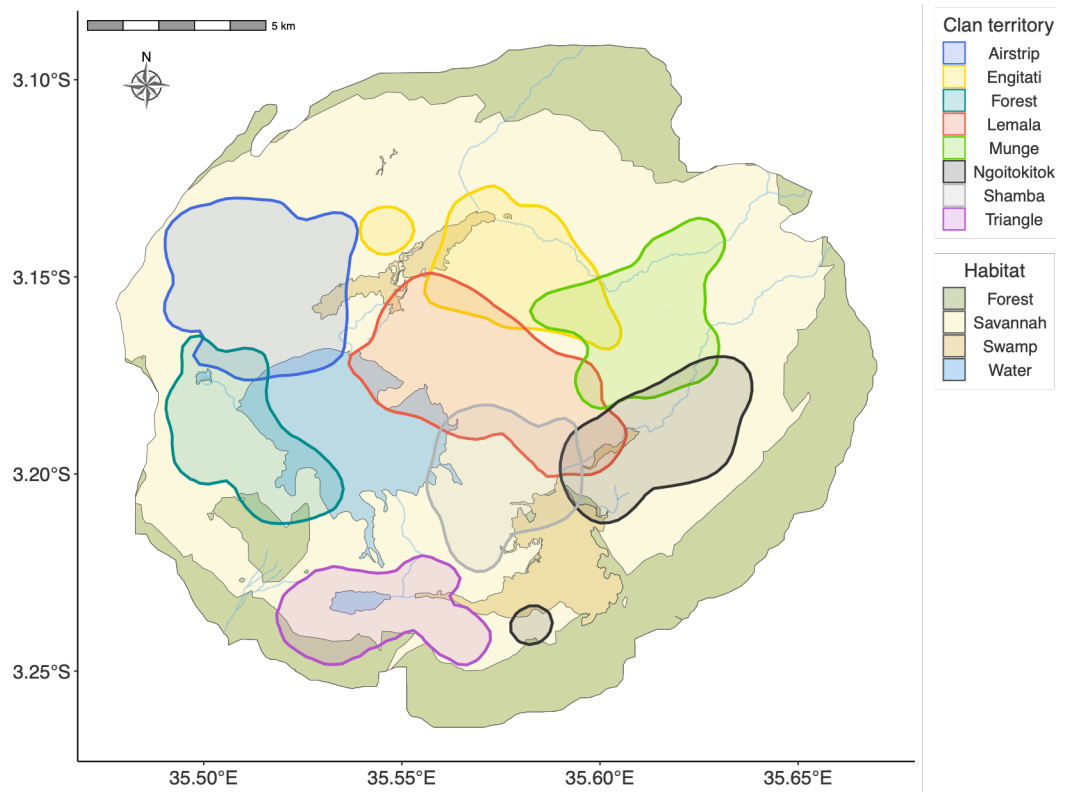


Figure 1. Map of the Ngorongoro Crater and each spotted hyena clan's territory together with broad habitat classifications.

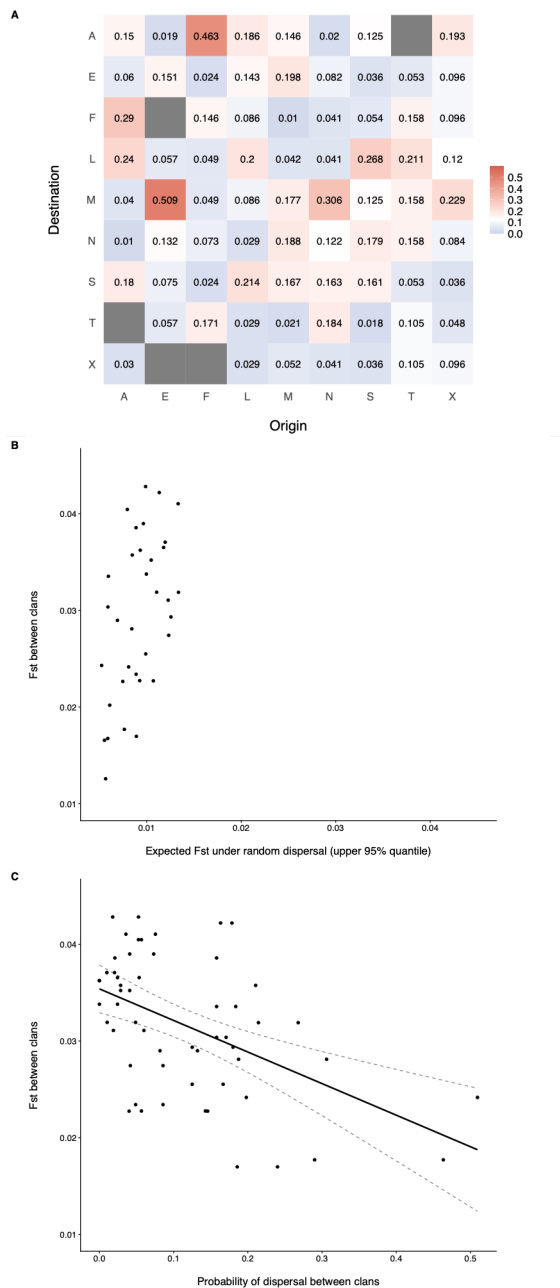


Figure 3. Relationship between genetic differentiation and male dispersal among spotted hyena clans in Ngorongoro Crater, Tanzania. (A) Heatmap showing the probability of male dispersal between clans. Diagonal elements represent the proportion of males remaining philopatric, and grey tiles indicate no dispersal. (B) Observed pairwise F_{ST} between clans plotted against expected pairwise F_{ST} under random male dispersal. The upper bound of the expected F_{ST} distribution indicates the threshold below which observed differentiation could have arisen by chance. (C) Relationship between the probability of male dispersal between clans and genetic differentiation F_{ST} . The solid line represents the mean predicted relationship, with standard errors shown as dashed lines. Diagonal elements were excluded from all matrices before analysis to focus on patterns of dispersal and genetic differentiation *between*, rather than *within*, clans.

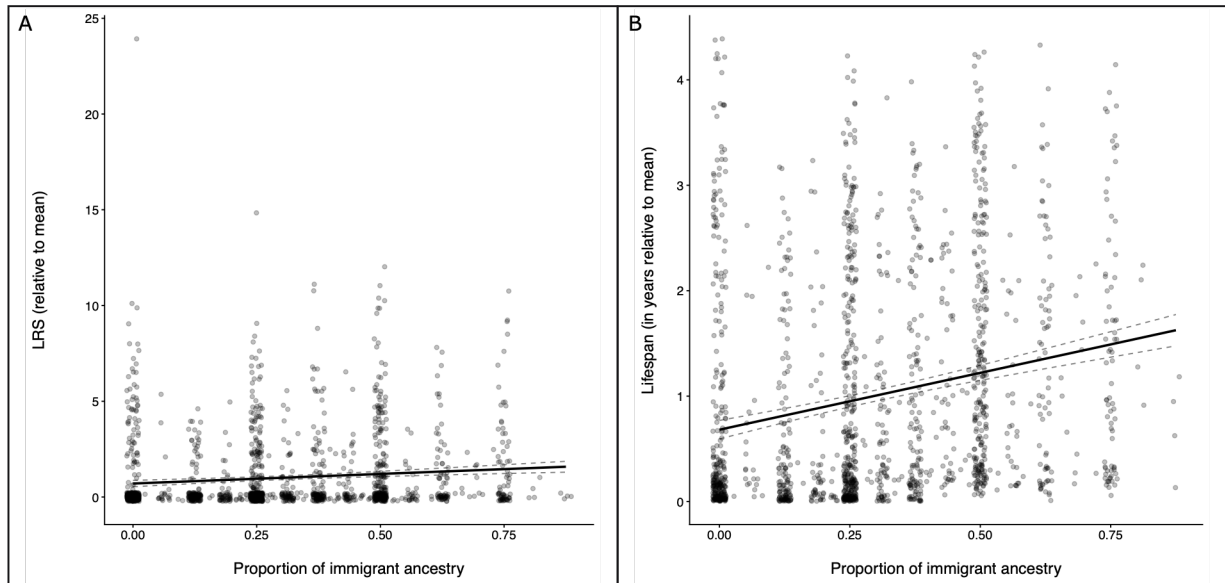


Figure 4. The relationship between immigrant ancestry and fitness, measured as lifetime reproductive success (LRS, A) and lifespan (B). Both fitness measures are plotted relative to the population mean (mean LRS = 1.74, mean lifespan = 4.15). Points have been jittered across the x axis, the solid black line demonstrates the predicted effect of immigrant ancestry and dotted lines demonstrate the 95% confidence intervals on that prediction.

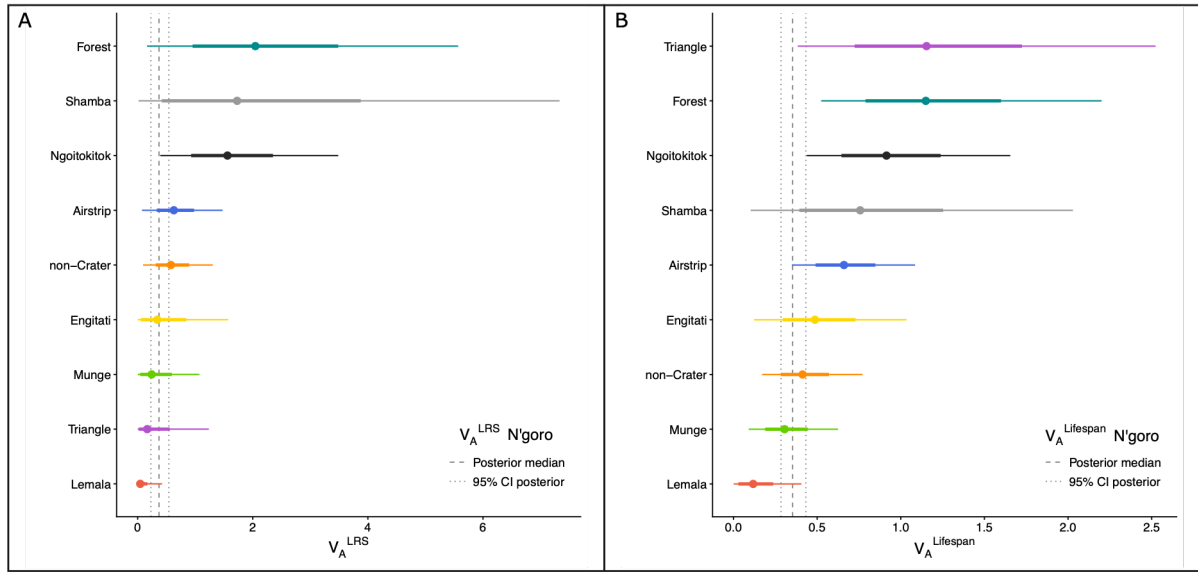


Figure 5. Estimates of additive genetic variance (V_A) for two lifetime reproductive success (LRS) and lifespan in each spotted hyena clan in Ngorongoro Crater, Tanzania. Fitness was modelled relative to the global population mean. Points indicate the median of the posterior distribution for each clan; thick bars show the 75% credible intervals, and thin lines show the 95% credible intervals. Vertical lines indicate the population-level V_A estimate from a model that did not estimate V_A separately for each clan. Clan estimates are ordered from highest to lowest median V_A , with a unique colour assigned to each clan. Dashed lines indicate the median of the posterior distribution of the population-level estimate, and dotted lines indicate its 95% credible intervals.

Tables.

Table 1. Genetic diversity within each clan of spotted hyenas in Ngorongoro Crater, Tanzania.

Clan	Mean observed heterozygosity	Mean expected heterozygosity	F _{IS}
Airstrip	0.262 (0.172)	0.256	-0.016 (-0.051; -0.023)
Engitati	0.259 (0.181)	0.251	-0.022 (-0.022; 0.014)
Forest	0.262 (0.18)	0.254	-0.024 (-0.065; -0.022)
Lemala	0.261 (0.176)	0.254	-0.02 (-0.045; -0.078)
Munge	0.26 (0.176)	0.254	-0.012 (-0.028; 0.008)
Ngoitokitok	0.26 (0.184)	0.25	-0.026 (-0.044; -0.003)
Shamba	0.261 (0.182)	0.251	-0.027 (-0.027; 0.008)
Triangle	0.264 (0.192)	0.251	-0.04 (-0.147; -0.077)
non-Crater	0.262 (0.168)	0.266	0.017 (-0.062; 0.022)

Mean observed heterozygosity estimated as the average heterozygosity of loci in the clan, with standard deviation of that mean in parentheses. Expected heterozygosity of loci estimated as $H_e = 2 * N_{ID} / (2 * N_{ID} - 1)$, where N_{ID} is the number of individuals in that clan. We present the mean expected Heterozygosity across loci within each clan. F_{IS} is the inbreeding coefficient and is estimated as $1 - (Heterozygosity / Expected heterozygosity)$, and we present the 95% quantiles of F_{IS} estimated at each locus in parentheses. All estimates calculated in the *dartR* R package (47).

Table 2. Parameter estimates for fixed and random effects estimated from a genetic group animal model used to estimate additive genetic variance for two measures of fitness (lifetime reproductive success, LRS, and lifespan). Both fitness measures were modelled relative to the global population mean and were fit with Gaussian errors. All parameter estimates shown are posterior medians with 95% credible intervals shown in parentheses.

Parameter	LRS	Lifespan
Intercept	3.384 (2.432; 4.379)	2.343 (1.806; 2.869)
Sex _M	-0.807 (-1.108; -0.498)	-0.241 (-0.391; -0.094)
Social rank	-0.02 (-0.03; -0.01)	-0.004 (-0.009; 0.001)
F	-5.482 (-10.339; -0.157)	-3.031 (-5.422; -0.406)
Size of clan	-0.024 (-0.033; -0.015)	-0.01 (-0.016; -0.005)
GG ^{Airstrip}	-1.17 (-1.939; -0.378)	-1.229 (-1.705; -0.762)
GG ^{Engitati}	-1.524 (-2.496; -0.494)	-2.094 (-2.639; -1.487)
GG ^{Forest}	-1.342 (-2.560; -0.094)	-1.739 (-2.486; -1.054)
GG ^{Lemala}	-1.591 (-2.455; -0.769)	-1.731 (-2.218; -1.216)
GG ^{Munge}	-0.79 (-1.586; -0.061)	-1.263 (-1.738; -0.803)
GG ^{Ngoitokitok}	-1.232 (-2.265; -0.244)	-1.582 (-2.185; -1.001)
GG ^{Shamba}	-1.771 (-3.188; -0.535)	-2.25 (-2.964; -1.493)
GG ^{Triangle}	-1.663 (-2.863; -0.29)	-1.583 (-2.250; -0.894)
Sex _M :Social rank	0.017 (0.007; 0.028)	0.003 (-0.002; 0.008)
V _A	0.376 (0.230; 0.542)	0.355 (0.284; 0.433)
V _{Mother}	0.148 (0.041; 0.265)	0.012 (0.001; 0.037)
V _{Cohort}	0.113 (0.029; 0.254)	0.161 (0.059; 0.330)
V _{BirthClan}	0.636 (0.115; 1.789)	0.077 (0.002; 0.229)
V _{AdultClan}	0.511 (0.102; 1.365)	0.118 (0.031; 0.302)
V _R	3.138 (2.918; 3.367)	0.609 (0.548; 0.670)

Social rank describes the position in the social hierarchy, where 1 is the highest rank and descends to N = clan size. F = individuals inbreeding coefficient estimated from the pedigree. GG = genetic group, which estimates the proportion of ancestry each individual has from each clan. Immigrant ancestry was fit as the reference level, so all parameter estimates show the effect of ancestry to each clan relative to immigrant ancestry. V_A is the additive genetic effects variance, V_{Mother} is the maternal effect, V_{Cohort} is the variance associated with between birth-year effects V_{BirthClan} is the variance between clan of birth, V_{AdultClan} is variance between the clans that individuals live in as adults, and V_R is the residual variance.

Table 3. Variance estimates for random effects from genetic group animal models used to estimate additive genetic variance for two measures of fitness (lifetime reproductive success, LRS, and lifespan) in each clan of spotted hyenas in Ngorongoro Crater. Both measures of fitness were modelled relative to the global population mean, and were fit with Gaussian errors. Results shown for set of models with clan-specific V_A estimates. Estimates shown are posterior medians with 95% credible intervals shown in subscript parentheses.

Parameter	LRS	Lifespan
V_A^{Airstrip}	0.662 (0.151; 1.293)	0.674 (0.391; 1.016)
V_A^{Engitati}	0.457 (0.004; 1.342)	0.512 (0.168; 0.944)
V_A^{Forest}	2.254 (0.340; 4.766)	1.2 (0.597; 1.989)
V_A^{Lemala}	0.089 (0.001; 0.329)	0.138 (0.004; 0.353)
V_A^{Munge}	0.322 (0.003; 0.919)	0.319 (0.120; 0.556)
$V_A^{\text{Ngoitokitok}}$	1.654 (0.563; 3.068)	0.946 (0.500; 1.525)
V_A^{Shamba}	2.218 (0.055; 6.260)	0.836 (0.185; 1.779)
V_A^{Triangle}	0.292 (0.002; 1.001)	1.234 (0.469; 2.240)
$V_A^{\text{non-Crater}}$	0.609 (0.157; 1.174)	0.428 (0.202; 0.708)
V_{Mother}	0.073 (0.003; 0.164)	0.009 (0.001; 0.030)
V_{Cohort}	0.227 (0.072; 0.482)	0.181 (0.069; 0.361)
$V_{\text{BirthClan}}$	0.35 (0.021; 1.066)	0.089 (0.005; 0.258)
$V_{\text{AdultClan}}$	0.33 (0.051; 0.915)	0.173 (0.046; 0.424)
V_R^{Airstrip}	4.521 (3.814; 5.292)	0.678 (0.541; 0.827)
V_R^{Engitati}	2.24 (1.807; 2.746)	0.624 (0.473; 0.804)
V_R^{Forest}	6.309 (4.821; 8.064)	0.478 (0.331; 0.650)
V_R^{Lemala}	2.088 (1.767; 2.418)	0.586 (0.482; 0.704)
V_R^{Munge}	3.302 (2.814; 3.856)	0.527 (0.418; 0.649)
$V_R^{\text{Ngoitokitok}}$	2.657 (2.097; 3.319)	0.67 (0.496; 0.864)
V_R^{Shamba}	2.93 (2.321; 3.651)	0.615 (0.447; 0.816)
V_R^{Triangle}	1.438 (0.966; 2.031)	0.893 (0.515; 1.361)

V_A is the additive genetic effects variance, V_{Mother} is the maternal effect, V_{Cohort} is the variance associated with between birth-year effects, $V_{\text{BirthClan}}$ is the variance between clan of birth, $V_{\text{AdultClan}}$ is variance between the clans that individuals live in as adults and V_R is the residual variance.

