# Social structure shapes gene flow and genetic variance in fitness in spotted hyenas

Kasha Strickland[1*], Oliver P. Höner[2,3], Larissa S. Arantes[4,5], Joel L Pick[1], Kenneth Aase[6], Loeske E. B. Kruuk[1], Eve Davidian[3]

1. Institute for Ecology and Evolution, School of Biological Sciences, University of Edinburgh, UK
2. Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
3. Evolutionary Anthropology Team, Institute of Evolutionary Sciences of Montpellier (ISEM), University of Montpellier, CNRS, IRD, Montpellier, France
4. Department of Evolutionary Genetics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
5. Berlin Centre for Genomics in Biodiversity Research (BeGenDiv), Berlin, Germany
6. Department of Mathematical Sciences, Norwegian University of Science and Technology, Trondheim, Norway

* corresponding author: kasha.strickland@ed.ac.uk

Short title: interplay between social and genetic evolution

**Abstract**

Many animal populations are structured by stable social relationships which influence dispersal, mating, and the spatial distribution of individuals. Although theory predicts that social structure should affect microevolutionary processes such as gene flow, genetic structure, and the distribution of genetic variation underlying fitness, these links have rarely been quantified in natural populations. Using nearly 30 years of behavioural, life-history, and genomic data from a population of spotted hyenas (*Crocuta crocuta*), we examined how social structure is associated with patterns of genetic structure and additive genetic variation in fitness. Genome-wide analyses revealed fine-scale genetic structure among social groups within a spatially continuous population, associated primarily with socially mediated dispersal. Individuals with greater immigrant ancestry exhibited higher fitness, measured as lifetime reproductive success and lifespan, indicating that gene flow from outside the population is associated with variation in fitness. Finally, quantitative genetic analyses showed that additive genetic variance in fitness differed among social groups, indicating heterogeneity across social groups in the expected rate of contemporary adaptive evolution. Together, these results show that socially defined population substructure is associated with variation in genetic connectivity, fitness, and rates of adaptive evolution. Our findings highlight the importance of integrating social structure into empirical descriptions of microevolutionary processes occurring in wild populations.

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

## *Introduction*

Social behaviours have evolved across a wide range of animal species and give rise to diverse forms of social structure, from transient pairwise associations to stable family groups and multilevel cooperative societies (1,2). These social structures are defined by differentiated social relationships which contribute to the non-random distribution of individuals across space. Accordingly, theory and empirical work across behavioural ecology, social evolution, and population genetics has long recognised that social structure can influence dispersal, gene flow, and population genetic structure (3–5). However, social structure may also affect how genetic variation underlying individual fitness is distributed within populations, generating heterogeneity among social groups in additive genetic variance for fitness which, under quantitative genetic theory, determines the expected rate of adaptive evolution (6,7). Understanding these links would help connect behavioural ecology with population and quantitative genetics and clarify how social structure is associated with microevolutionary processes in the wild.

Social structure emerges from individual and group-level behaviours such as mating, grouping, and dispersal (8), and these behaviours collectively influence how genetic variation is distributed within populations. Social interactions and dispersal are highly interdependent and are jointly shaped by kinship, sex and ecological context (4,9,10). For instance, dispersal decisions are often coordinated among social partners, frequently kin, and are further influenced by mate choice (11–14). As a result, social structure and dispersal behaviour can influence the rate and direction of gene flow, generating fine-scale genetic structure even in continuous populations (3,15). Links between dispersal, social structure, and genetic differentiation have been demonstrated across diverse taxa (16–19) and theory predicts that socially structured patterns of gene flow may generate within-population heterogeneity in relatedness, ancestry and

63 fitness (8,20–22). Such heterogeneity may influence the rate of adaptive evolution, but empirical
64 tests in natural populations remain rare because they require integrated behavioural,
65 demographic, pedigree, and genomic data. Consequently, our empirical understanding remains
66 limited regarding whether socially defined population substructure corresponds to differences
67 in genetic variance in fitness and, therefore, in opportunities for contemporary adaptive evolution
68 (6).

69 We address this gap by leveraging an exceptionally rich dataset from a well-characterised
70 population of spotted hyenas (*Crocuta crocuta*) living in Tanzania's Ngorongoro Crater. Spotted
71 hyenas provide a valuable system for examining how social structure and dispersal behaviour
72 are associated with patterns of genetic structure and quantitative genetic variation under natural
73 conditions because their societies generate clear, biologically interpretable axes of social
74 structure (17,23–26). Their multilevel fission–fusion social groups (called clans), stable female-
75 dominated dominance hierarchies, low rates of extra-group mating and pronounced
76 reproductive skew create social environments in which individuals experience different
77 opportunities for mating, competition, and kin interactions (17,27–30). Moreover, male-biased
78 dispersal between clans is often coordinated among kin and based on female availability
79 (14,29,31), which may result in structured patterns of gene flow, which could impact relatedness
80 within clans and connectivity between them.

81 The Ngorongoro Crater population is one of the best-characterised wild mammal
82 systems, with nearly three decades of continuous behavioural monitoring, detailed
83 demographic records for more than 3,200 individuals, a nine-generation genetic pedigree, and
84 genome-wide SNP data from 1181 animals. Previous work in this population has estimated
85 additive genetic variance in fitness (7), providing evidence for contemporary adaptive evolution
86 and creating an opportunity to examine how social and demographic structure coincide with

87 population- and quantitative-genetic variation. The population is structured into eight resident
88 social groups whose territories vary along key ecological axes such as group size (e.g., min = 22,
89 max = 90 individuals in June 2024), habitat type, territory size, exposure to pastoralism and sex
90 ratio (Fig 1A, (32)). These differences create social subunits that may differ in the distribution of
91 genetic variation and in ecological conditions experienced by individuals.

92 We addressed four specific questions: (1) is genetic variation structured among clans?
93 (2) how are patterns of dispersal associated with observed genetic structure? (3) how does clan
94 ancestry relate to fitness, and (4) does additive genetic variance in fitness, and therefore
95 expected rates of adaptive evolution, vary among clans? By addressing these questions, we
96 evaluate whether socially defined population structure corresponds to heterogeneity in additive
97 genetic variance for fitness, and provide empirical insight into how behavioural and demographic
98 organisation may contribute to microevolutionary processes in natural populations.

99 ***Results***

100 *Is genetic variation structured among clans?*

101 Using a panel of genome-wide SNPs (N = 27,219) sequenced for 1,181 individuals, we first ran a
102 suite of analyses to characterise the genetic structure of the population, including estimating the
103 extent of genetic differentiation between clans. Genomic PCA revealed that genetic variation
104 was distributed continuously throughout the population. The first two axes (PC1 and PC2) of the
105 PCA each explained a relatively low proportion (2%) of the genetic variation in the population,
106 and individuals generally sat continuously across both of these axes. However, individuals that
107 were born into the same clan clustered together across PC1 and PC2 (Figure 1C). This suggests
108 that individuals born into the same clan were more genetically similar to each other than to
109 individuals from other clans. Individuals born into the same clan also clustered together across
110 a continuum of genetic variation in the third and fourth PCA axes (Figure S1), further suggesting

111 that individuals that were from the same clan were more similar to each other than to individuals
112 from other clans. Genetic differentiation between clans was estimated as pairwise $F_{ST,}$ which
113 measures the proportion of genetic variation that is different between pairs of populations.
114 Pairwise $F_{ST}$ between clans varied between 0.013 and 0.043 and were all significantly different
115 from zero (i.e., none of the confidence intervals for the pairwise $F_{ST}$ estimates overlap 0.001,
116 Figure 1D). Most $F_{ST}$ estimates were also significantly different from each other, but two pairs of
117 $F_{ST}$ values (out of a possible of 630 pairs) were found to be not significantly different to each other
118 (at a significance threshold of = 0.001 to correct for multiple testing: $F_{ST}$ between Airstrip and
119 Munge was not different to Engitati-Lemala, and Munge-Forest was not different to Lemal-
120 Shamba). We also found evidence for isolation-by-distance between individuals born into the
121 Crater, whereby individuals that lived further apart from each other were less genetically similar
122 than those living closer (Figure 2D). Genetic variation, estimated as average heterozygosity
123 across individuals, differed significantly among most pairs of clans, but the magnitude of
124 difference in heterozygosity was very small (see Table 1). Heterozygosity in the Lemala and
125 Munge clans were not significantly different from each other, nor were Engitati, Ngoitokitok and
126 Triangle (Table 1). The Triangle clan had the lowest inbreeding coefficient ($F_{IS}$) of all of the clans,
127 indicating that they were marginally more heterozygous than expected (Table 1). However, while
128 the confidence intervals for Triangles $F_{IS}$ did not overlap with that of most other clans, it did
129 marginally overlap with $F_{IS}$ of Lemala, suggesting the difference in $F_{IS}$ between these clans had
130 little statistical support.

131 *How are patterns of dispersal associated with observed genetic structure?*

132 We next measured geographic distance and dispersal rates between clans to test whether these
133 factors predicted $F_{ST}$ between clans (see Figure 1 and methods). Dispersal rates between clans

were highly heterogeneous across the population, ranging from 0% of males from Airstrip clan dispersing to Triangle clan (and vice versa), to 51% males from Engitati clan dispersing to Munge clan (Figure 1B). Dispersal rates were often very asymmetric in that the exchange of males between clans via dispersal was rarely reciprocal (Figure 1B). For instance, 21% of males from Triangle clan dispersed to the Lemala clan, but only 3% of males from Lemala clan dispersed to the Triangle clan. Geographic distance between clans varied between 2,768m (Lemala to Shamba clans) and 11,976m (Forest to Munge clans) (Figure 1A). 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 contribute to generating heterogeneous rates of male dispersal between clans.

There were multiple lines of evidence to suggest that genetic differentiation between clans was driven by differential rates of male dispersal between clans. First, we compared observed $F_{ST}$ to that expected under a null model which randomly distributed males among clans, thus creating a range of $F_{ST}$ expected if males dispersed at random. We found that, for all pairs of clans, observed $F_{ST}$ was larger than that expected if males dispersed between clans at random (Figure 2A, methods). Second, dispersal rates between clans were negatively correlated with pairwise $F_{ST}$ between clans, as pairs of clans that exchanged fewer males were more genetically differentiated than those that had a higher rate of male dispersal (MRQAP: mean $\beta$ [95% bootstrapped CI's] = -0.036 [-0.037; -0.035], p = 0.017, Figure 2B). This remained true even when controlling for the effect of geographic distance, which did not have an effect on $F_{ST}$ when fitted in a model together with dispersal rates (MRQAP: mean $\beta$ [95% bootstrapped CI's] = $-2.15 \times 10^{-7}$ [$-2.22 \times 10^{-7}$; $-2.13 \times 10^{-7}$], p = 0.750, Figure 2C) or when estimated alone (MRQAP: mean $\beta$ [95% bootstrapped CI's] = $5.047 \times 10^{-7}$ [$5.047 \times 10^{-7}$; $5.048 \times 10^{-7}$], p = 0.379). This suggests that

158 dispersal between clans, rather than geographic distance, was the mechanism through which
159 genetic structure emerges in the population. We also found that when males were assigned to
160 their adult clans (i.e., the clan that they disperse into), $F_{ST}$ between clans were lower than when
161 assigned to their natal clan (as is presented above), although they were still all significantly
162 different from 0.001, further suggesting that male dispersal acts to facilitate gene flow through
163 the population (Figure S2).

164 *How does clan ancestry relate to fitness?*

165 When individuals disperse, they introduce new alleles to recipient groups and, if these alleles are
166 associated with fitness-related traits, dispersal can affect the distribution of additive genetic
167 (breeding) values for fitness (i.e., survival and reproduction) in the recipient group. These
168 changes can modify the genetic variance available for selection (21,33). We examined whether
169 dispersal between social groups had the potential to affect genetic variation for fitness by testing
170 if genetic ancestry from different clans, including from non-Crater clans, was associated with
171 different breeding values for fitness. To do this, we used "genetic group animal models" (as
172 described in (34)) to estimate the effect of ancestry from different clans using two estimates of
173 individual fitness, lifespan (in years) and lifetime reproductive success (LRS, total number of
174 offspring), estimated for 1,635 Crater-born individuals born between 1996 and 2015 together
175 with the population pedigree of 3,239 individuals with known natal clans (see methods for
176 details).

177 Among the 1,635 individuals included in the phenotypic analyses (i.e., those with data on
178 lifetime reproductive success and lifespan), the number of individuals with non-zero genetic
179 ancestry from each clan ranged from 105 to 1,318 (Lemala = 722, Munge = 877, Shamba = 105,
180 Triangle = 117, Ngoitokitok = 346, Engitati = 413, Forest = 256, Airstrip = 840, non-Crater = 1,318).

Because individuals could have ancestry from multiple clans, these counts are not mutually exclusive and reflect the number of analysed individuals who could trace at least some ancestry to each clan. Although the phenotypic analyses were restricted to individuals born into Crater clans, many of these individuals had ancestry from (non-Crater) immigrants (i.e., individuals born outside the Crater). Accordingly, individuals with a greater proportion of immigrant genetic ancestry had higher lifetime reproductive success and longer lifespans (Table 2, Figure 3). 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 between Crater and immigrant ancestry, the relative contributions of individual Crater clans did not significantly affect either lifetime reproductive success or lifespan (Table 2).

*Does additive genetic variance in fitness vary among clans?*

We estimated the expected rate of adaptive evolution following the fundamental theorem of natural selection which states that the expected per generation change in mean fitness caused by selection is equivalent to the additive genetic variance ($V_A$) in fitness (6). As a baseline estimate of $V_A$, we first fit our genetic group model assuming homogeneous variance across clans. 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 reported by (7), although our estimates had narrower credible intervals. We then used genetic group animal models to estimate heterogeneous $V_A$ in fitness by estimating a single estimate of $V_A$ per clan (6,7). Following methods outlined in (34), we identified whether there was evidence for among-clan differences

by assessing the proportion of the posterior distribution of clan-specific $V_A$ estimates (presented in Table 3) overlapped with each other (see methods). Despite increased uncertainty associated with smaller sample sizes within clans, we found evidence that $V_A$ in fitness differed among some clans (Table 3, Figure 4). All pairwise contrasts are provided in Figures S6–S7. For LRS, there was statistical support for differences in $V_A$ in six pairwise comparisons (out of a possible 72) (Figure S6). The Lemala clan had lower $V_A$ in LRS than Ngoitokitok, Forest, Airstrip and non-Crater clans. Ngoitokitok clan further had a higher $V_A$ in LRS that Triangle and Munge clans. For lifespan, there was statistical support for differences in $V_A$ in 11 of a possible 72 pairwise comparisons (Figure S7). The Lemala clan again had one of the lowest $V_A$ in lifespan which was lower than five other clans (Forest, Triangle, Ngoitokitok, Airstrip and Shamba). Non-crater had a lower $V_A$ in lifespan than Ngoitokitok, Triangle and Forest clans, and Munge clan also had lower $V_A$ in lifespan than Ngoitokitok, Triangle and Forest clans (Figure S7). Overall, these results suggest that Forest, Triangle and Ngoitokitok clans had the highest estimates of $V_A$ in fitness, whereas Lemala has the lowest.

Prior–posterior comparisons indicated that estimates of $V_A$ in LRS for the Lemala clan remained only weakly informed by the data, as the posterior distribution closely resembled the prior distribution (Figure S8). Posterior distributions for $V_A$ in LRS for the Munge, Engitati and Triangle clans also showed relatively limited contraction relative to the prior, suggesting less information in the data for these estimates. Posterior distributions for all other clan-specific estimates of $V_A$ in LRS, and for all estimates of $V_A$ in lifespan, were substantially contracted from the prior, indicating stronger information from the data. To further assess prior sensitivity, we re-ran the models using a substantially broader prior on random-effect variances (scale = 10,000). Estimates of $V_A$ showed strong similarity across prior specifications (Table S2), indicating that the results were not strongly dependent on the choice of prior. In addition, estimates of $V_A$ in lifespan

appeared consistently well supported, relative differences among clans were broadly similar for lifespan and LRS, and estimated $V_A$ showed no relationship with clan sample size for either trait. Taken together, these results suggest that although estimates of $V_A$ in LRS for some clans, particularly Lemala, should be interpreted cautiously, the overall pattern of heterogeneity in additive genetic variance among clans is likely to be robust.

Residual variance (which reflects the remaining phenotypic variance which is 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 (27,29,35). 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, suggesting evidence for inbreeding depression (Table 2). There was evidence for a negative relationship with natal clan size for both fitness measures (Table 2), suggesting evidence for an effect of density in early life on fitness (36). 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 the interaction between ecological and evolutionary processes (37). However, in addition to being shaped by evolution, social structure may influence microevolutionary processes by altering patterns of gene flow, modulating genetic drift, or structuring populations in ways that may generate variation in natural selection (2,3,5,15). In a wild population of spotted hyenas composed of eight social groups, we combined nearly 30 years of behavioural, life-history, and fitness data with a new genome-wide SNP dataset to show that social structure is associated with core microevolutionary processes. We found small but meaningful genetic differentiation among clans that was predicted by heterogeneous dispersal patterns, suggesting that dispersal between social groups contributes to the patterns of gene flow through the population. Furthermore, additive genetic variance in fitness varied among clans, suggesting that different social groups within the population differ in the expected rate of adaptive evolution.

While theory and empirical work suggests that social structure should shape population genetic patterns (5,11,16,38), empirical tests of the associated mechanisms are challenging because dispersal is hard to observe directly. In our study, genetic variation was distributed continuously across the population, but clans inhabiting the 250 $km^2$ Ngorongoro Crater were genetically differentiated to an extent comparable to metapopulations separated across island archipelagos (e.g., house sparrows, islands of Helgeland, Norway (39)). The patterns we observed likely reflects the combined effect of the kinship structure inherent to hyena social groups (25,40) and reproductive skew in both sexes (27,28,30,41), which results in recent coalescence to common ancestors within clans. Our findings also identify some of the mechanisms by which social structure may mediate genetic structure: while male dispersal

appeared to facilitate gene flow, rates of dispersal were only weakly predicted by geographic distance. Instead, local variation in clan density, sex ratio and kin structure, may underlie dispersal dynamics (14,29). Furthermore, the tendency for male relatives to disperse to the same clan may limit genetic mixing and amplify genetic differentiation (42).

Dispersal can shape adaptive evolution by introducing alleles that alter the additive genetic variance for fitness in recipient groups, provided these introduced alleles are associated with fitness-related traits. In our study, analyses suggested there were no differences in breeding values for fitness among clans. This supports previous findings that suggest dispersal between Crater clans does not confer a fitness advantage over philopatry (29). However, ancestry from immigrants originating from outside the Crater, sometimes from individuals who migrated from as far as 150km away (43), was associated with higher fitness, consistent with findings from other animal populations (44). This is an important finding because group-living animals, including hyenas, often show mating bias toward members of their own group (45), increasing the risk of inbreeding. Dispersal is therefore widely considered a mechanism to reduce inbreeding in kin-biased societies (46,47). Our results support this hypothesis because the high proportion of immigrant ancestry in the population might have resulted from biased mate choice toward males that immigrate from outside the population. Our findings also suggest there is unlikely to be selection against immigrants in the population, under which we would have expected lower fitness for immigrant ancestry (48). Although immigration from outside the Crater is rare (9% breeding males are immigrants), having immigrant ancestry is extremely common in the population (approximately 80% individuals have immigrant ancestry), and our results suggest that it plays a disproportionate role in shaping the quantitative genetic architecture of fitness related traits in the population (33). However, further work would be

298 needed to formally identify whether contemporary patterns of dispersal result in changes of
299 breeding values within clans.

300 Most wild populations are subdivided to some extent, resulting in population genetic
301 structure (15). In structured populations, genotypes are distributed non-randomly across
302 heterogeneous environments, where both the availability of mates and ecological selection
303 pressures vary spatially (5,22). As such, population structure may significantly affect
304 evolutionary dynamics (49–51). Our findings suggest that social structure not only impacts gene
305 flow via dispersal between social groups, but group membership also corresponds with
306 heterogeneity in additive genetic variance in fitness, and therefore the rate of adaptive evolution
307 (6,7), within the population. While the factors underlying among-clan differences in additive
308 genetic variance in fitness remain uncertain, the Lemala clan provides an illustrative case: it has
309 the lowest additive genetic variance in fitness, the lowest male-to-female sex ratio, the highest
310 proportion of philopatric males, and the most stable social hierarchy. It also shows some of the
311 strongest reproductive skew in females, with a few individuals contributing disproportionately to
312 the next generation (unpublished). These socio-demographic features likely reduce genetic
313 variance for fitness by limiting mate pools and increasing relatedness, highlighting how fine-
314 scale variation in social structure may influence genetic variance for fitness, and therefore
315 expected rates of adaptive evolution.

316 It is important to note that our analyses were not able to identify the causal mechanisms
317 generating differences in additive genetic variation among clans. Social structure itself emerges
318 from ecological and evolutionary processes, and environmental heterogeneity, reproductive
319 skew, historical demography, social behaviour, and finer-scale social genetic processes are all
320 likely to contribute jointly to the observed patterns. For example, indirect genetic effects (IGEs),
321 whereby the genotypes of social partners influence an individual's phenotype and fitness, can

alter both the expression and evolutionary consequences of genetic variation in socially structured populations (52,53). Because clan members experience repeated interactions within relatively stable social environments, IGEs could contribute to variation in fitness within and among clans. Our analyses were not able to disentangle such processes while simultaneously estimating clan-specific additive genetic variances and differences among social groups given the large statistical power required. Nevertheless, the inclusion of natal-clan and adult-clan random effects, together with clan-specific residual variances, should capture broad-scale differences in shared environmental and social conditions among clans. More broadly, the combination of higher fitness associated with immigrant ancestry and among-clan heterogeneity in additive genetic variance raises questions about how gene flow interacts with local demographic, social, and selective processes within socially structured populations. Distinguishing among these mechanisms will require future work that explicitly links dispersal decisions, social interactions, selection, and realised evolutionary change through time.

In conclusion, our study integrates behavioural, genomic, pedigree, and fitness data to provide a rare, comprehensive empirical examination of how social structure might impact microevolutionary processes like gene flow and adaptive evolution in the wild. Interestingly, our results suggest broadly similar inferences from either LRS and lifespan, despite them reflecting different combinations of the core fitness components of survival and fecundity. The broadly similar inferences obtained from LRS and lifespan suggest that associations between ancestry and quantitative genetic variation were not driven exclusively by either survival or reproductive output. We cannot yet quantify how population structure or clan-level variation in the rate of adaptive evolution correspond to realised genetic evolution, which traits may be under selection, or if these are the same across all clans. Nonetheless, our findings illustrate that social

behaviours and group structure are key mediators of gene flow and the distribution of genetic variance for fitness, and should be more fully integrated into evolutionary theory and empirical study design.

## ***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 $km^2$, $3^{\circ}11'$ S, $35^{\circ}34'$ 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 via surveys conducted on five to seven days a week, during which observations are made from a vehicle that hyenas are well habituated to from birth (31,54). 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 (54,55). 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 (29,54). The majority of males (>90%) dispersed to a breeding clan once and remained there for their entire adult life (Figure 1B). 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. 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 (28,56). 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 (57). Briefly, library construction followed the 3RADseq

protocol (58) using the restriction enzymes *EcoRI*, *XbaI*, and *NheI* and incorporating a modification to remove PCR duplicates (59), which enabled sequencing approximately 23500 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 (57)). Final libraries were sequenced on an Illumina NovaSeq S4 platform using 150 bp paired-end reads targeting ≥30× coverage per individual. Reads were then trimmed of their adapters using Cutadapt (60) before being demultiplexed using Flexbar (61). 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 (62)). Unmerged reads were trimmed to a maximum length of 130 bp and a minimum quality score of 30 using Trimmomatic (63). 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 (64) were excluded using Samtools (65). SNP calling was performed using Stacks reference-based pipeline v2.61 (66,67) and loci were retained if genotyped in ≥60% of individuals. Individuals with >2.5M reads were subsampled to normalize coverage (~60×). In total, 1187 spotted hyenas were genotyped at a total of 69816 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 1181 individuals and 27219 unlinked SNPs.

*is genetic variation structured among clans?*

Using a panel of genome-wide SNPs (N = 27219) sequenced for 1181 individuals, we first ran a suite of analyses to characterise the genetic structure of the population. To characterise genetic substructure and differentiation in our study population, we ran two analyses: genomic principal component analysis (PCA) and isolation-by-distance. Genomic PCA was used to describe patterns in genetic variation through the population, and was run in the *ADEGENET* package in R (68), retaining all of the principal components as per (69). Isolation-by-distance was estimated via the correlation between geographic distance and genetic distance between individuals. Geographic distance between pairs of 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 when the individuals were sighted (70). Centroids of MCPs were calculated using geometric unary operations via the *sf* R package (70,71). Individuals with less than five sightings were removed to ensure precision in estimation of home ranges (and therefore centroids). Genetic distance between individuals was calculated using Nei's genetic distance (72) using the *StAMPP* R package (73). Genetic differentiation between clans was estimated as pairwise $F_{ST}$ using the *StAMPP* R package (73). Individuals were assigned to their natal clan and all individuals and all clans were retained when calculating $F_{ST}$,

437 including individuals born to non-Crater clans that dispersed into a Crater clan. We identified
438 whether $F_{ST}$'s were different from zero by bootstrapping across loci, generating confidence
439 intervals of the estimated $F_{ST}$. $F_{ST}$ were considered different from zero if the 95% confidence
440 intervals from bootstraps did not include 0.001. Pairs of clans were considered to have different
441 $F_{ST}$ to each other when their 99.9% confidence intervals of estimated $F_{ST}$ from bootstraps did not
442 overlap with each other, using a stricter threshold to correct for multiple testing.

443 *Are patterns of dispersal associated with observed genetic structure?*

444 We next tested whether either distance between clans or dispersal rates predicted $F_{ST}$ between
445 clans. Geographic distance between clans was estimated as the distance in metres between the
446 centroid of clans' territories (Figure 1A). Clans and territories have remained very stable across
447 time: the territory boundaries have remained largely the same across time and there have been
448 no instances of clan replacement or formation during the study period (Figure 1A (74,75)). Clan
449 territories were estimated as utilisation distributions (UD) via the kernel density methods in the
450 *adehabitatHR* R package (76) using sightings of resident individuals of each clan. UDs for each
451 clan were estimated with a smoothing parameter of 440 metres, which was identified as the
452 maximum value used when optimised per clan and when assuming a bivariate normal
453 distribution of geographic coordinates. We decided to use a single smoothing parameter for all
454 clans, rather than different parameters for each clan via the *href* option to standardise the
455 estimation of clan territories across the population. Centroids per clan territory and geographic
456 distance between all centroids were then identified as described above for individuals. While
457 distance between territory centroids is a simplified estimate of spatial separation, our aim was
458 to assess the effect of broad spatial proximity among clans rather than model dispersal pathways
459 explicitly. We therefore considered centroid distance an appropriate first-order measure of

460 geographic separation (55). Although alternative measures could incorporate landscape
461 features or movement costs, we do not consider water bodies within the Crater to constitute
462 substantial barriers to hyena movement, as hyenas readily cross water and these areas are
463 greatly reduced during the dry season (Figure 1A). Furthermore, the observed dispersal patterns
464 were asymmetric among clans and were not fully explained by spatial proximity, suggesting that
465 factors other than geographic distance alone contribute to patterns of dispersal and genetic
466 differentiation.

467 Dispersal rates between pairs of clans were estimated as the proportion of males that
468 dispersed from one clan to another clan. We calculated the probability of dispersal between
469 clans as the proportion of males that dispersed from one clan to another, relative to the total
470 number of dispersing males from the first clan. This generated an asymmetric matrix that
471 described the probability of dispersal between clans and where the diagonal element of the
472 matrix describes the proportion of adult males that are philopatric and reproduce in their natal
473 clan.

474 To test whether pairwise $F_{ST}$ between clans was greater than expected given the rate of
475 dispersal in the population, we first ran a null model to generate pairwise $F_{ST}$ between clans that
476 would be expected if males dispersed at random. This model randomly permuted adult clan
477 membership between males, randomly distributing them through the population and simulating
478 random dispersal. This permutation model was run a total of 1000 times, calculating pairwise $F_{ST}$
479 between clans in each permutation to generate an expected range of pairwise $F_{ST}$ under random
480 male dispersal. We then identified whether observed pairwise $F_{ST}$ between clans were greater
481 than expected if the confidence intervals of observed $F_{ST}$ (estimated from the bootstraps
482 explained above) did not overlap with the 95$^{th}$ percentile of the distribution of the $F_{ST}$ generated

483 in the null model. This model was run in R using custom scripts and the *StAMPP* R package to
484 calculate $F_{ST}$ for each iteration of the permutation model.

485 Next, to test if either the probability of dispersal or geographic distance between clans
486 predicted pairwise $F_{ST}$, we ran a multiple regression quadratic assignment procedure (MRQAP)
487 with the matrix of $F_{ST}$ as the response matrix and the matrices of probability of dispersal and
488 geographic distance as the predictor matrices. MRQAP is an extension of the mantel test (a
489 statistical procedure commonly used to identify correlations between matrices) which allows
490 the user to concurrently test for the effects of multiple predictor matrices. We ran MRQAP using
491 the *asnipe* R package (77) and we calculated confidence intervals of effect sizes for each MRQAP
492 by propagating the bootstrapped estimates of $F_{ST}$ through and re-running the MRQAP for each
493 bootstrap permutation. However, we used the double semi-partialling method (DSP) to assess
494 significance using the mean estimate of $F_{ST}$ as this method has been found to be robust against
495 statistical violations of autocorrelation, confounder effect sizes and skewness in the data (78).
496 This method permutes (N = 1000 randomisations) the matrix of residuals from the ordinary least
497 regression of the dependent matrix on the independent matrices to estimate error and calculate
498 the effects. These analyses were conducted using the 8 Crater clans. Non-Crater clans were
499 discarded because their estimated rate of dispersal and home range are likely to be inaccurate
500 due to lower monitoring effort.

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

503 *Data selection*

504 We used two measures associated with realised lifetime fitness: lifetime reproductive success
505 (LRS), defined as the total number of offspring produced by an individual, and lifespan, defined

as age at death (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 but distinct aspects of life-history and lifetime fitness (79,80). LRS integrates both survival and reproductive output, whereas lifespan reflects the survival component of fitness but does not directly quantify reproductive success. Although LRS and lifespan were positively correlated ($r = 0.78$), analysing both allowed us to assess whether inferences regarding genetic variance and differences among clans were consistent across alternative fitness measures. In addition, reproductive success can be challenging to represent as a single, directly comparable measure of fitness because it is influenced by multiple demographic and life-history processes. Lifespan therefore provides a complementary and comparatively straightforward measure of fitness-related variation.

To ensure that we had observations across the complete lifespans of individuals, we only included individuals who were born after the beginning of the study period (1996) and were known to have died by February 2025. To ensure measures of fitness were accurate for each cohort in the dataset, we also 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 either 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 $\beta_{SEX}^{MALE}$ = -0.814 (-1.134 - -0.547), random assignment of sex $\beta_{SEX}^{MALE}$ = -0.814 (-1.114 - -0.519); Lifespan: without N = 204 individuals $\beta_{SEX}^{MALE}$ = -0.228 (-0.372 - -0.068), random assignment of sex $\beta_{SEX}^{MALE}$ = -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 =1635 Crater-born individuals for which mothers and social ranks at birth were known.

*Statistical models*

All models described below were fitted in a Bayesian framework using *MCMCglmm* package in R (81). We used the default weakly informative parameter expanded priors set to $F_{1,1}$ distribution setting the scale to 1000 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 10000) 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 60000 iterations, with a 10000 burn-in period and a thinning interval of 10. This was sufficient in all cases to achieve effective sample sizes of at least 1000 for all parameters and low autocorrelation. Model convergence was assessed using effective sample sizes and visual inspection of trace plots.

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 that partition breeding values according to ancestry from different clans and estimate

551 clan-specific additive genetic variances (21,34,82,83). Animal models are linear mixed-effects
552 models that incorporate relatedness information as a covariance matrix to estimate additive
553 genetic variance, i.e., the variance of additive genetic values for a response variable (84,85).
554 Genetic group animal models further allow the distribution of the genetic values to differ
555 according to genetic substructures (so-called "genetic groups") in the population. In our case,
556 each genetic group corresponded to one of the clans, in addition to a group lumping together
557 non-Crater (immigrant) individuals. Pedigree-based genetic group animal models assume that
558 founder individuals are unrelated both within and among genetic groups (21,86). We
559 acknowledge that this assumption is unlikely to be fully met in our study system because clans
560 are connected by low levels of dispersal and are therefore not completely reproductively
561 isolated. As is typical of genetic group models applied to natural populations, the fitted groups
562 should therefore be interpreted as pedigree-defined ancestry partitions rather than completely
563 isolated demes (33,34). Moreover, any resulting shared ancestry among founder groups would
564 be expected to reduce, rather than inflate, genetic differences among groups, making inference
565 of group-specific effects conservative.

566 LRS and lifespan were analysed relative to the global population mean fitness (i.e.,
567 individual fitness divided by the overall mean fitness across the dataset) using a Gaussian
568 distribution. This scaling placed fitness measures on a comparable scale and improved fitting of
569 these relatively complex models while retaining variation in fitness across cohorts and sexes. We
570 did not standardize fitness separately within cohort or sex because these effects were modelled
571 directly through fixed and random effects in the animal models (sex as a fixed effect and cohort
572 as a random effect). Correlations between mean fitness and additive genetic variance among
573 clans were low for both fitness measures ($r^2$ ($V_A^{LRS}$ and mean LRS) = -0.42, $r^2$ ($V_A^{Lifespan}$ and mean

lifespan) = 0.27) (see also Table 2, Table 3 and Figure 4), 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 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 (21,83)). Ancestry proportions were calculated using the full pedigree using the *nadiv* R package (87) following methodology and code provided in (21,34). 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 (28,88). Adult clan was included to account for environmental conditions experienced after dispersal or during adulthood. The models that estimated homogeneous variances were therefore:

$$w_i = \mu + \beta_1 F_i + \beta_2 sex_i + \beta_3 socialrank_i + \beta_4 clansize_i + \beta_5 (sex_i \times socialrank_i) + \beta_6 qA_i + \beta_7 qE_i + \beta_8 qF_i + \beta_9 qL_i + \beta_{10} qM_i + \beta_{11} qN_i + \beta_{12} qT_i + \beta_{13} qS_i + m_j + cb_l + cd_k + y_z + a_i + \varepsilon_i \quad \text{(Equation 1)}$$

where $w_i$ is the estimate of fitness (w) for individual i, $\mu$ 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

596 distributed as $(a_1,....,a_n) \sim N(0,V_A A)$ with additive genetic variance $V_A$ and genetic relatedness
597 matrix A (estimated via the population pedigree), and ε is the residual term.

598 Because ancestry proportions sum to one, one genetic group must be used as the
599 reference level, analogous to fitting a categorical fixed effect (34,83). We used non-Crater
600 ancestry as the reference group. Although the analysed dataset did not include individuals born
601 outside the Crater, some individuals possessed ancestry from outside the Crater and ancestry
602 proportions were therefore estimated using the full pedigree. To ensure that ancestry effects were
603 not confounded with inbreeding, we tested for collinearity between inbreeding coefficient and
604 non-Crater ancestry. These variables were only weakly correlated ($r^2 = 0.11$). In standard animal
605 models, breeding values ($a_i$) describe deviations from the mean of a single genetically
606 homogeneous population and therefore have a mean of zero. The genetic group model in
607 Equation 1 relaxes this assumption by allowing clans to differ in mean breeding value.
608 Accordingly, coefficients $\beta_6 - \beta_{13}$ represent the deviation of each groups mean breeding value
609 from the reference groups mean breeding value, while additive genetic variance remains
610 homogeneous across clans.

611 To allow the additive genetic variances to differ among clans, we fitted a second model
612 that partitioned individuals' genetic breeding values ($a_i$) into clan specific contributions.
613 Following methods explained in (34), we estimated partial genetic breeding values ($a_{ij}$) for each
614 group (clan), where $a_{ij}$ represents the contribution to the breeding value of individual *i* from group
615 *j*. These partial genetic breeding values are estimated for all groups (j=1,...,r) and are distributed
616 as $(a_{1j},....,a_{nj}) \sim N(0, V_{Aj} A_j)$, where $V_{Aj}$ is the additive genetic variance in group *j* and $A_j$ is a group-
617 specific relatedness matrix. Clan-specific relatedness matrices were specified following (34)
618 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 (82), we used a pedigree-based approach following (34) to maximise sample size (the full pedigree contains 3239 individuals, whereas the genomic dataset contains 1181 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 VA 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 (89). Instead, following (34,90), 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.

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***Author contributions:***

Conceptualisation: KS, OPH, ED; Data curation: OPH, ED, LSA; Resources: OPH, ED, LSA; Investigation: KS, OPH, LSA, ED; Formal analysis: KS, LSA; Methodology: KS, LSA, JLP, KA; Software: KS, LSA; Validation: KS, OPH, ED, JLP, KA; Visualisation: KS; Supervision: LEBK; Project administration: KS, LEBK; Funding acquisition: LEBK, OPH; Writing – original draft: KS; Writing – review and editing: all

***Competing interest statement***

Authors declare that they have no competing interests.

***Data and code availability***

The raw sequencing data are deposited in the Genbank with the NCBI BioProject accession no. PRJNA951614. Code used for bioinformatic analyses of genetic data can be found at:

https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-/blob/main/scripts/filterPCRdups/filterPCRdups_CM.py and https://git.imp.fu-berlin.de/begendiv/radseq-preprocessing-pipeline/-/blob/main/scripts/digestion/checkRestrictionSites.py). R code and data needed to reproduce analyses and results, including all tables and figures, can be found at https://github.com/kashastrickland/HyenaGroups.

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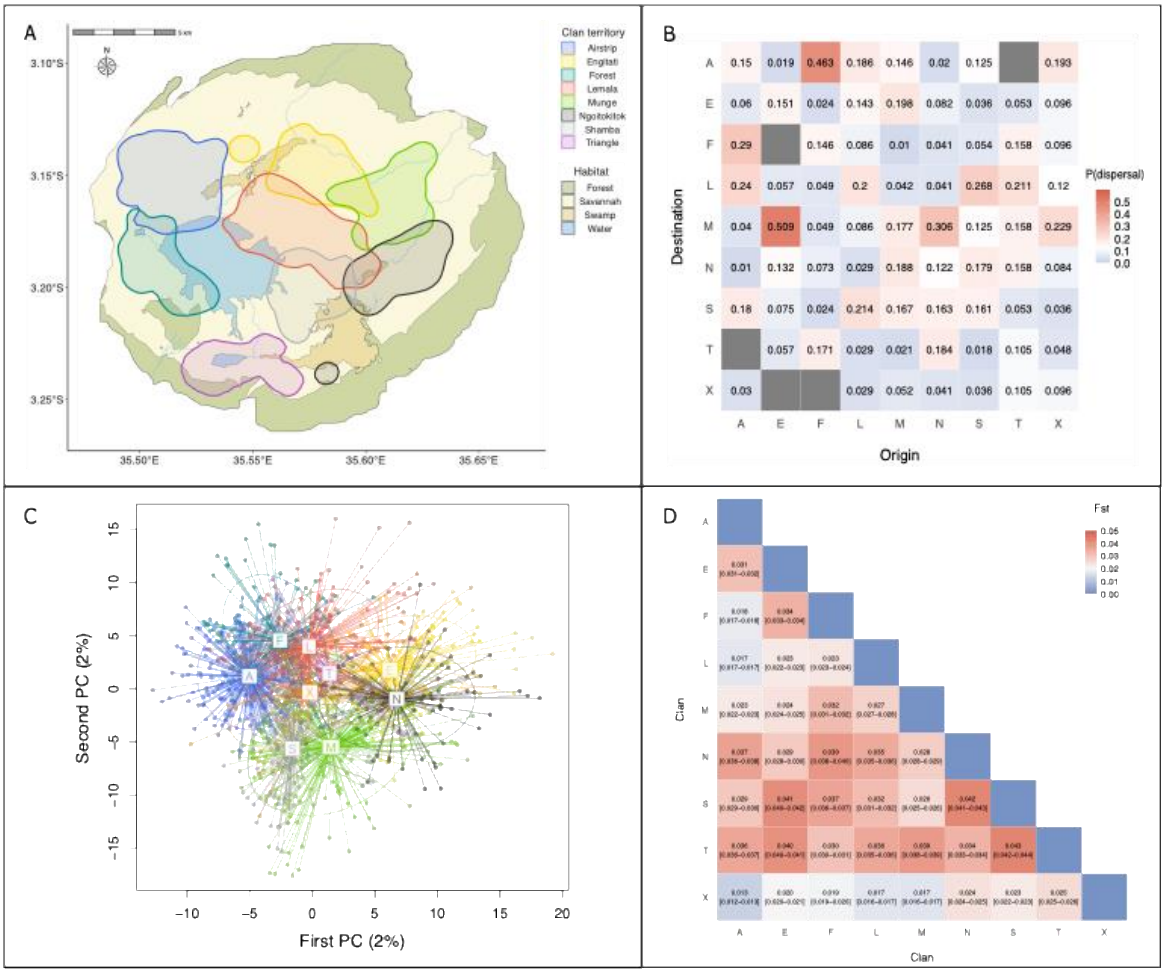


**Figure 1.** Summary plots describing the distribution of individuals and genetic variation across the population of spotted hyenas in Ngorongoro Crater, Tanzania. (A) Map of the Ngorongoro Crater and each clan's territory (see methods) (B) Heatmap showing the probability of male dispersal between all clans, where the diagonal element of the matrix describes the proportion of males that remain philopatric to each clan and grey tiles represent no dispersal. (C) Summary of the first two axes of genomic PCA analysis describing the distribution of genetic variation. Each point is an individual and is coloured by the clan they were born into, and ellipses group individuals born into the same clan. (D) Heatmap of pairwise $F_{ST}$'s between clans, with confidence intervals for each $F_{ST}$ in parentheses which were estimated via bootstrapping across all loci. All $F_{ST}$ estimates were significantly different from zero. Clan names: A = Airstrip, F = Forest, T = Triangle, E = Engitati, L = Lemala, S = Shamba, M = Munge, N = Ngoitokitok, X = non-Crater (i.e., immigrant).

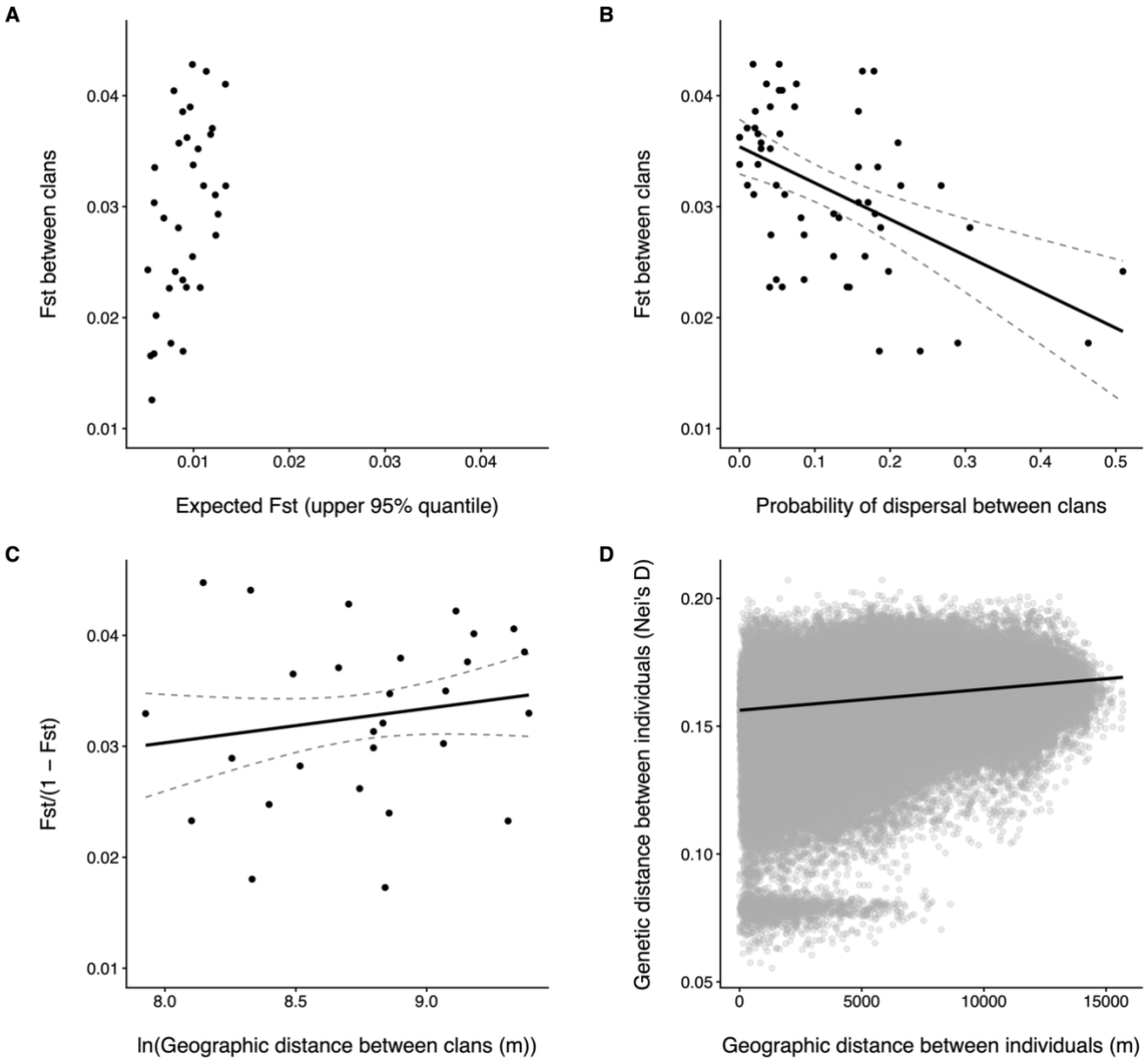


**Figure 2.** Results from analyses used to test for a relationship between genetic differentiation, male dispersal and geographic distance between clans in spotted hyenas in Ngorongoro Crater. (A) Relationship between pairwise $F_{ST}$ between clans expected when male dispersal between clans is random (x axis) and observed $F_{ST}$ between all clans. Upper bound of that range of expected $F_{ST}$ under random dispersal is shown under the expectation that if observed $F_{ST}$ was equal or lower to this expected value, it could have occurred by chance, (B) relationship between probability of dispersal between clans and genetic differentiation between clans, which is measured as $F_{ST}$ (solid line shows the mean predicted relationship with standard errors as dashed lines), (C) relationship between geographic distance (in metres) between the centroid of each clan's territory and genetic differentiation between clans, which is measured as $F_{ST}$ (solid line shows the mean predicted relationship with standard errors as dashed lines), (D) Isolation-by-distance. Each point is an individual and genetic distance on the y axis is measured as Nei's genetic distance between individuals. Geographic distance on the x axis is measured as linear distance in metres between the centroids of individuals home ranges. Note that diagonals of all matrices were removed prior to running analyses as we were interested in patterns occurring *between* clans rather than *within* clans.

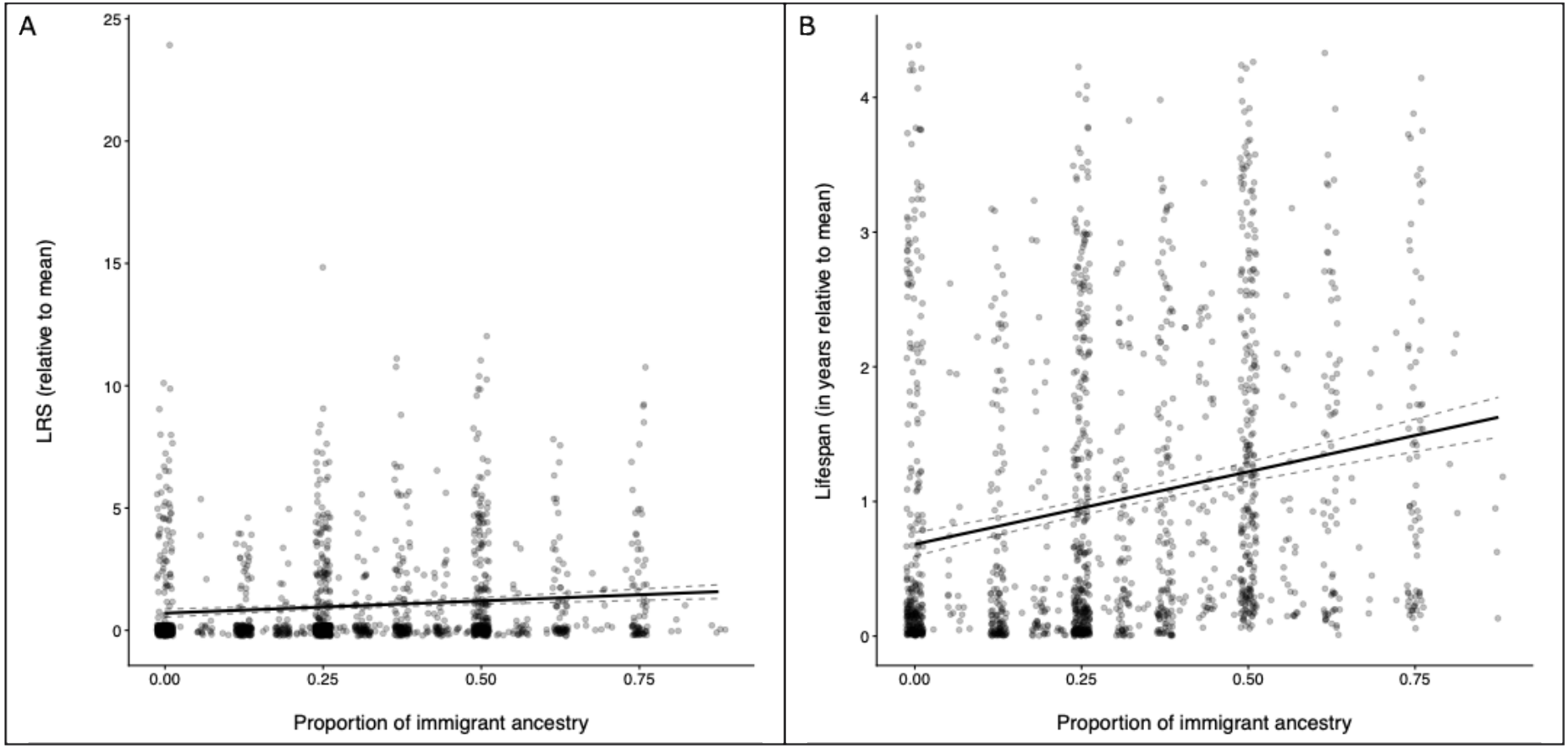


**Figure 3.** The relationship between the proportion of ancestry an individual has from immigrants (i.e., ancestors that immigrated into the Crater from outside the Crater) and fitness, measured as lifetime reproductive success (LRS, A) and lifespan (B). Both fitness measures are plotted relative to 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.

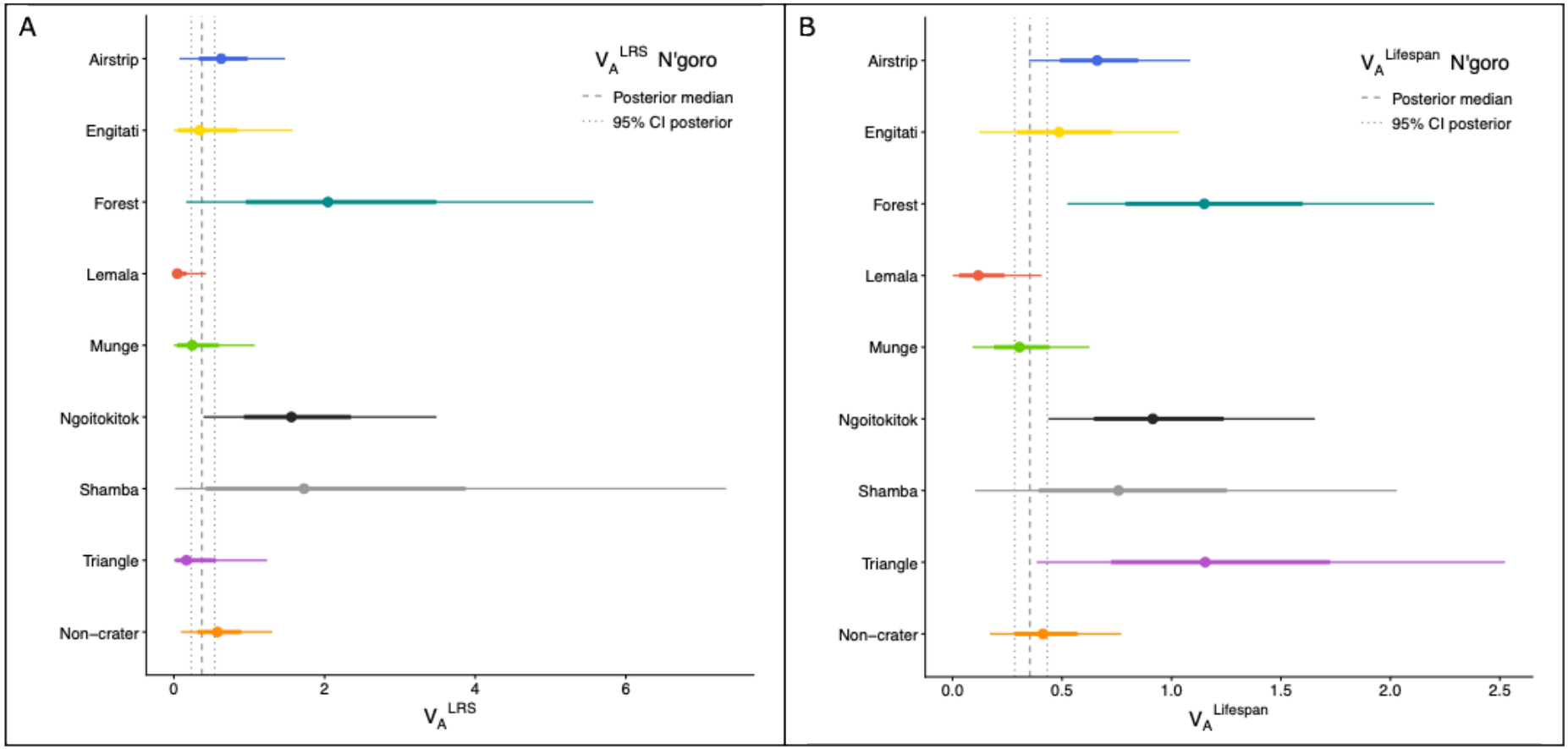


**Figure 4.** Estimates of additive genetic variance ($V_A$) for two measures of fitness (lifetime reproductive success, LRS, and lifespan) in each clan of spotted hyenas in Ngorongoro Crater. Estimates of $V_A$ are on relative fitness (i.e., relative to the global population mean). Points show the median estimate of $V_A$, thick bars show the 75% credible intervals of the full posterior distribution and thin lines show 95% credible intervals of the full posterior. Vertical lines intersect estimated $V_A$ for the population that was derived from a model that does not estimate $V_A$ for each clan independently. Dashed lines show the median of the posterior of those estimates and dotted lines show the 95% credible intervals of the posterior.

**Table 1.** Genetic diversity of each clan of spotted hyenas in Ngorongoro Crater, Tanzania. Standard deviations for heterozygosity estimates and confidence intervals of $F_{IS}$ given in parentheses.

| Clan | Observed heterozygosity | Expected heterozygosity | $F_{IS}$ |
|---|---|---|---|
| Airstrip | 0.262 (0.172) | 0.256 (0.164) | -0.016 (-0.051; -0.023) |
| Engitati | 0.259 (0.181) | 0.251 (0.17) | -0.022 (-0.022; 0.014) |
| Forest | 0.262 (0.18) | 0.254 (0.168) | -0.024 (-0.065; -0.022) |
| Lemala | 0.261 (0.176) | 0.254 (0.166) | -0.02 (-0.078; -0.045) |
| Munge | 0.26 (0.176) | 0.254 (0.167) | -0.012 (-0.028; 0.008) |
| Ngoitokitok | 0.26 (0.184) | 0.25 (0.171) | -0.026 (-0.044; -0.003) |
| Shamba | 0.261 (0.182) | 0.251 (0.169) | -0.027 (-0.027; 0.008) |
| Triangle | 0.264 (0.192) | 0.251 (0.173) | -0.04 (-0.147; -0.077) |
| non-Crater | 0.262 (0.168) | 0.266 (0.159) | 0.017 (-0.062; 0.022) |

Observed heterozygosity (He) estimated as the proportion of heterozygous loci per individual, averaged across the population. Expected heterozygosity estimated as $He * (2 * N_{ID} / (2 * N_{ID} - 1))$, where $N_{ID}$ is the number of individuals in that clan. $F_{IS}$ is the inbreeding coefficient and is estimated as 1 – (Heterozygosity / Expected heterozygosity). All estimates calculated in the *dartR* R package (91). Confidence intervals estimated via leave-one-out estimation.

**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) |
| $V_A^{Ngoitokitok}$ | 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) |
| $V_A^{Non-crater}$ | 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) |
| $V_{BirthClan}$ | 0.35 (0.021; 1.066) | 0.089 (0.005; 0.258) |
| $V_{AdultClan}$ | 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) |
| $V_R^{Ngoitokitok}$ | 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, $V_{BirthClan}$ 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.