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ORIGINAL RESEARCH

Population genetics of a lethally managed medium-sized predator

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Abstract

Globally, levels of human–wildlife conflict are increasing as a direct consequence of the expansion of people into natural areas resulting in competition with wildlife for food and other resources. By being forced into increasingly smaller pockets of suitable habitat, many animal species are at risk of becoming susceptible to loss of genetic diversity, inbreeding depression and the associated inability to adapt to environmental changes. Predators are often lethally controlled due to their threat to livestock. Predators such as jackals (black backed, golden and side striped; *Canis mesomelas*, *C. aureus* and *C. adustus*, respectively), red foxes (*Vulpes vulpes*) and coyotes (*C. latrans*) are highly adaptable and may respond to ongoing persecution through compensatory reproduction such as reproducing at a younger age, producing larger litters and/or compensatory immigration including dispersal into vacant territories. Despite decades of lethal management, jackals are problematic predators of livestock in South Africa and, although considered a temporary measure, culling of jackals is still common. Culling may affect social groups, kinship structure, reproductive strategies and sex-biased dispersal in this species. Here, we investigated genetic structure, variation and relatedness of 178 culled jackals on private small-livestock farms in the central Karoo of South Africa using 13 microsatellites. Genetic variation was moderate to high and was similar per year and per farm. An absence of genetic differentiation was observed based on STRUCTURE, principal component analysis and AMOVA. Relatedness was significantly higher within farms (r = 0.189) than between farms (r = 0.077), a result corroborated by spatial autocorrelation analysis. We documented 18 occurrences of dispersal events where full siblings were detected on different farms (range: 0.78–42.93 km). Distance between identified parent–offspring varied from 0 to 36.49 km. No evidence for sex-biased dispersal was found. Our results suggest that in response to ongoing lethal management, this population is most likely able to maintain genetic diversity through physiological and behavioural compensation mechanisms.

Introduction

Habitat loss, fragmentation and human persecution pose the greatest threats to the persistence of carnivore populations (Ripple et al., 2014). Populations are forced into smaller pockets of habitat and small, isolated populations are susceptible to loss of genetic diversity due to inadequate gene flow (Wright, 1931). This can reduce effective population size, lead to inbreeding depression (Keller & Waller, 2002; Ralls et al., 1979; Spielman et al., 2004), reduced reproductive fitness, a compromised ability to adapt to environmental changes (Markert et al., 2010), and an elevated extinction risk (Frankham, 2005; Spielman et al., 2004). In addition, demographic factors (low population growth rates and skewed sex ratios) may result in a population being susceptible to the effects of inbreeding depression (Mills & Smouse, 1994). Furthermore, if animals are selectively removed from a population due to specific traits by activities such as hunting, there may be additional genetic consequences, such as changes in the rate of gene flow between neighbouring populations, alteration in

effective population size and a decrease in fitness due to loss of rare alleles with evolutionary importance to the population (Harris et al., 2002).

Predators have been persecuted by humans for all recorded history. Lethal control of large predators such as jaguars (*Panthera onca*), grey wolves (*Canis lupus*), lions (*P. leo*), leopards (*P. pardus*), African wild dogs (*Lycaon pictus*) and cheetah (*Acinonyx jubatus)* has resulted in severe range reduction in these species (Gittleman & Gompper, 2001). Although apex predators play a fundamental role in ecosystem functioning, their importance is underestimated because their effects are only understood once they have been exterminated from an area (Estes et al., 2011). One of these effects can be "mesopredator release", where populations of previously suppressed predators may increase in an ecosystem after reducing/removing apex predators (Minnie, Avenant, et al., 2018; Prugh et al., 2009; Ritchie & Johnson, 2009). This phenomenon may be further exacerbated on livestock farms due to high and constant supply of food resources (Blaum et al., 2009).

To reduce predation on livestock, farmers often resort to lethal management (Thorn et al., 2013; Treves & Karanth, 2003), which may disrupt social structures resulting in predators compensating reproductively by having higher proportions of young breeders and larger litter sizes (Haber, 1996; Minnie, Gaylard et al., 2016). Disrupting social structures in territorial species may also create vacant spaces which facilitates compensatory immigration (Minnie, Zalewski, et al., 2018; Pulliam, 1988). Additionally, increasing movements of targeted species may increase disease transmission (e.g. badgers; Pope et al., 2007). As with other regions of South Africa, large apex predators were historically removed from the Karoo (Van Sittert, 1998). Karoo farmers historically received government support (subsidized fencing, access to poison and hunting dogs) to protect their livestock from predation (Nattrass et al., 2017). However, due to changes in policies and attitudes towards conservation and predator management, government support was discontinued and by the mid-1990s, farmers were fully responsible for the protection of their livestock (Nattrass & Conradie, 2013). Consequently, together with the historical removal of large predators from these areas, this provided opportunities for an influx of mesopredators onto farms (Van Sittert, 1998), and an increase in lethal management to protect livestock.

Black-backed jackals (*Canis mesomelas*; hereafter, jackals) are common and widespread throughout South Africa (Mills & Bester, 2005), and occur in most habitat types (Minnie, Avenant, et al., 2016). Despite decades of lethal management, jackals are considered problematic livestock predators (Kerley et al., 2018). Similar to other mesopredators [(e.g. coyotes (*C. latrans*; Knowlton et al., 1999) and red foxes (*Vulpes vulpes*; Kierepka et al., 2017)], jackals show physiological and behavioural flexibility to local conditions (e.g. compensatory reproduction and immigration (Minnie, Gaylard et al., 2016; Minnie, Zalewski, et al., 2018)), resulting in lethal management having little effect on jackal densities (Thorn et al., 2013).

Jackals are monogamous (Ferguson, 1978) and form mating pairs in stable lifelong territories which they defend against other jackals (Moehlman, 1983; Walton & Jolly, 2003). From 6 months to 1 year of age, jackal pups will either disperse, find their own mate and move into a vacant territory, or remain with parents and act as "helpers" of subsequent litters (Ferguson et al., 1983; Moehlman, 1979b; Rowe-Rowe, 1982). However, in the presence of regular/high food resource availability such as at vulture supplementary feeding sites (Yarnell et al., 2015) and livestock farms (Newsome et al., 2015), the exclusive territorial behaviour of jackal pairs may collapse (James, 2014) and territorial pairs may tolerate dispersing juveniles within their natal home range (Ferguson et al., 1983; Hiscocks & Perrin, 1988; Loveridge & Macdonald, 2003). This may increase the density of related jackals within an area resulting in populations that are relatively stable with higher levels of relatedness. Furthermore, regular removal of individuals from controlled populations of bobcats (*Lynx rufus*; Anderson et al., 2015), coyotes (Kierepka et al., 2017; Knowlton et al., 1999), dingo (*C. lupus dingo*; Allen, 2015), Eurasian lynx (*L. lynx*; Bagrade et al., 2016) and jackal (Minnie, Zalewski, et al., 2018) creates multiple spatial vacancies facilitating compensatory immigration resulting in low genetic relatedness between individuals within these populations (Williams et al., 2003; James et al., 2017; Minnie, Zalewski, et al., 2018; Tensen et al., 2018; Tensen et al., 2019).

As historical methods of predator management in South Africa are unlikely to be reinitiated, it is imperative that the behavioural and physiological responses of jackal to lethal management are understood and how these responses in turn influence genetic structure (Abdelkrim et al., 2007; Gervasi et al., 2015). In this study, we investigated genetic structure, variation and relatedness of lethally managed jackals on small-livestock farms (high resource availability, i.e. food resources) in the central Karoo region of South Africa. We hypothesized that due to the ongoing and regular lethal removal of jackal, vacant territories are created leading to genetic structure and increased genetic diversity. We predicted that the genetic relatedness between individuals of the overall study population would be relatively low and that genetic diversity would be unaffected, or possibly increase, over time (James et al., 2017; Minnie, Zalewski, et al., 2018; Williams et al., 2003). Furthermore, because young jackals remain within their natal area for at least 6 months after birth and young jackals are more likely to respond to "call-ins" by culling operators (I. du Preez pers. obs.), we hypothesized that relatedness between individuals would be higher within than between farms.

Materials and methods

Study area

The study took place in the Pixley ka Seme District of the Northern Cape province of South Africa which falls within the Nama Karoo biome, characterized by sparse vegetation with xeric shrubland and grasses being dominant (Mucina & Rutherford, 2006). The topography is predominantly flat, interspersed with dry riverbeds. A mountain that rises 1572 m above sea level is also present. Small-livestock farming [mainly Dorper and Merino sheep (*Ovis aries*) and goats

(*Capra hircus*)] is the leading farming practice in the study area. Farms are partially fenced with jackal proof or stock proof fences, thus movement on and between farms is possible.

Ethics and sample collection

Ethics approval was obtained from the University of South Africa's Animal Ethics Committee (2015/CAES/050) and the Research Ethics and Scientific Committee of the South African National Biodiversity Institute (SANBI, NZG/RES/P17/25). The Department of Agriculture, Forestry and Fisheries of South Africa granted a permit under Section 20 of the Animal Diseases Act of 1984 (Ref: 12/11/1/1/18(816)) and the Department of Environment and Nature Conservation, Northern Cape, granted a research permit (Fauna 293/2/2015). Over 4 years, 190 ear samples were collected opportunistically from jackals that were culled during predator control operations across 26 livestock farms (approximately 92 918 hectares). No jackals were killed for the purpose of this study and carcasses were donated by farmers. Samples were stored in ethanol at room temperature. Jackals were aged based on tooth eruption patterns as per Lombard (1971).

Molecular methods

DNA was extracted using the ZR Genomic DNA™ Tissue MiniPrep (Zymo) following the manufacturer's protocol. Microsatellite markers developed from domestic dog (*C. familiaris*) were amplified for jackal (Table S1; Francisco et al., 1996; Halverson & Basten, 2005; Wictum et al., 2012). Polymerase chain reaction (PCR) amplification was conducted in a 12.5 microlitre (μL) reaction volume consisting of Ampliqon *Taq* DNA polymerase RED (Lasec), forward and reverse primers (0.5 micromolar (μM)) and 10 nanogram (ng) genomic DNA. The PCR conditions were as follows: 5 min at 95°C denaturation, 35 cycles for 30 s at 95°C, 30 s at 45–58°C (Table S1) and 30 s at 72°C, followed by extension at 72°C for 10 min in a SimpliAmp™ Thermal Cycler. PCR products were run against a Genescan™ 500 LIZ™ internal size standard on an ABI 3130 genetic analyser (Applied Biosystems, Inc.) and were genotyped using GeneMapper® v. 4.0.

Genetic variation

All samples were included in each analysis, unless stated otherwise. We used MICRO-CHECKER 2.2.3 (Van Oosterhout et al., 2004) to detect genotyping errors, allele dropout and null alleles. Summary statistics per locus and non-exclusion probabilities were calculated in Cervus 3.0.7 (Kalinowski et al., 2007). Summary statistics per farm (six farms where $n = 1$ were excluded) and per year were calculated using the basicStats function implemented in the R package diveRsity 1.9.90 (Keenan et al., 2013), in R 3.6.2 (R Core Team, 2019) and RStudio 1.2.5033 (RStudio Team, 2019), implementing 1000 bootstrap replicates to calculate 95% confidence intervals for both inbreeding coefficient (F_{IS}) and allelic richness (A_R). Arlequin 3.5.2.2 (Excoffier et al., 2005; Excoffier & Lischer, 2010) was used to evaluate loci for linkage disequilibrium (LD) (100 initial conditions followed by 10 permutations, as described by Guo and Thompson (1992)) and to test for deviations from expected Hardy–Weinberg (HW) proportions (Markov Chain length of 105 and 100 000 dememorization steps).

Effective population size and generation length

Effective population size (N_e) was estimated using three estimators: the sibship assignment method (Wang, 2009), implemented in Colony 2.0.6.6 (Jones & Wang, 2010); the linkage disequilibrium method in NeEstimator 2.01 (Do et al., 2014); and the "estimator by parentage assignments" (EPA), implemented in AgeStructure 1.1 (Wang et al., 2010). Full details for the three estimators are provided in Supplementary Methods in Appendix S1.

Genetic structure

Hierarchical analysis of molecular variance (AMOVA; Excoffier et al., 1992) and pairwise F_{ST} were calculated using Arlequin 3.5.2.2 (Excoffier et al., 2005; Excoffier & Lischer, 2010) to assess genetic differentiation. Population structure was assessed in STRUCTURE 2.3.4 (Pritchard et al., 2000) and via principal component analysis (PCA). STRUCTURE was run with the admixture model "allele frequency correlated" and without prior population information for 20 replicates each of $K = 1$–27, and a run length of 700 000 Markov Chain Monte Carlo iterations, following a burn-in period of 200 000 iterations. The optimum number of subpopulations was estimated by identifying the K with greatest increase in posterior probability (ΔK, Evanno et al., 2005) and by evaluating the log likelihood of K (Ln Pr(X|K)) curve, using STRUCTURE HARVESTER (Earl & von Holdt, 2012). CLUMPAK (Cluster Markov Packager Across K; Kopelman et al., 2015) employs DISTRUCT (Rosenberg, 2004) and was used to graphically represent STRUCTURE runs. CLUMPAK obtains the membership coefficient matrices of replicate runs using CLUMPP (Jakobsson & Rosenberg, 2007), employing as a default, the LargeKGreedy algorithm with 2000 random input sequences. STRUCTURE analysis was repeated, with the above parameters with close relatives removed, using a relatedness cut-off of 0.25 in the software Friends and Family 21 (de Jager et al., 2017). The R package Adegenet 2.1.1 (Jombart, 2008) was used to construct a PCA of the complete dataset.

Relatedness

To determine the appropriate estimator, we used the R package related (Pew et al., 2015) to simulate, from the allele frequencies, 100 pairs of each of the following relatedness categories: parent–offspring (PO), full siblings (FS), half siblings (HS) and unrelated (UR). The performance of six estimators was tested by estimating relatedness of these simulated pairs and

determining which estimator correlated best with the simulated values by calculating Spearman's correlation coefficient (cor.test function in R). The estimators tested included: dyadic maximum likelihood "DyadML" (Milligan, 2003), Lynch-Li (Li et al., 1993), Lynch and Ritland (Lynch & Ritland, 1999), Queller and Goodnight (Queller & Goodnight, 1989), triadic maximum likelihood "TrioML" (Wang, 2007) and Wang (Wang, 2002). Based on the simulation and PCA results, pairwise relatedness (r) and individual inbreeding coefficients (F) were estimated using the entire dataset, with the TrioML estimator in Coancestry 1.0.1.8 (Wang, 2011), assuming monogamy and inbreeding to obtain estimates of F.

Spatial analyses

To investigate genetic substructure at finer scales, we compared relatedness within (six farms where $n = 1$ were excluded) and between farms by testing for a difference in means using the non-parametric two-sample Wilcoxon test in *R* (wilcox.test function), where H_0 = no difference in means. A 95% confidence level was applied for all tests. We conducted a spatial autocorrelation analysis (H_0 = random distribution of genotypes in space, i.e. $r_{auto} = 0$) in GenAlEx using 50 even distance classes of 1 km each (the largest distance between two samples was ~49 km), with 1000 bootstrap replicates of pairwise comparisons within each distance class (with replacement) used to generate 95% confidence intervals to determine significance of correlation within each distance class.

To determine if either sex dispersed significantly more than the other, we compared mean relatedness between sexes (mean relatedness is lower in the dispersing sex), using the Wilcoxon test. We also conducted spatial autocorrelation tests in GenAlEx for each sex separately, using the same parameters as before.

Temporal analyses

To investigate whether culling influenced the levels of relatedness or inbreeding over time, we tested for a difference in mean relatedness and individual inbreeding between years, using the Wilcoxon test.

Dispersal

To identify dispersing individuals and dispersal distance, we reconstructed full-sib families and parent–offspring relationships in Colony. Samples were classified as potential fathers, mothers and/or offspring based on the following age categories: (1) ≤1 year were classified as offspring only (jackals do not breed until 1–2 years of age; Mills & Bester, 2005); (2) 1–3 years were classified as potential fathers/mothers and potential offspring and (3) ≥3 years were classified as potential fathers/mothers only. While animals older than 3 years could be offspring of even older individuals (e.g. 5- or 6-year-old animals), the age classifications in this category become broader (e.g. >4 years, or 3–5 years), making discrete subdivision of these older individuals increasingly uncertain, with few samples per category, which in turn would increase the uncertainty of parent–offspring designations. Thus, we decided on a conservative approach to classify all individuals older than or equal to 3 years as potential parents only, likely leading to an underestimation of number of parent–offspring pairs, but increased confidence in those pairs that were identified. Two samples had unknown ages and were classified as potential fathers/mothers and potential offspring. This resulted in 152 potential offspring, 33 potential fathers and 29 potential mothers.

Relationships were reconstructed in Colony with a medium-length run assuming monogamous mating for both sexes (Mills & Bester, 2005), with no inbreeding and no clones, using the full-likelihood method, a weak sibship prior of 1.0 for both paternal and maternal sibship sizes, sibship scaling, no updating of allele frequencies and accounting for potential genotyping errors as before. To investigate dispersal, full sibs sampled on different farms were identified (using the *.BestFSfamily output file from Colony) and distance between these individuals was measured using the GPS location of where they were culled. Distance was measured between parent–offspring pairs regardless of whether they were sampled on different farms (using the *.ParentPair output file).

Results

Between 1 and 16 jackal samples were collected from 26 farms ranging from 1633 to 6624 ha in size. Females were made up of 47% ($n = 83$) and males 53% ($n = 95$) of the samples. Ages of sampled jackals ranged from approximately 2 weeks to 7 years (<3 weeks: $n = 12$; >3 weeks to 13 weeks: $n = 4$; 14–23 weeks: $n = 54$; >23 weeks−1 year: $n = 42$; 1–4 years: $n = 44$; >4 years: $n = 18$; unknown = 4). The mean distance between jackal samples was 20.145 km (range: 0–49.78 km; SE: 0.136).

A total of 178 of 190 individuals were successfully genotyped at 14 loci with a low level of missing data (one marker in three individuals). The number of alleles ranged from 5 (VGL2009) to 15 (PEZ6), with a mean of 8.7 alleles per locus and a total of 122 different alleles. Linkage disequilibrium, deviations from HWE and null alleles were detected; however, as deviations were most likely due to the presence of highly related individuals, we subsequently performed the analysis following their removal. Here, LD was not found and only one marker (VGL1165) deviated from HWE with evidence of null alleles and was removed from further analysis. The remaining 13 markers showed no evidence for linkage or null alleles.

Genetic variation

Expected heterozygosity was 0.733 and the mean polymorphic information content (PIC) value, used to measure the informativeness of a genetic marker, was 0.698. The combined non-exclusion probability of identity (NE-I; probability that the genotypes at a single locus do not differ between two randomly chosen individuals) was 7.91E-14, while for sib identity (NE-SI) this was 8.68E-06 and for parent pair (NE-PP) it was

4E-08. This indicated the loci had sufficient statistical power to identify individuals and siblings with high confidence and were appropriate for conducting sibship and parentage analysis (Table S2).

Genetic variation per farm: Observed and expected heterozygosity varied from moderate [(H_O = 0.596 (farm: DS), H_E = 0.519 (farm: KW)) to high (H_O = 0.846 (farm: RE), H_E = 0.731 (farm: BB)] (Fig. 1a, Table S3). Allelic richness (A_R) was not significantly different between farms, as indicated by the overlapping 95% confidence intervals (Fig. 1b). The inbreeding coefficient, F_{IS}, for all farms was low (0.054), but significantly greater than 0, as shown by the 95% confidence intervals, indicating a slight deficit of heterozygous genotypes (Fig. 1c). Estimates of F_{IS} varied among farms and, while confidence limits were strongly influenced by sample size, the majority displayed significantly negative F_{IS} values, indicating heterozygosity excess on those farms (Fig. 1c).

Genetic variation per year (full dataset): Genetic diversity did not change significantly year on year (Fig. 2). Observed and expected heterozygosity (Fig. 2a, Table S4) ranged from 0.687 to 0.705 (mean = 0.702) and 0.587 to 0.732 (mean = 0.731) respectively. The A_R values (Fig. 2b) per year were similar (2.88 to 3.892). Estimates of F_{IS} (Fig. 2c) did not change significantly year on year, except from year 1 to year 2, most likely due to the small sample size (n = 4) for year 1. F_{IS} was significantly negative for year 1 (−0.194), indicating an excess of heterozygotes, but was also likely due to the small sample size. The remaining 3 years had positive but low F_{IS} values (year 2 = 0.052, year

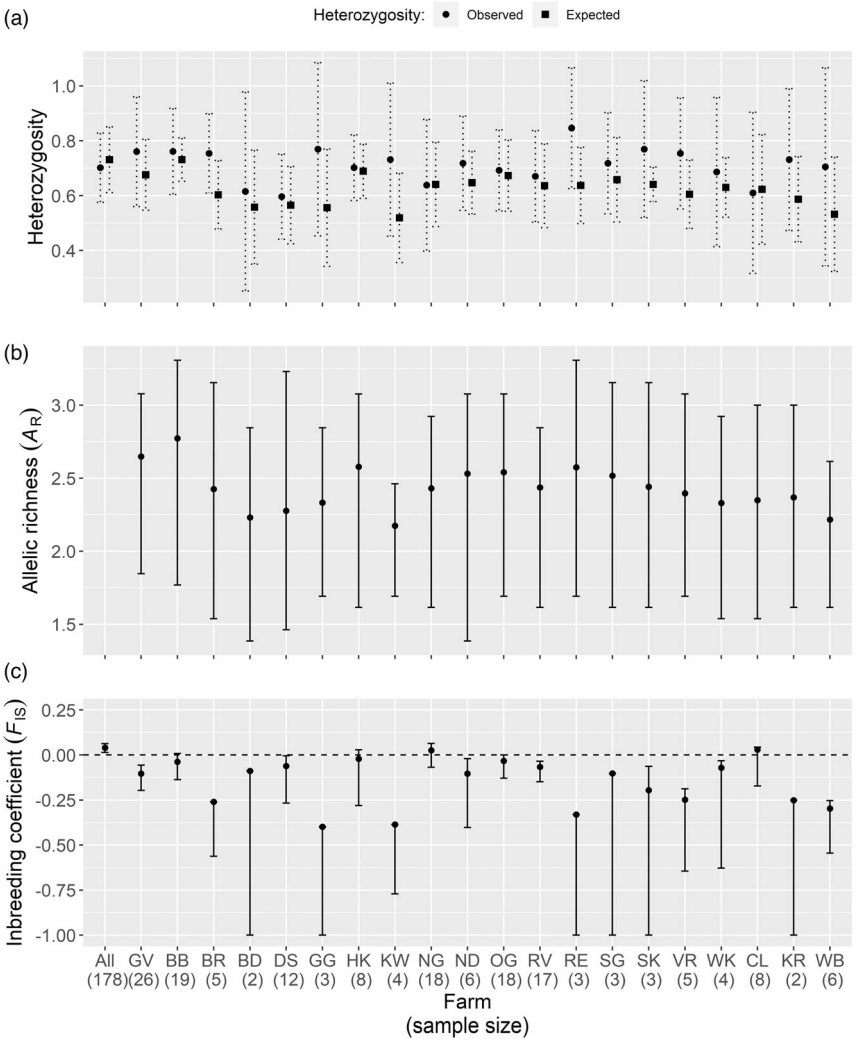

Figure 1 Summary statistics for 20 farms (farm ID is indicated in brackets) with >1 sample and for all farms pooled (see Table S3 for raw data). (a) Observed and expected heterozygosity, with the dotted lines showing the standard deviation across loci, indicative of the spread of the heterozygosity values. (b) Allelic richness, where no data are available for all samples pooled ("All"). Allelic richness is a measure of relative genetic diversity between groups and thus cannot be calculated when there is only one group. (c) Inbreeding coefficient, with the dashed line indicating 0. Solid lines in (b) and (c) show 95% confidence intervals.

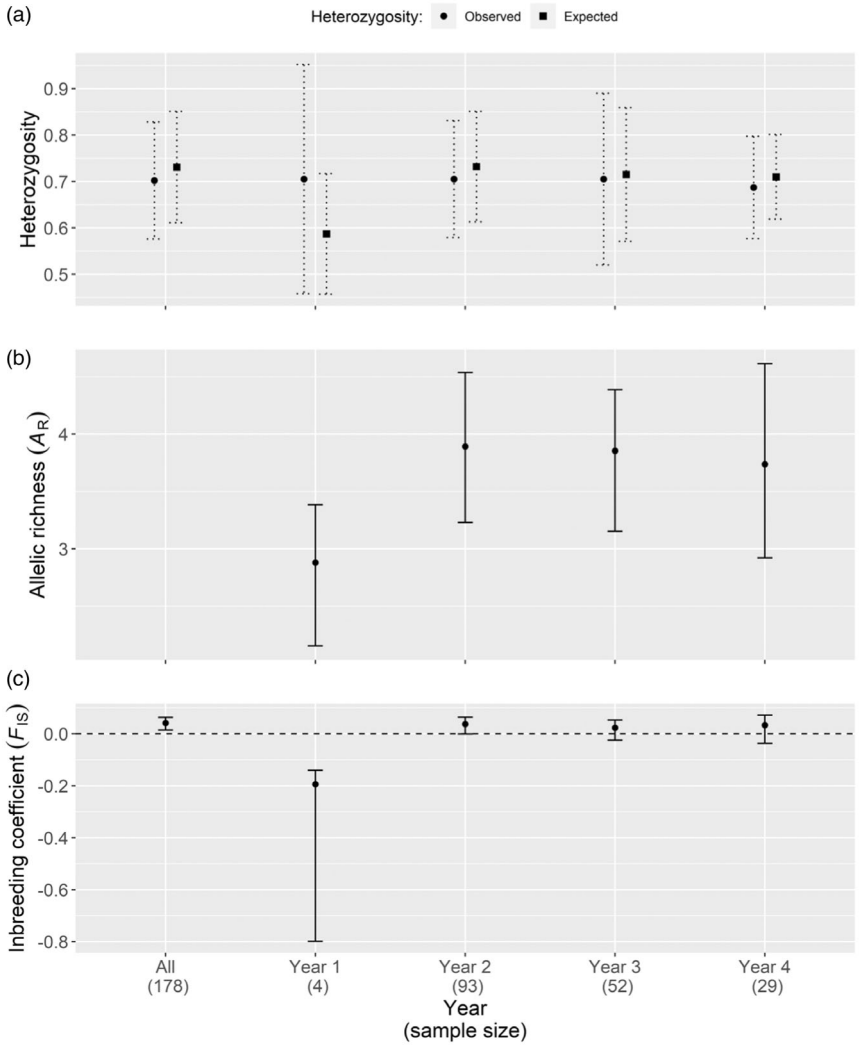

Figure 2 Summary statistics per year and for all years together (see Table S4). (a) Observed and expected heterozygosity, with the dotted lines showing the standard deviation across loci, indicative of the spread of the heterozygosity values. (b) Allelic richness, where no data are available for all samples pooled ("All"). Allelic richness is a measure of relative genetic diversity between groups and thus cannot be calculated when there is only one group. (c) Inbreeding coefficient, with the dashed line indicating 0. Solid lines in (b) and (c) show 95% confidence intervals.

3 = 0.035 and year 4 = 0.045), although only year 2 was significantly greater than 0, indicating a slight deficit of heterozygotes.

Effective population size and generation length

The three methods used to calculate N_e were similar, as indicated by overlapping 95% confidence intervals. The estimated N_e for the sibship assignment method in Colony (alpha = 0) was 46 (95% CI: 29–82) when assuming monogamy and 28 (95% CI: 16–50) when assuming polygamy, while that obtained with the LD method in NeEstimator was 51.6 (parametric 95% CI: 37.8–77.3), with a lowest allele frequency allowed of 0.01. The EPA method in AgeStructure provided a N_e estimate of 47 (95% CI: 36–66). AgeStructure estimated the generation length (L) to be 2.72 years (95% CI: 2.50–3.18), with females (2.25 years [95% CI: 2.06–2.98]) having a shorter generation length than males (3.19 years [95% CI: 2.60–3.66]).

Genetic structure

STRUCTURE analysis using the entire dataset suggested $K = 9$ according to the Delta K method and log probabilities of K values (Fig. S1). Inspection of the clusters indicated that they consisted of closely related individuals. Therefore, STRUCTURE analysis was conducted excluding related individuals and results suggested $K = 14$, but with very low Delta K values, while the log probability plot indicated $K = 1$ was the most likely (Fig. S2). Assignment plots showed no distinct genetic clusters and we thus interpreted $K = 1$ as the most

likely structuring scheme. The PCA identified that farms formed a single, largely overlapping cluster (Fig. 3) with two farms (DS and KD) being marginally separated. An absence of genetic structure was further observed in the PCA when related individuals were excluded (Fig. S3).

An F_{ST} value greater than 0.15 indicates significant population differentiation (Frankham et al., 2002). Here, a statistically significant but low F_{ST} value (0.077, $P < 0.001$) was obtained using AMOVA, indicating low overall genetic differentiation between farms. Furthermore, high genetic variation was identified within individuals (97.06%) and low genetic differentiation was observed among individuals within farms (−1.74%) and among farms (7.68%). Using the full dataset, pairwise F_{ST} values between farms were low to moderate, with 98 of 325 comparisons being significant at a level of 0.05 (Table S5). Two farms, KD and KW, showed high F_{ST} values, however, these results appear to be driven by KD's small sample size ($n = 1$), and small sample size and high relatedness for KW ($n = 4$, mean relatedness = 0.55). When the analysis was repeated with close relatives removed, only two pairwise comparisons were significant, RV-GV ($F_{ST} = 0.028$) and RV-BB ($F_{ST} = 0.039$), and these F_{ST} values were low (Table S6). In general, when relatives were removed from the dataset, F_{ST} values were lower (Tables S5 and S6).

Relatedness and individual inbreeding

Due to an absence of genetic structure at a broad population-level scale, we investigated whether genetic structure exists at finer scales, using relatedness and spatial autocorrelation analyses. All six different relatedness estimators correlated significantly with the simulated values (*P*-values <2.2E-16), with Spearman's *rho* correlation coefficients as follows: DyadML = 0.794, Lynch-Li = 0.792, Lynch and Ritland = 0.770, Queller and Goodnight = 0.791, TrioML = 0.794 and Wang = 0.805 (Fig. S4). Given these similar results, the TrioML estimator was used to estimate pairwise relatedness as it provides relatedness estimates between 0 and 1, thus facilitating interpretation.

Spatial analyses

Relatedness (r) and individual inbreeding (F) were relatively low for the whole dataset (mean $r = 0.085$, $F = 0.089$, Fig. 4). However, relatedness was significantly higher within (mean $r = 0.189$) compared to between (mean $r = 0.077$) farms (*P*-value < 2.2e-16, Fig. 5). Spatial autocorrelation analysis indicated a significant positive correlation of genetic and geographic distance in distance classes of ≤2 km, but not in >2 km distance classes, indicating that individuals in distance classes of ≤2 km were genetically more similar than expected by chance (Fig. 6). There were some instances of significant negative correlation of genetic and geographic distance at larger distance classes, indicating that individuals were genetically less similar than expected by chance (Fig. 6). However, low sample sizes in these larger distance classes are likely the cause of this signal.

We found no evidence of sex-biased dispersal. Relatedness was not significantly different within females compared to within males (Wilcoxon test, *P*-value = 0.51). The spatial autocorrelation analyses for each sex also mirrored those of the whole dataset, with no clear differences between sexes (Fig. S5).

There were no significant differences in F (inbreeding) between years (Table S7). While mean r (relatedness) appears to have been higher in year 1 compared to year 2 (Wilcoxon test, *P*-value = 0.040) and year 3 (Wilcoxon test, *P*-value = 0.048), the low sample size from year 1 ($n = 4$) limited the power of these comparisons.

Dispersal

Colony identified 28 full-sib groups with a probability of inclusion >0.95, comprising 97 full-sib dyads. Of these 97 dyads, there were 18 occurrences where an individual was sampled on a different farm to its full sibling/s, indicating potential dispersal events (Fig. 7). The mean distance between full sibs on different farms was 16.00 km (range: 0.78–42.93 km; Fig. 7). Most distances (13 of 18) fall within the range of 5–135 km reported by Ferguson et al. (1983) for dispersing individuals. If only distances of >5 km represent true dispersal events, the mean dispersal distance of full siblings was 19.2 km (range: 5.1–42.93). Of the 13 dispersal events ≥5 km, 11 involved jackals of at least 1 year old, likely indicating true dispersal events.

Colony assigned parent pairs with >0.95 probability to 149 of the 152 individuals classified as offspring. Of these, 54 (35.5%) had at least one parent in the dataset (i.e. parent was sampled), while 98 (64.5%) had parents assigned that were not in the dataset (i.e. parent was not sampled). Of the 54 offspring with at least one parent in the dataset, there were nine instances with no GPS coordinates. Thus, we were able to determine a mean distance of 2.96 km (range: 0–36.49 km) for 45 parent–offspring pairs. In these cases (10 of 45), where distances were ≥5 km (based on Ferguson et al., 1983), the mean distance between parent and offspring was 10.34 km (range: 5.37–36.49), half of that between full siblings.

Discussion

We investigated genetic diversity, relatedness and inbreeding of lethally managed jackals on private small-livestock farms in the central Karoo region. We provide genetic estimates of important life history traits: effective population size (N_e), generation length and identify individuals that likely dispersed from their natal site. We found that genetic diversity was high overall and varied from moderate to high per farm. Our genetic diversity estimates (mean $H_0 = 0.70$) are similar to previously published studies on jackals: Minnie (2016) reported that H_0 of jackals in the Eastern and Western Cape province of South Africa varied from 0.59 to 0.69, while Tensen et al. (2018) reported a mean H_0 of 0.73 ($n = 82$) in jackals from the Western Cape province. In our study, genetic diversity on farms has been maintained over a 4-year period which

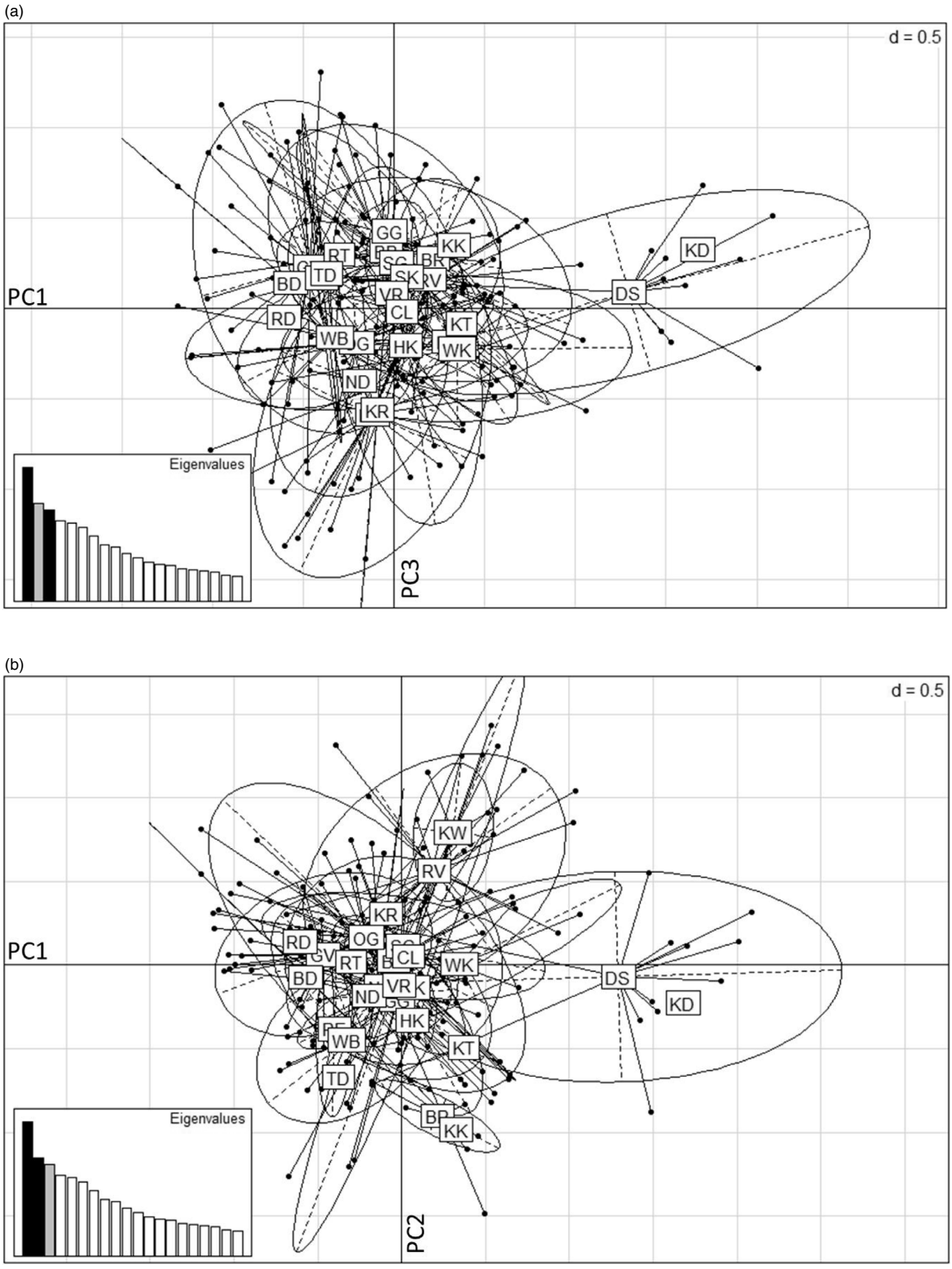

Figure 3 Principal component analysis (PCA) of the different jackal sampling locations (farms) indicating (a) PCA1 and 3 and (b) PCA1 and 2.

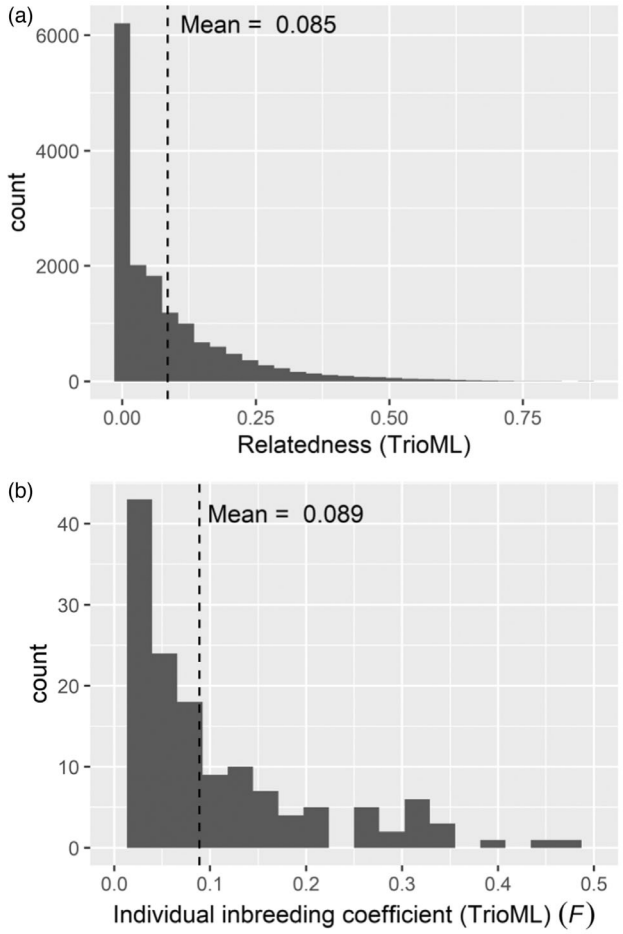

Figure 4 Distribution of (a) relatedness and (b) individual inbreeding coefficients of jackal across all sampling localities (farms).

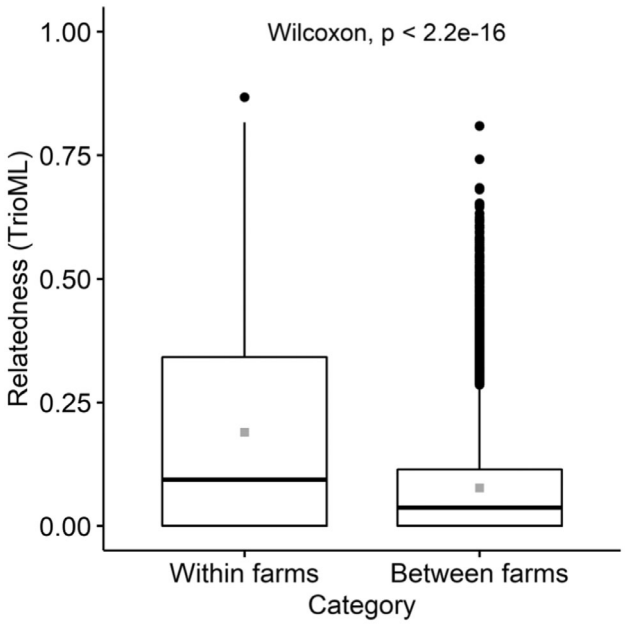

Figure 5 Boxplots showing the distribution of relatedness within and between farms. The lower and upper hinges of the box indicate the interquartile range (IQR), with the median shown by the horizontal line in each box. The whiskers show the values at 1.5 x IQR, while outliers are shown by points. The grey squares show the mean. The text inset shows the result (*P*-value) of the two-sample Wilcoxon test for a difference in means.

is unsurprising considering the mean generation length was 2.72 years. The study period is therefore likely not long enough to detect significant changes in genetic diversity, as it only represents 1.47 jackal generations. Thus, further analysis over a longer period to monitor changes in diversity is suggested.

In support of our hypothesis, young jackals were within their natal ranges and in close proximity to siblings and other family members when culled, explaining why relatedness was significantly higher within farms than between farms, a finding supported by spatial autocorrelation analysis. These fine-scale patterns are likely indicative of family groups sampled on farms, suggesting that while no population-level structuring was observed, family-level structure is present. This is also likely the cause of the significant but low F_{ST} values.

A significantly positive but low F_{IS} value (0.054) observed for the entire dataset indicated a slight heterozygote deficit. However, given the low overall relatedness (r = 0.085) and individual inbreeding levels (mean F = 0.089), the significantly positive F_{IS} value is likely not due to biologically significant inbreeding. Our results are similar to Tensen et al. (2018): F_{IS} = 0.085; r = 0.081. A slight heterozygote deficit has been reported in coyote populations that have undergone intensive removal for several decades (Williams et al., 2003). Thus, while mating is monogamous, jackals may be employing inbreeding avoidance strategies such as kin recognition to maintain genetic diversity. Although F_{IS} was significantly negative on several farms, this is likely a statistical artefact, as most farms had sample sizes of <10. Farms where sample sizes were > 10 and F_{IS} was negative (e.g., GV, NG, RV) may be an indication of an excess of heterozygotes (Wright, 1965). This may be due to an influx of unrelated dispersers due to spaces being created after culling, which are then occupied by immigrants via compensatory migration (Minnie, Avenant, et al., 2016).

Our findings may be explained by several factors. Firstly, very young jackal of the same litter are most likely found together inside a den (<3 weeks), in relative close proximity to each other and a den (3–14 weeks) or out foraging with parents (>14 weeks until dispersal; Moehlman, 1979b). Therefore, it is not unexpected that multiple jackals killed on the same farm were often found to be closely related. Secondly, under natural/stable conditions, two-thirds of pups will disperse from their natal site by about 1 year of age (Ferguson et al., 1983; Moehlman, 1979b). However, in areas with regular high food resources, such as in this study, territorial mating pairs tolerate other jackals (Hiscocks & Perrin, 1988; Jenner et al., 2011), thereby delaying density-regulated dispersal and increasing

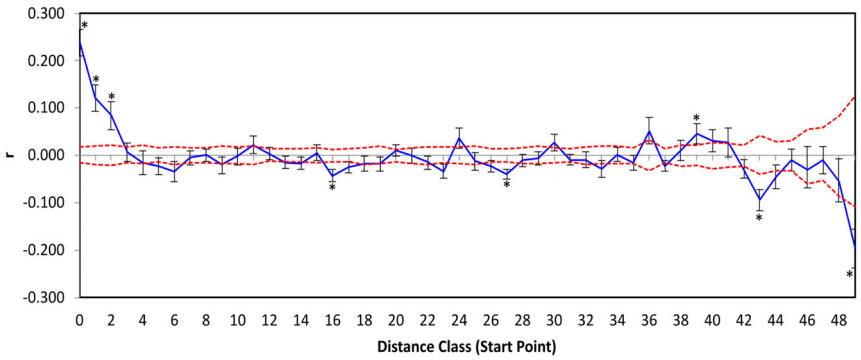

Figure 6 Results of the spatial autocorrelation analysis for the whole dataset. The blue line indicates the autocorrelation coefficient of the data, with the 95% confidence interval at each distance class indicated by the black error bars (determined by 1000 bootstrap resampling replicates). The red dashed lines indicate the 95% confidence interval around the null hypothesis (no spatial structure, i.e. $r_{auto} = 0$), as determined by permutation (999 steps). Thus, if the error bars around the blue line do not overlap with the red dashed lines in a distance class, then genotypes were more (positive r_{auto}) or less (negative r_{auto}) similar than expected under the null hypothesis in that distance class. Such cases are indicated with an asterisk (*).

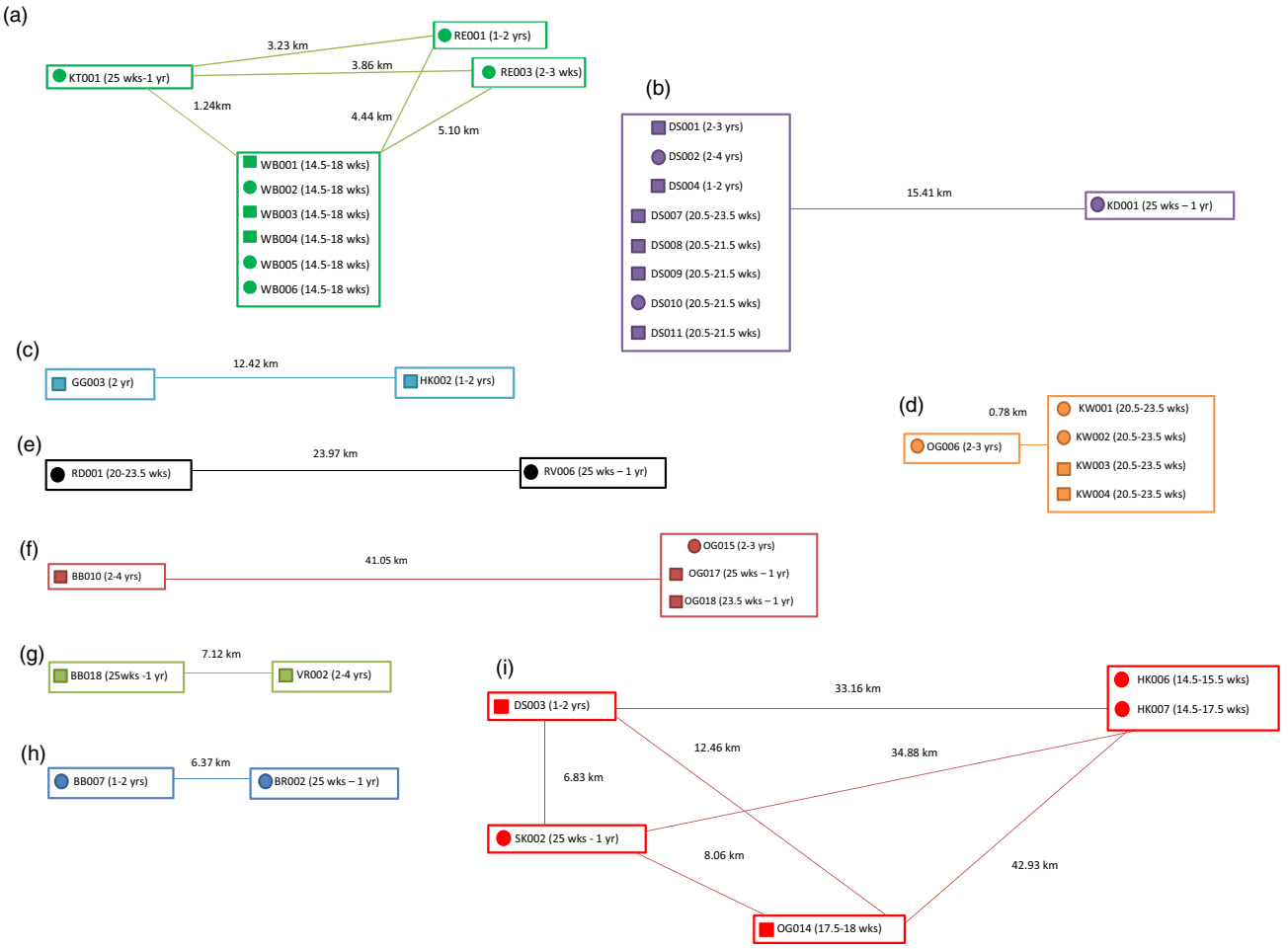

Figure 7 Diagrammatical representation of 18 occurrences ([a–i] represents sibling groups) where related siblings were detected on different farms. Distance between related individuals is shown above the line. Squares represent males and circles females. Estimated age of individuals is provided in brackets.

jackal density and relatedness. However, if unrelated jackals are also tolerated within territories, relatedness between individuals may be decreased. Thirdly, the expectation under intensive lethal control would be that natural social patterns break down and spatial vacancies are created. Relatedness would be randomly distributed across the study area and individuals found close together would not be any more likely to be related than those found further apart. The motivation for this being that intense culling on a farm would result in a sink (Delibes et al., 2001), which will be filled by unrelated jackals immigrating from neighbouring areas, resulting in low relatedness on farms and no correlation of genetic and geographic distance, particularly on a relatively small scale such as this study area (92 918 ha). The results presented here do not support this scenario, but rather of a distribution of relatedness expected in a more natural system with regular high resource availability. Thus, as jackals have access to both high food resource (livestock) and are intensively managed, a combination of responses are present in the study population.

Our study is consistent with Tensen et al. (2018) that lethal management thus far does not have a negative effect on genetic diversity of jackals in the study area. Genetic diversity may be maintained through compensatory migration within and from outside the study area, as it is not a closed system, whereas social/family structure may be maintained by compensatory reproduction (Minnie, Gaylard et al., 2016). Similar suggestions are reported for lethally managed coyote (Kierepka et al., 2017), red fox, (Cavallini & Santini, 1996; Marlow et al., 2016), wolverine, *Gulo gulo* (Gervasi et al., 2015) and cougar, *Pumo concolor* (Robinson et al., 2008). Furthermore, lower genetic diversity has been found in unhunted populations when compared to hunted populations of red foxes in Europe (Fratti et al., 2000) and grey-winged francolin (*Scleroptila africanus*) in South Africa (Little et al., 1993), further supporting compensatory immigration as an adaptive mechanism in lethally controlled populations.

Subpopulation differentiation was not observed here, which suggests gene flow between farms (92 918 ha). The pairwise F_{ST} and STRUCTURE results indicated that differentiation identified between farms was driven by family structure (close relatives sampled on the same farm). This was supported by the spatial autocorrelation results, and the relatedness within and between farms. Additionally, the PCA showed no distinct clusters. Thus, we can conclude that genetic subdivision in this population occurs only at the family level, which is what is expected in a free-roaming population of jackal. Therefore, neither culling, fences, nor landscape features are hindering gene flow. Although previous studies (Minnie, 2016; Minnie, Zalewski, et al., 2018; Tensen et al., 2018) reported genetic structure in jackal, the study areas were larger and subdivision was weak, with admixture in the intervening areas due to dispersal and/or immigration.

Genetic diversity and adaptability to future environmental change can be affected by breeding population size, proportion of males/females breeding, generation length and adult longevity (Martinez et al., 2002; Ryman et al., 1981). Culling of jackals has the potential of altering characteristics of the breeding population which in turn can reduce N_e and generation length. Our estimation of N_e was 46–51.6 (monogamy assumed) or 29–51.6 (polygamy assumed), which is substantially lower than the target of 500 suggested to maintain evolutionary potential of a population (Hoban et al., 2020). However, jackals from our study likely form part of a population occupying a larger area with a high rate of migration in and out of the study area. Therefore, the N_e estimated here may be an underestimate, and likely reflects the effective number of breeders. The mean generation length was 2.72 years, which is lower than the estimated 5 years suggested by Pacifici et al. (2013). However, without estimates of generation length from unmanaged jackal populations, the shorter generation length observed here may be due to various external forces (i.e. culling). Nonetheless, for the first time, we provide a direct genetic estimate of this important, and notoriously difficult to estimate, life-history trait for this species.

Finally, we used full-sib and parent–offspring assignments to identify individuals that had likely dispersed from their natal site (or away from their siblings) and directly measured their dispersal distance. This is, to the best of our knowledge, the first instance where dispersal distances of individual black-backed jackal were measured using genetic techniques. We identified full siblings that were sampled on different farms as potential cases of dispersal and found 18 such occurrences (Fig. 7). The 11 instances of full sibs at least 1 year old and sampled >5 km from each other represent true dispersal events, i.e. individuals that did not stay with their parents as helpers but left to establish their own territory. Dispersal distances were all within the dispersal range 5–135 km identified by Ferguson et al. (1983), with the mean (19.2 km) being at the lower end of this range, possibly due to high abundance of food sources.

The observation that the dispersal distance of parent–offspring pairs was half of that of full siblings suggests that full siblings are possibly more likely to disperse further distances from each other than from parents, perhaps in different directions from the natal range. In all except one case (discussed below), dispersed offspring were older than 6 months and the parent was at least 1 year older than the offspring, indicating that these were likely true dispersal events. In six cases, offspring older than 1 year of age were killed less than 4 km (range: 0–3.8) from a parent, suggesting that these individuals had remained as helpers or were tolerated within the parent's territories. However, as many intrinsic and extrinsic factors influence range sizes, this should be further investigated as currently there is no information on territory/home range size of jackals in this population. In one case, three offspring were 2–3 weeks old, and their inferred parent (mother) was sampled 5.79 km away. It is most likely that the mother was foraging away from the den at the time that she was culled as jackal pups remain within the den until about 3 weeks of age.

Our study confirms that despite decades of lethal management of jackals in the central Karoo, genetic diversity may not have been detrimentally affected, with gene flow occurring between farms. Lethal control-induced increase in gene flow is likely to be one explanation as to why lethal management alone is considered to be counter-productive (Bergman et al., 2013; Eklund et al., 2017; Minnie, Zalewski,

et al., 2018) and why there is often an increase in loss of livestock in subsequent years (Nattrass et al., 2019). This study supports the idea that compensatory immigration and associated genetic robustness are most likely at least partially responsible for the ineffectiveness of ongoing lethal management in the region. Here, we show the value and power of genetic data from a time series of sexed and aged individuals (rare in population genetics studies) to explore population dynamics and estimate ecologically important life-history traits. Limitations include insufficient information on overall population size, genetic samples and age-sex information of individuals not culled or a control population (jackals not lethally managed). This information could be used to investigate impacts on the greater population in terms of immigration/dispersal, relatedness and N_e in response to ongoing lethal management. We made the assumption that culled individuals represent the population, but it is probable that rates of lethal management differ between farms, and that jackal behaviour affects the likelihood of an individual being culled. Nonetheless, we believe that sampling across 26 farms, and our relatively large sample sizes across multiple years, adequately reduced these potential biases.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods.

Table S1. Primer details for microsatellite loci used to genotype black-backed jackals (*Canis Mesomelas*).

Table S2. Per-locus summary statistics as calculated in Cervus v3.0.7. The non-exclusion probabilities and combined non-exclusion probabilities (final row, italics) are relevant indicators of the power of the loci for parentage and sibship analyses.

Table S3. Summary statistics for 20 sampling localities (farms) with >1 sample and for all farms pooled. Produced using the basicStats command of the diveRsity package v1.9.90 in R v3.6.2 and RStudio v1.2.5033. Standard deviation was calculated across loci in Microsoft Excel (stdev.s). Sampling localities with only one sample are not shown.

Table S4. Summary statistics per year and for all years pooled. Produced using the basicStats command of the diveRsity package v1.9.90 in R v3.6.2 and RStudio v1.2.5033. Standard deviation was calculated across loci in Microsoft Excel (STDEV.S).

Table S5. Pairwise F_{ST} values between farms with the full dataset (below diagonal) and associated significance at a level of 0.05 (above diagonal), where significant values are indicated by a "+" and non-significant values by a "−". Calculated in Arlequin 3.5.2.2.

Table S6. Pairwise F_{ST} values between farms with relatives removed (below diagonal) and associated significance at a level of 0.05 (above diagonal), where significant values are indicated by a "+" and non-significant values by a "−". Calculated in Arlequin 3.5.2.2.

Table S7. Comparison of mean pairwise relatedness (r) between years and mean individual inbreeding coefficients (F)

between years. *P*-values for the Wilcoxon tests for difference in means are shown on the inside of the table (bordered by grey), with *P*-values for inbreeding comparisons shown below the diagonal (bottom left) and *P*-values for relatedness comparisons shown above the diagonal (top right). The mean *F* for each year is shown in the left-most column "outside" the main table, with the mean *r* for each year shown in the top row "outside" the main table. The numbers in parentheses after each year are the number of observations/data points for that year (number of samples for *F* and number of pairwise relatedness comparisons for *r*).

Figure S1. STRUCTURE HARVESTER results for (a) Delta *K* values and (b) probability (-LnPr) of *K* = 1–27 averaged over 20 runs and (c) genetic differentiation between the jackal sample locations (farms) based on STRUCTURE analysis (performed with *K* = 2–6) of 1 = GV, 2 = BB, 3 = BR, 4 = BD, 5 = DS, 6 = GG, 7 = HK, 8 = KD, 9 = KW, 10 = KK, 11 = KT, 12 = NG, 13 = ND, 14 = OG, 15 = RV, 16 = RE, 17 = RT, 18 = RD, 19 = SG, 20 = SK, 21 = VR, 22 = WK, 23 = CL, 24 = KR, 25 = WB and 26 = TD.

Figure S2. STRUCTURE HARVESTER results for (a) Delta *K* values and (b) probability (-LnPr) of *K* = 1–27 averaged over 20 runs and (c) genetic differentiation between the jackal sample locations (farms) based on STRUCTURE analysis (performed with *K* = 2–6 and *K* = 14) of 1 = GV, 2 = BB, 3 = BD, 4 = DS, 5 = GG, 6 = HK, 7 = KW, 8 = KT, 9 = NG, 10 = ND, 11 = OG, 12 = RV, 13 = RE, 14 = RD, 15 = SG, 16 = SK, 17 = VR, 18 = WK and 19 = CL. After removing relatives, some localities had no samples, hence fewer sampling localities as compared to the full dataset. Note: The Evanno method (DeltaK) does not evaluate *K* = 1.

Figure S3. Principal component analysis (PCA) of the different jackal sampling locations (farms) with related individuals removed.

Figure S4. Plot comparing the relatedness estimates using six estimators and simulated individuals of known relatedness. Di, Dyadic likelihood estimator "DyadML"; LL, Lynch-Li estimator; LR, Lynch and Ritland estimator; QG, Queller and Goodnight estimator; Tri, Triadic likelihood estimator "TrioML"; W, Wang estimator. Plot produced with ggplot2 3.3.0 (Wickham, 2016).

Figure S5. Results of the spatial autocorrelation analysis for **A** females and **B** males. The blue line indicates the autocorrelation coefficient of the data, with the 95% confidence interval at each distance class indicated by the black error bars, as determined by 1000 bootstrap resampling replicates. The red dashed lines indicate the 95% confidence interval around the null hypothesis (no spatial structure, i.e. $r_{auto} = 0$), as determined by permutation (999 steps). Thus, if the error bars around the blue line do not overlap with the red dashed lines in a distance class, then genotypes were more (positive r_{auto}) or less (negative r_{auto}) similar than expected under the null hypothesis in that distance class. Such cases are indicated with an asterisk (*).