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REVIEW

Food availability and population structure: How do clumped and abundant sources of carrion affect the genetic diversity of the black-backed jackal?

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Abstract

Carnivores frequently come into conflict with humans in agricultural and livestock-producing areas around the world. Understanding their fidelity and dispersal patterns in response to food availability is therefore important given the effort invested in conflict mitigation strategies. In this study, we investigated the influence of clumped and abundant sources of carrion on the genetic diversity of the black-backed jackal *Canis mesomelas* within six private game farms in the North-West and Gauteng provinces of South Africa. It is predicted that clumped and abundant sources of carrion will increase immigration and thus genetic diversity in the local subpopulation. By quantifying the variability in microsatellite loci in black-backed jackals subjected to artificially increased carrion availability, and comparing them with individuals from control sites, we were able to describe patterns of historic gene flow within the total sampled population. The results of this investigation indicate that clumped and abundant sources of carrion promote genetic structuring (F_{ST} = 0.0302) which implies a lack of gene flow and a degree of isolation. Genetic artefacts of three populations could be identified through Bayesian clustering analysis of individuals based on their genetic identity. Individuals sampled from the two supplementary feeding sites could be assigned to one of two ancestral populations with an average population assignment of 69 and 82%, while individuals from the remaining four control sites, originate from a third population with percentage assignments of 63%, 46%, 53% and 42%. It is therefore likely that clumped and abundant sources of carrion in the agricultural landscape of South Africa can affect the population dynamics of the black-backed jackal and result in subpopulations with limited migration and dispersal when compared with the total population.

Introduction

It is generally recognized that carnivores play a fundamental role in the structure and function of an ecosystem (Ripple & Beschta, 2004; Ripple *et al.*, 2014). However, factors such as disease transmission and livestock depredation frequently promote conflict in areas where humans and carnivores exist in close proximity (Woodroffe, Thirgood & Rabinowitz, 2005). Understanding the ecological factors that drive the spatial organization of free-ranging carnivores is therefore important when considering both conservation and management of species in the human-modified landscape. Thus, this study follows a microsatellite-based approach to investigate the short-term historic effects of 4 years of supplementary feeding on the genetic diversity of black-backed jackals *Canis mesomelas* at private game farms in South Africa.

Following the expectations of the resource dispersion hypothesis (Macdonald, 1983), an increase in localized food availability will often result in a breakdown in territorial stability and subsequently lead to an increase in local density (Johnson *et al.*, 2001, 2002). Indeed, anthropogenically derived sources of food, synonymous with agricultural and human-modified landscapes, have been shown to strongly influence the spatial organization of many omnivorous canids including the golden jackal *Canis aureus* (Rotem *et al.*, 2011), red fox *Vulpes vulpes* (Contesse *et al.*, 2004), coyote *Canis latrans* (Fedriani, Fuller & Sauvajot, 2001) and dingo *Canis lupus dingo* (Newsome *et al.*, 2013). Furthermore, studies in both Namibia and South Africa have recorded the black-backed jackal at far greater abundances than expected in areas where scavenging opportunities are high and carrion availability is clumped, stable and abundant (Hiscocks & Perrin, 1988;

Jenner, Goombridge & Funk, 2001; Yarnell *et al.*, 2014). Studies using both radio-telemetry and behavioural observations in the Cape Cross Seal Reserve (CCSR) have also concluded that territorial boundaries of the black-backed jackal often overlap in close proximity to clumped, abundant resources such as seal colonies (Hiscocks & Perrin, 1988), and that home range sizes significantly increase with distance from the colony itself (Jenner *et al.*, 2001). As the social structure of the black-backed jackal is commonly reported to consist of a monogamous breeding pair, which holds and aggressively defends territory from transient individuals and neighbouring residents (Ferguson, Nel & De Wet, 1983; Estes, 1991), it is clear that an increase in local abundance of food can dramatically affect both the territorial behaviour and spatial organization of this species. However, what remains unclear from contemporary observations is the effect that increased food availability has on the fidelity and dispersal of such subpopulations over time. Therefore, by examining the genetic diversity of black-backed jackals in the game farms of South Africa, this study aims to elucidate the genetic consequences of clumped and abundant sources of food on the dispersal of a free-ranging canid within a human-modified landscape.

The black-backed jackal is a medium-sized canid (5–15 kg) with two discrete distributions that span the majority of the Southern African subregion, and parts of Eastern Africa (Estes, 1991; Skinner & Chimimba, 2005). This study focuses on the southern African subspecies *C. m. mesomelas*, henceforth "black-backed jackal", due to the high rate of human–carnivore conflict associated with this region (Thorn *et al.*, 2012). As a vector of rabies and canine distemper (Zulu, Sabeta & Nel, 2009; Bellan *et al.*, 2012), and an opportunistic hunter of small game and livestock (Estes, 1991), the black-backed jackal is frequently controlled as a pest species throughout its range (Ginsberg & Macdonald, 2004; Thorn *et al.*, 2012). With an omnivorous diet consisting of small mammals, livestock, forage and carrion (Klare *et al.*, 2010), this species is considered a generalist carnivore that is able to undertake diet switching in response to changes in local food availability (Rowe-Rowe, 1983; Van der Merwe *et al.*, 2009; Kamler, Klare & Macdonald, 2012; Fourie *et al.*, 2015; Humphries, Ramesh & Downs, 2016). Therefore, to further investigate the effect of food availability on the population dynamics of the black-backed jackal, this study used carrion stations, known as vulture restaurants, to measure the historic effect of artificially increasing scavenging material on the gene flow and variation in genetic diversity within and between local subpopulations. Vulture restaurants were originally introduced in participating game farms and nature reserves across South Africa with an aim to supply declining vulture species with a safe and consistent source of carrion which originates from hunted or slaughtered livestock destined for the human food chain. Subsequent analysis has shown that the regular deposition of carcasses at these sites has resulted in an unintentional increase in the local abundance of many scavenging carnivores, including the black-backed jackal (Yarnell *et al.*, 2014). As the abundance of black-backed jackals residing in close proximity to vulture feeding sites are often far in excess of those in the surrounding area (James, pers. obs.), it is predicted that clumped and abundant sources of carrion will have resulted in an increase in genetic diversity within local subpopulations as it is hypothesized that increased food availability increases migration.

Materials and methods

Sampling and study sites

This study was undertaken in the North-West and Gauteng provinces of South Africa. Individual black-backed jackals ($n = 65$) were sampled for genetic material from six game breeding farms (Fig. 1) between March 2011 and September 2012 for an analysis of population structure. Two game farms, Site VR1 and Site VR2, had active vulture restaurants initiated approximately 4 years prior to sampling ($n = 27$ and 19 jackal DNA samples, respectively). The remaining four game farms, Site C1, C2, C3 and C4, acted as control sites with no additional scavenging material provided ($n = 6$, 6, 3 and 4). Carrion, consisting of recently deceased ungulates, was placed at each vulture restaurant on a regular basis with an average of 797 kg a month being recorded between 2008 and 2011 at site VR1 (Yarnell *et al.*, 2013). A non-invasive genetic recovery protocol was used to acquire genetic material from 63 recently deposited faecal samples along with two tissue biopsies opportunistically collected from the ear lobe of deceased individuals. The non-invasive genetic recovery protocol used in this investigation was specifically designed for use with this species and had previously been tested for adequate recovery of host DNA prior to undertaking analysis (James *et al.*, 2015). Tissue samples were placed in 1.5 mL of absolute ethanol (EtOH) after collection and stored at −20°C prior to transport to the UK for further analysis.

To sample faecal deposits for genetic source material, driven transects of 5 km were undertaken along the road networks within each site. Transect routes were chosen to maximize an even coverage of area and habitat types. Transect width was standardized at 2 m from the edge of the road to minimize the variation in detection probability. All transects were undertaken by two experienced observers and were driven at a speed maintained between 5 and 10 km h^{-1} to maintain sampling effort. Sampling effort was maintained between sites at 1.4 km of transect driven per 1 km^2 of reserve area. Upon discovery of fresh faecal material, the outer-most layers of the faecal sample were collected using a sterile razor blade and stored in a biologically inert buffer (Roche diagnostics S.T.A.R. buffer cat no: 03335208001). Samples were then stored at −20°C prior to DNA extraction and purification. Scat identification was aided with field guides and expert advice where necessary, and the spatial location of each faecal sample was recorded using a Garmin GPSmap 62 (Fig. S1A–F and Table S1).

Microsatellite loci

Previous research has successfully used domestic dog *Canis lupus familiaris* microsatellite markers to describe the genetic structure and dispersal of jackal populations (e.g. Jenner, 2008; Minnie, 2016). However, the markers used for this study were specifically characterized for the black-backed jackal (Table 1;

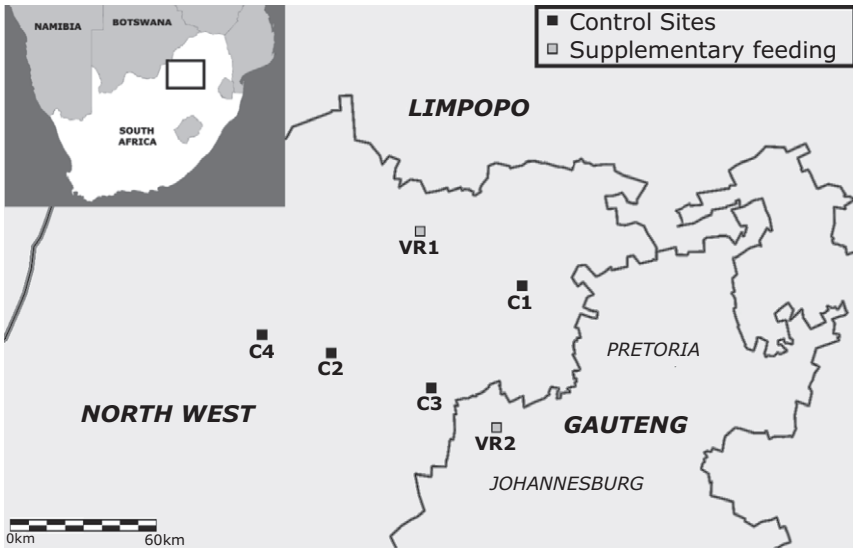

Figure 1 A map depicting the six study sites and the three subpopulations of black-backed jackals sampled in this investigation. Subpopulations are denoted by black circles.

Table 1 Microsatellite loci, 5′ modification, forward (F) and reverse (R) primer sequences (5′–3′), Tm and NCBI accession numbers (AN)

Locus	5′ mod	F primer	Tm °C	R primer	Tm °C	AN
cme144	FAM	aactttaagccacacttctgca	57.9	acttgcctctggcttttaagc	58.4	KU050829
cme136	FAM	aactggccaaacataaacacg	58.5	ttcattaacccttttgccctg	58.5	KU050830
cme206	HEX	cgagagcaacataggcatga	58.4	caaagtgctgtggcaggtc	58.8	KU050831
cme196	HEX	aggaggacagaaagacagaagg	57.5	atggatgtattgtgagggtgg	58.0	KU050832
cme193	FAM	gagctcctgatggaagagctta	58.6	catcctgtccgtgacttcaa	58.0	KU050833
cme210	HEX	cttgtgcaatcatcatcttga	57.2	cccgaggtacctatggct	57.5	KU050834

James *et al.*, 2015) and examined for selective neutrality before estimates of population structure were undertaken. Furthermore, the predictive power, resolution and allelic drop-out rate and null allele estimates were evaluated for this marker set and were shown to be suitable for use in this analysis. These markers were used to estimate the population structure and inbreeding coefficients of the black-backed jackal. Individual multi-locus genotype profiles that matched were considered to derive from the same source and were hence removed prior to the analysis. Results were pooled by site for an analysis of population structure.

Sample processing and PCR conditions

Approximately 25 mg of black-backed jackal tissue, fixed in absolute EtOH, underwent DNA extraction using the Qiagen DNeasy blood and Tissue Kit (cat No: 69504; Valencia, CA, USA), following the manufacturer-based spin column tissue extraction protocol. Dermal and epidermal cells were isolated manually from cartilaginous tissue before proteinase *K* digestion at 56°C. DNA was then eluted using 150 μL of manufacturer-supplied PCR-compatible buffer.

A chloroform extraction protocol was used in conjunction with a Qiagen DNeasy spin column method to isolate and purify DNA templates from faecal samples collected in the field. Faecal samples stored in S.T.A.R. buffer were defrosted in batches at 4°C prior to DNA extraction. Individual samples were homogenized by shaking, then 10 mL of sample was transferred to a sterile collection tube. One millilitre of $\geq$ 99.8% chloroform-EtOH (GC) was then mixed with the sample solution and vortexed to form an emulsion. Emulsified samples then underwent centrifugation at $1000\times\boldsymbol{g}$ for 3 min and the subsequent supernatant was removed for further processing. A Qiagen blood and tissue extraction protocol was followed to recover DNA from the supernatant. Spin columns were centrifuged at $1400\times\boldsymbol{g}$ for 3 min prior to elution, to remove excess EtOH and chloroform from the silica membrane, and were stood to dry at room temperature for 5 min. DNA elution was undertaken using 75 μL of warmed elution buffer at 54°C (James *et al.*, 2015).

PCR reactions were undertaken in 25 μL volumes containing approximately 40 ng of DNA template, estimated in triplicate using a nanodrop 2000 spectrophotometer, 1× Invitrogen PCR buffer, 1.5-mM $MgCl_2$, 1 unit of Invitrogen hot start PlatinumTaq DNA polymerase (cat No: 10966–018; Invitrogen, Carlsbad, CA, USA), 1 unit of Qiagen Q-solution, 0.5 μL ng^{-1} BSA, 0.2 mM dNTP mix and 0.2 μM primer mix. Amplification conditions used on a Techne TC-4000

thermal cycler consisted of an initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C for 1 min, 55°C for 45 sec and 72°C for 1 min finishing with a final extension stage of 72°C for 5 min.

Statistical analysis

The probability for exact Hardy–Weinberg proportions, F-statistics (Weir & Cockerham 1984) and estimates of allele frequencies between the six sampled subpopulations and each STRUCTURE-identified cluster was calculated using the program GENEPOP v. 4.2.1 (Rousset & Raymond, 1995; Rousset, 2008). Population differentiation between sites was examined using the exact G test.

Evidence for genetic isolation by distance was assessed by plotting a pairwise genetic distance matrix (F_{ST}) against a pairwise spatial distance matrix. A Mantel test for dissimilarity was performed against the two matrices using R v. 3.0.2 (R Core Team, 2013) (permutation = 999 model = strata). Significance values were ascertained using the Monte-Carlo Markov Chain algorithm (Dememorization = 1000, batches = 100, and iterations/batch = 1000). Pairwise F_{ST} significance values and Bonferroni *P*-value corrections for multiple comparisons were undertaken using the program GENEPOP v. 4.2.1 (Rousset & Raymond, 1995; Rousset, 2008) and R v. 3.0.2 (R Core Team, 2013). The significance of the correlation between genetic and geographic distances at the individual level was ascertained by Monte-Carlo simulation (based on 999 replicates) using the R package adegenet v 2.0 (Jombart, 2008).

The program STRUCTURE v2.3.4 (Pritchard, Stephens & Donnelly, 2000) was used to estimate rate of migration and degree of isolation between subpopulations assuming unbalanced and limited sample sizes (Pritchard *et al.*, 2000). This analysis employs a Bayesian clustering algorithm to correlate microsatellite allele frequency dissimilarities between individuals with prior knowledge of sample location. The inclusion of sample location is specifically recommended when determining low levels of population structuring under small spatial scales, where a significant F_{ST} value has been determined (Hubisz *et al.*, 2009). This approach assigns individuals to the most relevant deme based on genetic dissimilarity between individuals and groups. The admixture model used in this analysis accounts for the possibility of admixture within clusters, as opposed to pure distributions of genotypes, while remaining robust to the absence of admixture. This method was employed to detect any indication of subtle population structure using the genotype data in this study. The number of subpopulations, K, was estimated to be between 1 and 6 using a burn-in of 10 000 runs; Markov Chain Monte-Carlo simulation (MCMC) run length of 100 000 with 10 iterations per simulation. Pairwise F_{ST} values between STRUCTURE-identified clusters were calculated using the program GENEPOP v. 4.2.1 (Rousset & Raymond, 1995; Rousset, 2008) and examined for significance using the exact *G* test.

Identification of the number of distinct and genetically consistent groups within the sampled population was estimated using the rate of change in the log probability of the data between successive estimates of the number of populations, termed delta *K* (ΔK) (Evanno, Regnaut & Goudet, 2005). The estimation of *K* was undertaken using the program Structure Harvester (Earl & von Holdt, 2012). The programs CLUMPP V1.1 (Jakobsson & Rosenberg, 2007) and DISTRUCT v1.1 (Rosenberg, 2004) were then used to produce graphical representations of the structure analysis. However, resent research suggests that unbalanced sample sizes from known localities may result in the identification of spurious clusters by the program STRUCTURE (Puechmaille, 2016), which is likely to result in an underestimation of *K* using the delta *K* method outlined in Evanno *et al.* (2005). As resampling a subset of genotypes to correct for unbalanced sample sizes is not appropriate in this case due to the small sample size, the approach of identifying a true value for *K* using the estimators MedMeaK, MaxMeaK, MedMedK and MaxMedK over 20 repeats per estimation of *K* was used (Puechmaille, 2016). The maximum value of *K* was interpreted by the number of clusters that contained at least one sampling locality at membership coefficient threshold of 0.5. The R package Kestimator (Puechmaille, 2016) was used to calculate the estimators listed above.

We used a cut-off assignment to test for the number of potential migrants within each structure-identified cluster (Sacks, Brown & Ernest, 2004). An arbitrary cut-off assignment of 70% was selected due to the limited sample size, local spatial arrangement and cluster assignment probability. A χ^2 test was used to assess the difference in the proportion of migrants between clusters.

The statistical power to reject the null hypothesis of genetic homogeneity in this investigation was assessed by undertaking a power test using the program POWSIM (Ryman & Palm, 2006) at F_{ST} values of 0.001, 0.0025, 0.01, 0.03 and 0.05. Effective population size (N_e), when simulated populations drifted apart, was maintained at 4000 and the number of simulations per run was set to 1000. It is generally regarded that power scores should be greater than 0.8 to be confident of adequate power.

Results

Hardy–Weinberg exact tests and fixation statistics

Genotype frequencies across all loci were found to be in general alignment with Hardy–Weinberg proportions at the total population level ($\chi^2 = 73.4136$, d.f. = 72, $P = 0.432$). When examined by locus, 3 of the 36 tests were shown to deviate significantly from Hardy–Weinberg proportions across the six sampling localities ($P < 0.05$). However, the exact Hardy–Weinberg test by population indicated that the majority of this deviation was partitioned to Site VR1 ($\chi^2 = 33.4919$, d.f. = 12, $P < 0.05$), showing a heterozygote excess at locus cme136 (Weir and Cockeram $F_{IS} = -0.2203$, $P < 0.05$). Weir & Cockerham fixation statistics indicated that a degree of sub-structuring was apparent in the total population as highlighted by the multi-locus F_{ST} estimate of 0.0302 (Table 2). Significant genetic differentiation was apparent between sample sites when examining the variation in allele frequencies between sites using the exact *G* test ($\chi^2 = 49.8182$, d.f. = 12, $P < 0.05$).

Table 2 Weir & Cockerham fixation statistics for individual and combined loci across all localities

Locus	F_{IS}	F_{ST}	F_{IT}
cme144	0.0819	−0.0080	0.0746
cme136	−0.1783	0.0067	−0.1705
cme206	−0.0024	0.0834	0.0812
cme196	0.0875	−0.0019	0.0858
cme193	0.0223	0.0062	0.0284
cme210	−0.1823	0.1146	−0.0468
All:	−0.0272	0.0302	0.0039

Isolation by distance

Analysis of the entire microsatellite dataset found no statistical correlation between Euclidian distance and pairwise F_{ST} values at the population level ($r = -0.1836$, $P = 0.75833$). Furthermore, no evidence of isolation by distance could be ascertained at the individual level when the correlation between distance matrices was compared to simulated values under the absence of spatial auto-correlation (simulated *P*-value: 0.707, Fig. 2).

Analysis of population structure

The analysis of genetic variation within and between individuals and sites using the Evanno method (2005) indicated that the number of ancestral populations genetically represented in the contemporary dataset can be inferred as $K = 3$ (Fig. 3).

STRUCTURE analysis indicated that the population structuring, highlighted by the inbreeding coefficient ($F_{ST} = 0.03$), was largely partitioned between feeding sites VR1 and VR2, being consistently dissimilar to each other and the remaining four sites in individual population assignment. Individuals from the remaining four control sites (C1, C2, C3 and C4) showed variable population assignment probabilities, thus a high degree of genetic admixture was inferred across these sites. The analysis of MedMeaK, MaxMeaK, MedMedK and MaxMedK indicates that the true value of $K = 3$.

Allelic richness, observed and expected heterozygosity, F_{IS} and the Hardy–Weinberg test for heterozygote excess and the proportion of potential migrants for each STRUCTURE-identified cluster are shown in Table 3. Contrary to our predictions a greater proportion of migrants were found in the STRUCTURE-identified cluster that included the four control sites (Cluster 3) when compared with the two supplementary feeding sites ($\chi^2 = 13.091$, d.f. = 2, $P < 0.05$).

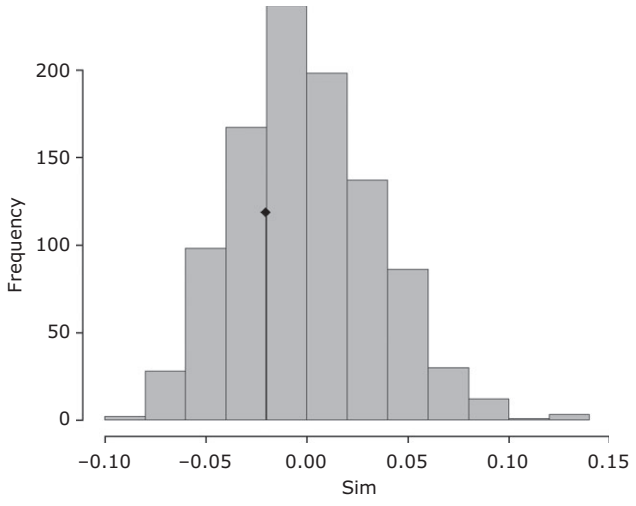

Figure 2 Genetic distance as a function of geographic distance between individual black-backed jackals showing the initial correlation (dot) and the distribution of simulated data under the absence of Isolation by distance.

Analysis of statistical power

Power analysis undertaken using the program POWSIM indicated that the suite of microsatellite loci used in this investigation was suitable for differentiating population structure at F_{ST} values of 0.03 and above, with a Fisher's exact test statistic >0.8. Power analysis with F_{ST} values of 0.001, 0.0025, 0.01, 0.03 and 0.05 were computed as 0.0760, 0.1660, 0.7580, 0.9980 and 1.000, respectively.

Discussion

Carnivore spatial organization is rarely, if ever, homogeneous in space and time. Resource-based explanations of spatial organization are able to describe such variation by exploring the relationship between the availability of resources (e.g. food) and the fitness cost associated with territorial defence (Johnson *et al.*, 2001, 2002). Theoretical models that link resource dispersion with spatial organization describe plasticity in territory size and stability when the distribution of food is heterogeneous across the environment (Macdonald, 1983; Johnson *et al.*, 2002). Thus, traditional explanations of the resource dispersion hypothesis place emphasis on the selective advantage gained by reducing territorial defence when the availability of food exceeds the requirements of the individual and group. For example, studies have concluded that populations of free-ranging red foxes residing in close proximity to human settlements are more likely to exist at higher densities than their rural counterparts due to the overabundance of anthropogenically derived sources of food (Bino *et al.*, 2010). However, the underlying mechanisms by which such populations are formed and maintained have been heavily veiled by their complexity. In this study we found evidence for a small degree of genetic structuring within the population as a whole (Table 2). Furthermore, a Bayesian analysis of population structure showed that black-backed jackals at supplementary feeding sites were genetically distinct relative to the total population (Fig. 3). However, contrary to our predictions, individuals from the remaining four control sites could not be accurately assigned to a single population of origin based upon their genetic identity alone, and showed a far greater number of potential migrants relative to the supplementary feeding sites (Table 3 and Table 4), which suggests a degree of historic gene flow between these sampling locations. In

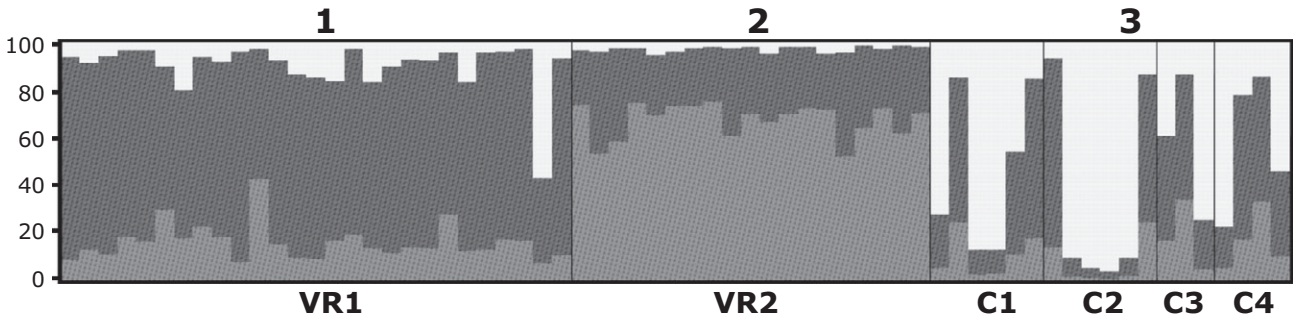

Figure 3 A graphical representation of population structure. Individual black-backed jackals are represented by vertical lines, with the population assignment represented in gray scale, $k = 3$.

Table 3 Genetic diversity estimators and proportion of migrants for each STRUCTURE-identified cluster

Cluster	Site	N	Ar	HO	HE	Overall F_{IS}	HWE (*P*-value)	Migrants (%)
1	VR1	27	47	103	105.2368	0.0217	0.7322	25.9
2	VR2	19	36	65	64.3377	−0.0103	0.6633	36.8
3	C1,C2,C3,C4	19	43	91	82.8843	−0.1009	0.3053	57.8

All pairwise F_{ST} values for each STRUCTURE-identified cluster (Table 4) were shown to be significantly different ($P < 0.05$).

addition, no evidence of spatial auto-correlation could be detected across the total population (Fig. 2), providing further evidence of a discontinuous population across the sampled area. We believe, therefore, that the results of this study show that far from increasing migration as predicted; clumped, abundant and stable sources of carrion can cause population structuring in the black-backed jackal by reducing gene flow between these sites. However, it should be noted that, while the identification of population sub-structuring is highly indicative of barriers to gene flow within the sampled population, evidence of slight outbreeding (Table 2) suggests that the genetic composition of the total breeding population has not been captured in its entirety. Despite this shortfall, the result of this study provides an informative estimation of the parameters of a population in flux and describes the genetic consequences of a population responding to increased food availability in the resource-rich agricultural landscape.

Competitive exclusion offers an attractive explanation for the degree of population structuring seen in this study. Once the carrying capacity of the environment has been reached, it is intuitive that a relative increase in competition for food would prompt territorial behaviour and limit or reduce migration and gene flow. Furthermore, due to the large diversity of alternate sources of prey available to the black-backed jackal within the agricultural landscape of South Africa (Kamler *et al.*, 2012), long distance commuting behaviour, as observed at the CCSR (Jenner *et al.*, 2001), may not be a cost-effective strategy in this system. Investigations into movement patterns of the dingo, which reside at resource-rich refuse sites in central Australia, have also shown that individuals do not always remain at refuse sites indefinitely. This indicates that further selective pressures above those predicted by the resource dispersion hypothesis, such as group hunting, may play an important role in the social structure of the Canidae (Newsome *et al.*, 2013). However, given that approximately 24–33% of offspring of territory-holding black-backed jackals have been recorded as delaying dispersal to provide alloparental care to subsequent kin (Ferguson *et al.*, 1983; Moehlman, 1983, 1986, 1987; Estes, 1991), a more likely explanation for the results of this study is that following a substantial increase in local food availability, the offspring of individuals in close proximity to supplementary feeding sites show a reduction in dispersal due to the high carrying capacity of the environment and reduced competition for resources between siblings. This would result in the formation of genetically distinct clusters of individuals. Previous studies have shown that pup survival rate is positively correlated with both food availability and alloparental care (Moehlman, 1987; Estes, 1991). Furthermore, the mechanisms dictating whether an individual chooses to disperse from its natal range or to remain and act as a helper has been correlated with food availability, competition for available resources and persecution (Ferguson *et al.*, 1983; Moehlman, 1987; Minnie, Gaylard & Kerley, 2016). Therefore, offspring that have failed to disperse from their natal range, in combination with an increase in dispersing offspring following disturbance from persecution at the control sites (Minnie *et al.*, 2016), would explain, at least in part, the degree of population structuring seen in this study. However, although previous studies have

Table 4 Pairwise F_{ST} values for each STRUCTURE-identified cluster

Clusters	Sites	Pairwise F_{ST}
1 + 2	VR1 + VR2	0.0329
1 + 3	VR1 + (C1, C2, C3, C4)	0.0274
2 + 3	VR2 + (C1, C2, C3, C4)	0.0647

suggested that a breakdown in territorial stability can result from clumped and abundant sources of food (Hiscocks & Perrin, 1988; Johnson *et al.*, 2002; Bino *et al.*, 2010), by sampling faeces for genetic material, a prominent territorial marker in many mammalian species, it is possible that transient individuals may have eluded genetic identification and potentially induced a sampling artefact to the analysis. Furthermore, the limited number of microsatellite loci used in this investigation has the potential to induce a type 2 statistical error in this analysis as statistical power is often reduced when both sample size and microsatellite loci are limited in number. To date, only six microsatellite markers have been published for the black-black jackal, which is relatively few by current standards. However, despite the limited resolution these markers offer for population structure analysis, they appear to be sufficient for identifying weak differentiation (F_{ST} = 0.03), which we regard as still biologically meaningful. It is, therefore, recommended that future studies focus on the characterization of further microsatellite loci with the aim of undertaking pedigree analysis using high-quality tissue samples to accurately infer relatedness between individuals at supplementary feeding sites.

Conclusions

Many previous studies have shown that excess food availability can dramatically affect the population dynamics of carnivores (Hiscocks & Perrin, 1988; Fedriani *et al.*, 2001; Jenner *et al.*, 2001; Johnson *et al.*, 2001; Bino *et al.*, 2010; Rotem *et al.*, 2011; Newsome *et al.*, 2013; Yarnell *et al.*, 2014). An increase in the abundance and density of local subpopulations is therefore expected following a substantial increase in carrion availability. The results of this study indicate that anthropogenically provisioned resources (e.g. carrion) results in genetically identifiable groups of black-backed jackals that show a degree of historic isolation from the surrounding population. Whether through kin selection or the principles of competitive exclusion, the formation of a structured population in response to excess carrion is not unexpected given the assumed territorial breakdown described by the resource dispersion hypothesis. However, the degree of genetic admixture at site VR1 suggests that immigration may play a substantial role in the formation of this cluster. The ability to identify genetically distinct groups, in response to a vastly increased local carrying capacity, provides additional insight into the group dynamics of a monogamous and territorial carnivore in the human-modified landscape.

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Supporting Information

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

Figure S1A–F. Maps depicting the spatial arrangement of faeces collected for genetic analysis within each game farm site. Faecal deposits of the black-backed jackal are denoted by black circles and carrion stations are represented by white circles.

Table S1. Individual black-backed jackal population assignment values for each structure-identified cluster.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main article.

Carnivores frequently come into conflict with humans in agricultural and livestock-producing areas around the world. Understanding their fidelity and dispersal patterns in response to food availability is therefore important given the effort invested in conflict mitigation strategies. In this study, we investigated the effect of clumped and abundant sources of food on the migration and dispersal of the black-backed jackal. We found that clumped and abundant sources of food promote population structuring, resulting in subpopulations with limited migration and dispersal when compared with the total population.