

Compensatory life-history responses of a mesopredator may undermine carnivore management efforts

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Summary

1. Lethal carnivore management, aimed at reducing carnivore impacts, is a global phenomenon threatening the persistence of many carnivores. Black-backed jackals *Canis mesomelas*, the dominant cause of livestock predation in southern Africa, are widely hunted to reduce livestock predation. Despite centuries of lethal management, jackals persist. Smaller canids, like jackals, are highly adaptable and display variable responses to mortality sources, which may affect management outcomes.

2. The effects of killing carnivores will depend on their behaviour, social organization, reproduction and dispersal patterns. We predicted that hunted jackals will alter demographic and reproductive patterns to compensate for increased mortality. Here, we collected demographic and reproductive information from harvested jackals and compared it between continually hunted (farms) and unmanaged populations (reserves).

3. The removal of jackals from farms results in a decrease in median age from 5–6 years (reserves) to 2–3 years (farms). Hunting also changed the age structure of jackal populations from a stable population to an expanding population. This may be ascribed to the compensatory immigration of individuals from neighbouring unmanaged areas, suggesting the formation of a source–sink system. Unmanaged areas may act as source populations exporting young, dispersing individuals to hunted areas which may act as sinks. This is likely driven by disruptions in the normal, mutually exclusive territorial system resulting in low densities of conspecifics on farms.

4. The low density of conspecifics allows younger individuals that would be socially precluded from reproducing to reproduce. Jackals on farms compensated for increased mortality by increasing the pregnancy rate of young individuals and increasing the litter size at younger ages, thereby increasing reproductive output.

5. *Synthesis and applications.* The lethal management of predators is the prevailing strategy to reduce livestock predation. However, the highly adaptable nature of jackals and the combination of compensatory mechanisms such as increased reproduction and potential for immigration allow these predators to persist in the face of severe anthropogenic mortality, possibly through the formation of a source–sink system. These compensatory processes will continue to counter population management actions as long as recruitment from unmanaged areas persists.

Key-words: black-backed jackal, *Canis mesomelas*, compensatory immigration, compensatory reproduction, harvest, human–carnivore conflict, hunting, livestock predation mesopredator, source–sink dynamics

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Introduction

Human–carnivore conflict is a global phenomenon threatening numerous species. The conflict arises because carnivores may prey on people, livestock and valued wildlife. To combat these losses, humans respond by killing

carnivores to reduce carnivore populations and the associated prey losses. In some cases this is believed to be effective in reducing carnivore populations and protecting prey populations (Robinson *et al.* 2008), whereas in other cases it is thought to be ineffectual (Knowlton, Gese & Jaeger 1999). The effects of hunting on carnivore populations is context-dependent and will vary depending on the behaviour, social organization, reproduction and dispersal patterns of the focal carnivore (Frank & Woodroffe 2001).

The variability in carnivore social structure makes it difficult to predict the effects of hunting (Frank & Woodroffe 2001). In many cases larger predators such as lions *Panthera leo* and wolves *Canis lupus* have been extirpated, owing in part to conflict with humans and livestock (Ripple *et al.* 2014). Conversely, small- to medium-sized predators are more resilient to mortality sources (i.e. compared to larger predators) and persist despite heavy hunting pressures. This is exemplified by the European red fox *Vulpes vulpes*, both in its natural and introduced ranges (Newsome, Crowther & Dickman 2014), and coyotes *Canis latrans* in the USA (Knowlton, Gese & Jaeger 1999) that are still present despite intensive population management. These canids are particularly plastic with respect to changes in behaviour, social organization, reproduction and dispersal in response to hunting. For example, Sacks (2005) suggested that coyotes may exhibit life-history strategies similar to both r-selected (high reproductive output and short-lived) and K-selected species (low reproductive output and long-lived), depending on the level of anthropogenic mortality. This shift between r- and K-strategies is often density-dependent and associated with compensatory mechanisms such as altered reproduction or immigration (Sacks 2005). The combination of compensatory immigration and reproduction has been suggested as processes contributing to the persistence of many hunted species (e.g. wolves: Fernández & Ruiz de Azua 2010). In addition, many larger predators have been locally extirpated allowing the proliferation of small- to medium-sized predators (mesopredator release, Prugh *et al.* 2009). This has further exacerbated the impacts of smaller predators on prey populations (see Prugh *et al.* 2009).

Small- to medium-sized predators, in particular, have high intrinsic growth rates which translate to strong demographic responses to increased mortality (Frank & Woodroffe 2001). Therefore, compensatory reproduction – a reallocation of resources to increase reproductive output and compensate for decreased survival – plays an important role in the persistence of hunted small- to medium-sized predators, and may manifest itself as increases in litter size (e.g. red fox: Cavallini & Santini 1996), proportion of breeding females (e.g. red wolf *Canis rufus*: Sparkman, Waits & Murray 2011), and a decrease in age at first reproduction (e.g. coyotes: Sterling, Conley & Conley 1983).

In addition, compensatory immigration – the net movement of individuals from unhunted (source) to hunted (sink) areas – plays a fundamental role in the recovery of hunted populations (Turgeon & Kramer 2012). For exam-

ple, cougar *Puma concolor* populations exhibit a source–sink population structure as a consequence of unevenly distributed hunting pressures, owing to compensatory immigration (Robinson *et al.* 2008; Stoner *et al.* 2013). Thus, many exploited carnivore populations are characterized by source–sink metapopulation structures, where spatial variation in the intensity of top-down regulation results in the immigration of individuals from neighbouring unhunted areas, and differing demographic patterns (e.g. cougar: Robinson *et al.* 2008).

However, we know little about how anthropogenic mortality affects the life history of predators and hence their populations, and there is a paucity of information confirming that changes in reproductive patterns contribute to carnivore persistence. It is important to gauge these impacts across the diverse range of carnivores to detect general patterns among these important predators, and to inform effective predator conservation and management regimes. Here we explore these patterns for black-backed jackals *Canis mesomelas* (hereafter referred to as jackal, Schreber 1775).

In South Africa, most of the larger carnivores, such as lions and spotted hyenas *Crocuta crocuta*, have been extirpated from most of their historical range (Skead 2007, 2011). These top predators now occur only in protected areas (Slowtow & Hunter 2009). Despite concerted population control efforts, mesopredators such as jackals and caracal *Caracal caracal* (Schreber 1775) are still abundant on rangelands and are the largest cause of livestock mortality across southern Africa. Hunting, in conjunction with other interventions such as fencing, may result in the local extirpation of jackals from certain areas (e.g. Kamler, Stenkewitz & Macdonald 2013). However, similar to coyotes (Knowlton, Gese & Jaeger 1999) and dingoes *Canis dingo* (Allen 2015), jackal populations may return to pre-management densities once lethal management ceases. Therefore, it is likely that compensatory reproduction and dispersal allows the persistence of jackals in the face of anthropogenic mortality. The combination of immigration and reproduction can result in skewed age and sex ratios which might further magnify or reduce the effects of hunting (Robinson *et al.* 2014).

Here we test whether hunted jackal populations display compensatory demographic and reproductive patterns by comparing these in hunted vs. unhunted areas. It is hypothesized that hunted jackal populations will show changes in sex ratios, age structure, and reproductive patterns to compensate for increased anthropogenic mortality. We predict that hunted populations will display: (i) a skewed sex ratio, as stressed populations produce more individuals of the sex that increases population fitness; (ii) a younger age structure due to the removal of territorial adults, and an influx of younger individuals from neighbouring unhunted areas; (iii) increased pregnancy rates for young jackals, as younger females typically do not reproduce in stable, unhunted populations and (iv) larger litter size to compensate for the additional anthropogenic

mortality. Our results indicate that the combined effects of reproductive compensation and, almost certainly, compensatory immigration are contributing to the persistence of jackal populations in the face of severe anthropogenic mortality. This suggests that unevenly distributed hunting may induce a source–sink system.

Materials and methods

STUDY AREA

Jackal samples were collected from three conservation areas, Karoo National Park (KrNP), Mountain Zebra National Park (MZNP), and Addo Elephant National Park (AENP), as well as various wildlife and livestock farms adjacent to these reserves in the Eastern and Western Cape, South Africa (Fig. 1). The study area is semi-arid, with an aridity gradient, being drier in the west (mean annual precipitation at KrNP = 274 mm) than in the east (MZNP = 403 mm, AENP = 401 mm). The western and central parts of the study area are dominated by Nama Karoo vegetation, which transitions to patches of Albany Thicket in the south-east and Grasslands in the north-east (Mucina & Rutherford 2006). Mosaic vegetation patterns are common within the study area, with different biomes interdigitating (Mucina & Rutherford 2006). The dominant land use is extensive small livestock (sheep and goat) grazing with wildlife farms scattered throughout.

Historically, the study area supported numerous carnivore species. However, due to conflict with humans most of the top predators have been extirpated (Skead 2007, 2011). Lions, hyenas and cheetahs *Acinonyx jubatus* only occur within protected areas, while leopards *Panthera pardus* may occur at low densities throughout the mountainous areas. Jackal and caracal are ubiquitous throughout the study area and are the dominant mammalian predators on farms. Due to the high predation pressures on livestock and wildlife, jackals are widely hunted as both a preventative and reactive measure to reduce livestock and wildlife losses. The intensity and methods of jackal management outside protected areas throughout the region are comparable. Jackal populations within National Parks are generally unmanaged, but samples became available during experimental jackal population reductions by South African National Parks to reduce predation on small- and medium-sized ungulates (South African National Parks project number: GAYA1167).

SAMPLE COLLECTION

Jackal carcasses were obtained from problem animal control specialists, reserve managers and farm managers between October 2011 and October 2013. These jackals were killed as part of livestock and ungulate predation control measures. Samples were separated into two treatments based on management regime: (i) reserves – National Parks that stock indigenous animals and

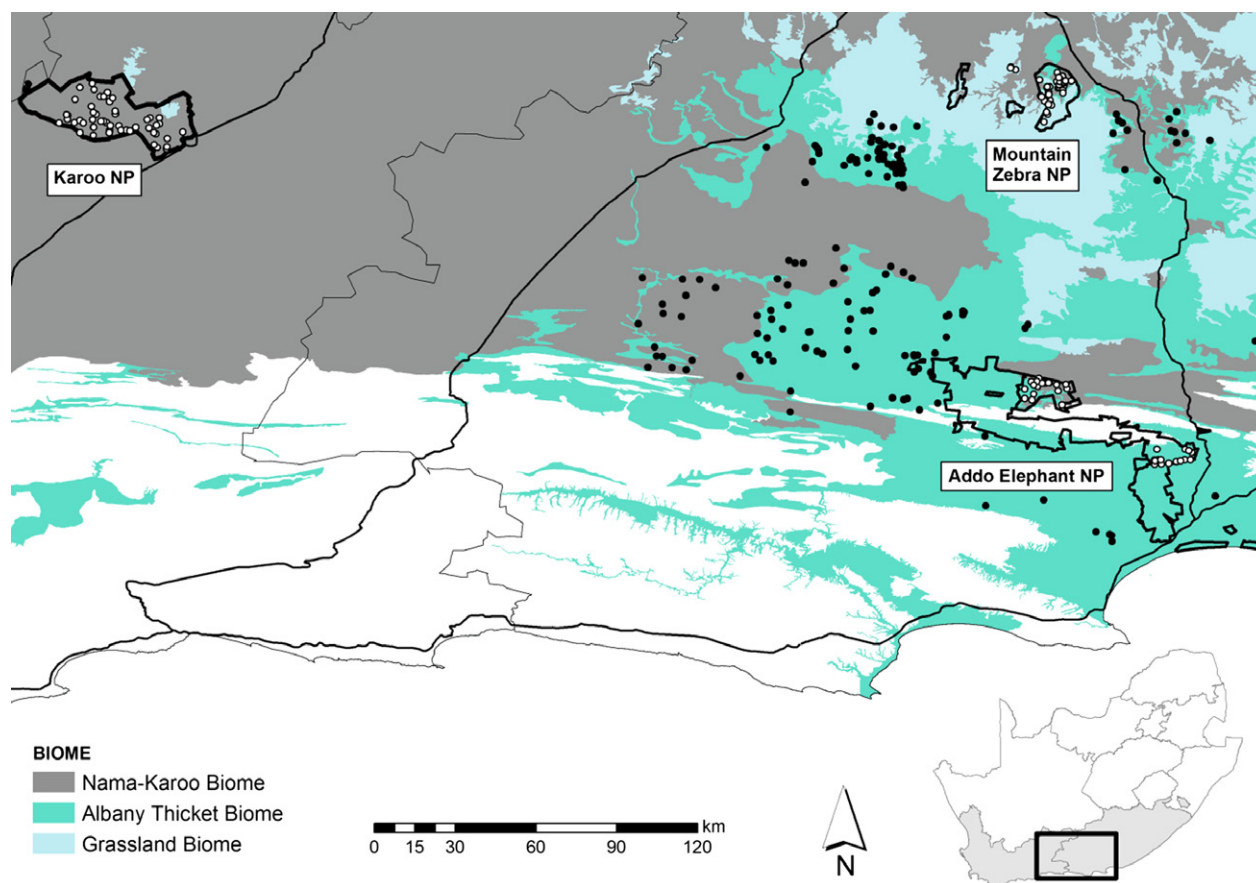


Fig. 1. The location of jackals collected from farms (black dots) and reserves (white dots). Samples were collected from reserves (black lines), Karoo National Park ($n = 108$), Mountain Zebra National Park ($n = 59$), Addo Elephant National Park ($n = 79$), and the farms surrounding the latter two reserves ($n = 327$).

seldom control jackal populations; and (ii) farms – stock live-stock and/or wildlife species with ongoing jackal control. Jackals were harvested using the same approach on reserves and farms (i.e. call-and-shoot), thereby reducing any potential biases in sample collection. Additionally, all individuals responding to calls, irrespective of age and sex, were shot, and this process was repeated several nights in a row to ensure that most of the jackals in an area were harvested. Carcasses were collected within 6–24 h after death. Jackals were weighed, sexed, aged based on tooth wear (Lombaard 1971), and necropsied to collect information on body condition and reproduction.

BODY CONDITION

Two indices of body condition were used: (i) body mass was used as an indicator of overall protein content (Sacks 2005) and was corrected for stomach mass (due to large variations in stomach mass: 42–1680 g) by subtracting the stomach content mass from body mass, and (ii) renal fat index (RFI) as a measure of total body fat. RFI is calculated by dividing the mass of the kidneys and the renal fat by the kidneys trimmed of fat (Cavallini 1996). The natural log of the mean RFI (lnRFI) was used as it provides a better estimate of total body fat (Torbit *et al.* 1988).

FEMALE REPRODUCTION

Uteri were removed, opened longitudinally, and examined for the presence of foetuses. Foetuses were sexed, and mass and total body length recorded. Uteri were examined over a light source for the presence of placental scars. Only dark placental scars were used to estimate litter size, as light placental scars represent foetuses from previous seasons' pregnancies (Heydon & Reynolds 2000; Elmeros & Hammershøj 2006). When no dark placental scars or foetuses were present, the presence of lighter placental scars (representing foetuses from previous pregnancies) was used to determine if the female was nulliparous or not. Determining litter size via placental scar counts does not reliably equate to postnatal litter size as it does not account for embryo resorption and prenatal mortality (Ruetter & Albaret 2011). As a consequence, placental scar counts often overestimate postnatal litter size (e.g. Allen 1983). However, placental scars represent the maximum number of foetuses that may have been born and reflect reproductive investment. Thus, placental scar counts remain a valuable technique in determining potential reproductive output.

DATA ANALYSIS

Sex ratio

We used chi-square goodness-of-fit tests (Zar 1999) to test whether the observed sex ratios of adults and foetuses were different from parity (expected sex ratio of 1:1), as hunting may skew sex ratios towards the sex that will increase the fitness of the population. We also used chi-square tests to determine if biases in adult and foetal sex ratios differed between treatments (Zar 1999).

Age distribution

Samples were not collected simultaneously owing to the *ad hoc* basis of jackal management. Farm samples were collected

throughout the year except during September and October. The majority of the farm samples were collected in March (35% of the sample) and May (32%), which corresponds with the periods when juveniles start foraging with their parents and yearlings start dispersing from natal territories (Skinner & Chimimba 2005). Thus, the farm sample may be biased towards juveniles and yearlings. All the reserve samples were collected during September (78%) and October (22%) which is the parturition period (Bingham & Purchase 2002). We standardized the ages of all jackals to March – the period when all the pups should be foraging with their parents – to minimize any biases related to differences in sample collection period. The standardized age distribution was only used for the age structure comparisons and the original ages were used for the analysis pertaining to reproduction. The standardized age distributions were compared between treatments, to test if hunting results in a younger age structure (i.e. higher frequency of younger individuals in the hunted population), via a Pearson's chi-square test (Zar 1999). The influence of hunting on the median population age was compared between treatments using an asymptotic Wilcoxon rank-sum test in the package 'exactRankTests' (Hothorn & Hornik 2013).

Body condition

The influence of reproductive status (pregnant, lactating, or both) on female body condition (lnRFI) was assessed using a Kruskal–Wallis ANOVA for each treatment. It is expected that body condition will respond to the stress of the various stages of reproduction. Thereafter, we used Welch *t*-tests for unequal variances (Zar 1999) to test if reproductive activity (active vs. inactive) and treatment influenced female body condition.

Reproduction

Adult females that were not pregnant or did not display any placental scarring were considered barren. Litter size (excluding barren females) was calculated as the number of dark placental scars or foetuses per adult (older than one) female, and fecundity (including all pregnant and barren females) was calculated as the average number of placental scars per adult female. The prediction that hunting induces an increase in reproductive output was assessed by comparing litter size and fecundity between treatments using a Welch *t*-test for unequal variances (Zar 1999). A generalized linear model (GLM) with a Gaussian error distribution and a log-link function was used to test for differences in litter size and fecundity between treatments, including body condition (lnRFI), and age as covariates. Corrected body mass was removed from the analysis as it was collinear (Spearman $Z = 3.10$, $P = 0.002$) with body condition. Model selection was conducted using small-sample Akaike Information Criterion (AICc; Burnham & Anderson 2002). Model averaging was used to estimate coefficients when no clear best model could be identified (models within 2 Δ AICc units of the best model). Interactions between predictor variables were further inspected using conditional plots. Age-specific fecundity and pregnancy rates were compared between treatments using a Kruskal–Wallis ANOVA and *post hoc* multiple comparisons (Welch *t*-tests) with Bonferroni-corrected *P*-values ($P = 0.007$). All data analyses were performed using the R statistical package (R Core Team 2013).

Results

AGE AND SEX STRUCTURE

We obtained a total of 246 jackals from reserves and 327 from farms. The sex ratio (M:F) of farm populations (1.05:1) did not differ ($\chi^2 = 0.45$, d.f. = 2, $P = 0.80$) from that of the reserve populations (0.94:1). Although slightly male-biased on farms and slightly female-biased on reserves, neither ratio differed from parity (farm: $\chi^2 = 0.24$, d.f. = 1, $P = 0.63$; reserve: $\chi^2 = 0.02$, d.f. = 1, $P = 0.90$); thus, hunting does not skew jackal sex ratios.

The age class distributions differed between treatments ($\chi^2 = 98.30$, d.f. = 12, $P < 0.0001$), with the farm population exhibiting an expanding population structure as opposed to the decreasing population pyramid of the reserve population (Fig. 2). Most jackals on reserves were older than 2 years, with the majority (32%) older than 7 years. In contrast, the farm population was dominated by individuals younger than 3 years and the majority (32%) were yearlings. The reserve population (median: 5–6 years) was significantly older than the farm population (median: 2–3 years; $W = 14405$, $P < 0.0001$). There was no difference in age between sexes in either of the treatments (farm: $W = 14728$, $P = 0.10$; reserve: $W = 6835$, $P = 0.44$).

BODY CONDITION

The reproductive status of females did not influence body condition estimates on farms ($\chi^2 = 5.66$, d.f. = 2, $P = 0.06$) or reserves ($\chi^2 = 0.80$, d.f. = 2, $P = 0.67$).

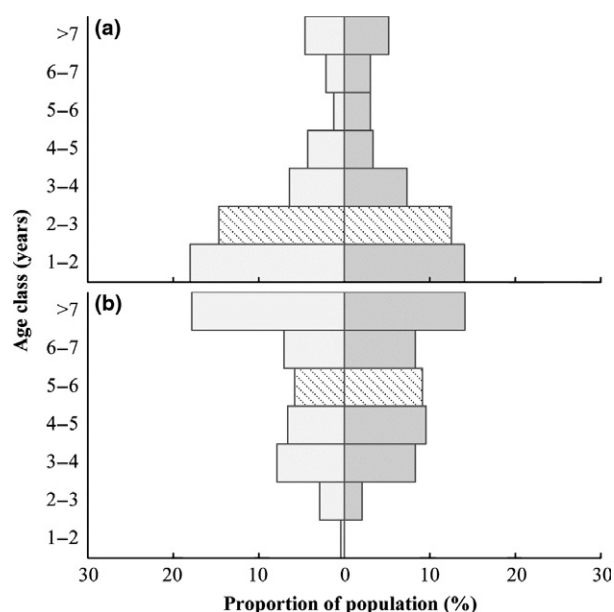


Fig. 2. Population pyramids and median age (hatched bars) of jackals showing (a) an expanding population on farms ($n = 327$), and (b) a stable/contracting population on reserves ($n = 246$). The left-hand side represents the males and the right-hand side the females.

Furthermore, female body condition was similar across treatments ($t = -0.15$, d.f. = 177.19, $P = 0.88$). Reproductively active females tended to be in better condition than inactive females. However, this relationship was only significant on reserves ($t = 2.18$, d.f. = 76.22, $P = 0.03$).

PREGNANCY

The proportion of females on farms that had been pregnant before was consistently high for all age classes, ranging between 68% and 88% for 1- to 5-year-old females (Fig. 3). All females on reserves and farms older than five had been pregnant before. The proportion of pregnant females on farms differed from that on reserves ($\chi^2 = 33.50$, d.f. = 6, $P < 0.0001$). The proportion of pregnant females on reserves was consistently lower than the farm population until the age of 4–5 years, after which there was no difference. The most notable difference was for the yearlings, where only 20% of the reserve females had been pregnant before, compared with 68% on farms. Approximately 80% of the farm females aged between one and four had been pregnant before, as opposed to the 20–50% observed on reserves.

LITTER SIZE & FECUNDITY

Litter size ($t = -1.20$, d.f. = 128, $P = 0.23$, Power = 0.14) and fecundity ($t = -1.18$, d.f. = 226, $P = 0.24$, Power = 0.10) were similar across treatments, contrary to our prediction. The average litter size was 3.30 ± 0.14 (range: 1–6) on reserves and 3.02 ± 0.19 (range: 1–7, Fig. 4) on farms. The average fecundity was 1.84 ± 0.17 for reserve and 1.56 ± 0.17 for farm populations. The best performing model for litter size included only age (coefficient = 0.23, 95% CL = 0.09–0.40) as a predictor variable (model 1, Table 1), accounting for 43% of the weight of evidence (w). The next best models were >2 Δ AICc units from the best model, accounting for only 15% w . Therefore, we did not consider the next best models to be competitive (Burnham & Anderson 2002). The best model for fecundity (21% w) included age, body condition, treatment and an interaction between age and

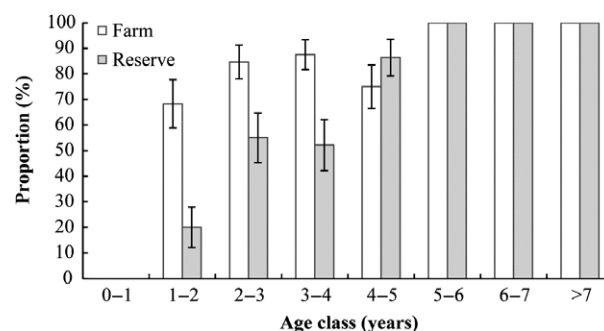


Fig. 3. The pregnancy rate (proportion pregnant \pm 95% CL) of females on farms and reserves.

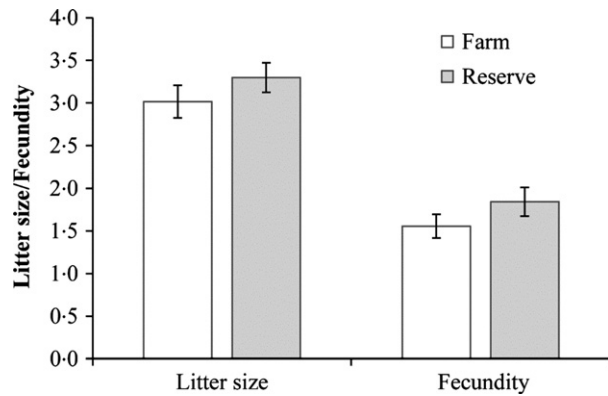


Fig. 4. Average litter size (\pm SE) and fecundity (\pm SE) of females on farms and reserves. Litter size excludes all barren females and fecundity includes barren females.

Table 1. The top models explaining variation in jackal litter size and fecundity based on model selection using small-sample Akaike Information Criterion (AICc; Burnham & Anderson 2002)

Rank	Model	k^*	$\Delta\text{AICc}^\dagger$	w^\ddagger
Litter size				
1	Age	3	0.00	0.43
2	Age + treatment	4	2.12	0.15
Fecundity				
1	Age + BC [§] + treatment + age: BC	6	0.00	0.21
2	Age + BC + age: BC	5	0.13	0.19
3	Age + BC	4	0.84	0.14
4	Age + BC + treatment + age: BC + age: treatment	7	1.83	0.08
5	Age + BC + treatment	5	2.11	0.07

*Number of parameters.

†Difference in relation to best model.

‡Model weight.

§Body condition.

body condition (model 1, Table 1). However, based on ΔAICc and w , the three next best models (model 2, $\Delta\text{AICc} = 0.13$, 19% w ; model 3, $\Delta\text{AICc} = 0.84$, 14% w ; model 4, $\Delta\text{AICc} = 1.83$, 8% w ; Table 1) were also supported. Age (model-averaged coefficient = 0.12 ± 0.19) and body condition (model-averaged coefficient = -1.14 ± 2.44) formed part of all the top models, with the interaction between age and body condition (model-averaged coefficient = 0.76 ± 0.42) included in three of the four top models. The interaction between age and body condition was the only significant ($P < 0.1$) predictor variable. Thus, the interaction between age and body condition suggests that older females with a higher body condition will have a relatively higher fecundity (Fig. 5). The age-specific fecundities of jackals on reserves increased steadily from 1 to 7 years of age (Fig. 6). The jackals on farms displayed a similar increase in fecundity with age. However, the fecundity of younger jackals (1–4 years) on farms tended to be higher than those on reserves; this was significantly higher for yearlings ($t = 5.20$, d.f. = 39, $P < 0.007$), as predicted.

FOETAL LITTER SIZE

Only ten litters with measurable foetuses were collected – four from farms and six from reserves. Foetuses were collected from July–September, which corresponds with the normal parturition period (Loveridge & Nel 2004). This small sample size allows only descriptive statistical analysis. The average number of foetuses was 4.25 ± 1.71 (range: 2–6), and 2.67 ± 1.21 (range: 1–4) for farms and reserves, respectively. All females with measurable foetuses were older than 6 years. The overall sex ratio (M:F) for foetuses was 0.7:1 for farms and 1:1 for reserves, neither of which differed from parity.

Discussion

The effects of anthropogenic mortality vary depending on the life histories and social structures of the focal carnivores. Therefore, interpreting the patterns observed here requires an understanding of jackal social structure. In a stable social system, jackals are strictly monogamous (Moehlman 1987), and defend mutually exclusive territories (Loveridge & Nel 2004), but other jackals may be tolerated when resources are locally abundant (Hiscocks & Perrin 1988; Jenner, Groombridge & Funk 2011). In addition, subordinates are tolerated on the fringes of territories (Ferguson, Nel & de Wet 1983). Jackals become sexually mature at 11 months, and typically disperse from their natal ranges at ca. 1 year of age (yearlings, Ferguson, Nel & de Wet 1983). Approximately two-thirds disperse from their natal range in search of mates and territories, with one-third remaining to assist their parents with raising the next litter (Ferguson, Nel & de Wet 1983; Moehlman 1983). In a system approaching social carrying capacity (saturated with territorial pairs), dispersing subordinates cannot establish territories (as there are no vacant territories available) and are thus socially precluded from reproducing. It is unclear what drives dispersal, but it is thought to be socially mediated (Loveridge & Macdonald 2001). Thus, young jackals show relatively low philopatry and recognize and disperse into vacant territories.

Anthropogenic mortality disrupts this stable social system by removing territorial individuals which may result in a wide variety of population-level responses. This includes changes seen in other carnivores, such as behaviour, social structure (e.g. lions: Snyman, Jackson & Funston 2015), demography (e.g. raccoons *Procyon lotor*: Beasley *et al.* 2013), and reproduction (e.g. coyotes: Sacks 2005). Hunting, the dominant form of predator control in this study, may also result in skewed sex ratios in populations with sex-biased dispersal (e.g. cougar: Robinson *et al.* 2008). Here, there is no evidence of sex-specific vulnerability to predator control. There was no difference in sex ratio between treatments and both approximate parity. Thus, a balanced sex ratio is to be expected owing to the monogamous mating of jackals. Long-term pair

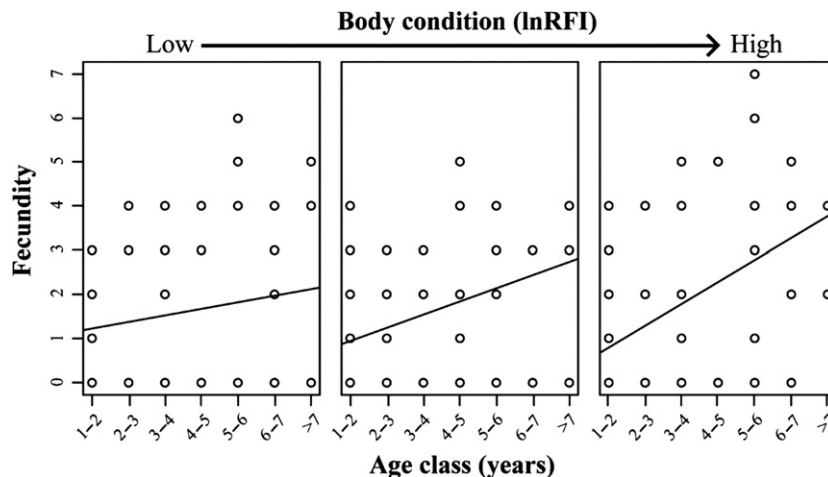


Fig. 5. Interactive relationship between age class and body condition (natural log of the mean renal fat index) and its influence on jackal fecundity.



Fig. 6. Age-specific fecundity (average number of placental scars per female) for jackal populations on reserves and farms.

bonding is critical for defending territories and successfully rearing pups, as single parents cannot successfully rear a litter (Moehlman 1987). Thus, males and females invest equally in the success of reproduction, reinforcing the prevalence of a balanced sex ratio.

As predicted, the farm population (hunted) was younger than the reserve population (unhunted), and displayed an expanding population structure dominated by younger individuals, as opposed to the declining population structure dominated by older individuals of the reserve populations. Similar differences in age structure have been documented for other hunted carnivores (e.g. coyotes: Gese 2005), and have been ascribed to a disruption in normal social structure. Gese, Rongstad & Mytton (1989) suggested that coyotes are regulated by social intolerances mediated by resource availability, and that within stable (unhunted) populations subordinates are excluded from territories and forced into suboptimal (hunted) habitats. This is likely the case for jackal populations. Hunting disrupts the mutually exclusive territorial structure of jackal populations by creating vacant territories on farms. Young jackals exhibit low philopatry, and populations experiencing high levels of mortality will have a reduction in social ties and dispersal will be favoured (Loveridge & Macdonald 2001). Therefore, hunting skews the age structure of the farm population towards younger individuals

by inducing an influx of dispersing yearlings, probably from neighbouring unhunted areas (compensatory immigration). According to habitat selection theory (Rosenzweig 1981), compensatory immigration will be driven in part by intraspecific density-dependent interference competition (Delibes, Gaona & Ferreras 2001) on reserves and by the lower density of conspecifics on farms. Compensatory immigration has been documented for several harvested organisms ranging from willow grouse *Lagopus lagopus* (Smith & Willebrand 1999) to cougars (Robinson *et al.* 2008). This in many cases induces source-sink dynamics, which may magnify, or in this case, reduce the effects of hunting (Robinson *et al.* 2014).

Further, hunting may also affect various aspects of reproduction. However, contrary to our prediction, both litter size and fecundity were comparable between treatments. In fact, there is little evidence to support an increase in litter size with increases in hunting (Frank & Woodroffe 2001). Knowlton (1972) showed that there was an increase in litter size for coyotes in response to hunting, but this has not been shown for other canids (e.g. red fox: Harris & Smith 1987; arctic fox *Alopex lagopus*: Hersteinsson 1992). However, the impacts of hunting are often masked by differences in resource availability and distribution, as the reproductive patterns of carnivores are highly correlated with the availability of resources (Fuller & Sievert 2001). For example, Gese (2005) found an increase in coyote litter size in response to hunting, but this was confounded by an increase in prey abundance. Conversely, a reduction in resource availability resulted in a decrease in coyote body condition and a significant reduction in litter size (Todd & Keith 1983). Similarly, differences in resource availability between treatments may influence jackal reproductive patterns. However, there was no difference in body condition between treatments, indicating that resource availability was similar across treatments. Age had a positive relationship with litter size and fecundity. Thus, it can be expected that reserves should display larger litter sizes and fecundities owing to an older population structure. In addition, body condition covaried with age, indicating that older females in better condition had relatively higher fecundities

(Fig. 5). However, this did not result in any difference in fecundity between treatments.

The fact that litter size and fecundity are similar between treatments despite the significant difference in age structure and associated body conditions can be attributed to the relatively larger fecundity of younger jackals (1–4 years) on farms. In addition, a much larger proportion of the younger jackals on farms are reproducing. In a jackal population with a stable social structure, such as those on reserves, dominant mated pairs prevent younger subordinates from reproducing by constant harassment (Loveridge & Nel 2004), and in so doing reduce competition for limited resources (Moehlman & Hofer 1997). This was reflected by the large proportion of sexually mature individuals that did not reproduce on reserves (50% of females aged 1 to 4 years). In contrast, when the territorial structure is disrupted, due to high levels of anthropogenic mortality, younger individuals are released from density-dependent regulation and social dominance, and may reproduce. This was the case for the jackal population on farms, which showed an increased pregnancy rate at younger ages relative to reserves. This is to be expected, as according to Frank & Woodroffe (2001), hunting increases the likelihood of an individual female to reproduce (e.g. red fox: Harris & Smith 1987; coyote: Gese 2005). Therefore, jackals show reproductive compensation to increases in anthropogenic mortality by producing relatively larger litters at younger ages.

The findings from this study indicate that the combined effects of reproductive compensation and, in all likelihood, compensatory immigration contribute to the persistence of jackal populations in the face of severe anthropogenic mortality, possibly via the formation of a source–sink system. Within a source–sink system, the reproductive surplus produced in source populations may sustain sink populations (Pulliam 1988). Unevenly distributed hunting pressures have been shown to induce source–sink dynamics in many carnivore populations (e.g. grizzly bears *Ursus arctos horribilis*: Doak 1995; lynx *Lynx lynx*: Slough & Mowat 1996; culpeo foxes *Pseudalopex culpaeus*: Novaro, Funes & Walker 2005; cougars: Robinson *et al.* 2008). In this study, hunting pressures are focussed on farms, resulting in social disruption, a collapse in territorial structure, and a decrease in jackal density. Therefore, immigrants will occupy these newly vacated areas (Frank & Woodroffe 2001), especially when densities are well below carrying capacity (e.g. red fox: Lieury *et al.* 2015). Hunting-induced source–sink systems function on what Delibes, Gaona & Ferreras (2001) describe as an ‘attractive sink’. Attractive sinks arise because of the inability of animals to recognize mortality risks in habitats that would otherwise provide adequate resources to allow for high reproduction. Farms likely act as attractive sinks where there are abundant resources (natural prey and livestock) and vacant territories with few competitors, thus driving compensatory immigration (Frank & Woodroffe 2001; Lieury *et al.* 2015). However, more information on the magnitude and

direction of dispersal is required to ascertain the connectance between potential sources and sinks. The results presented here indicate that the lethal control of mesopredator populations, to reduce livestock losses, may be counteracted by compensatory immigration and reproduction. These compensatory processes are mediated by disruptions in social structure and may continue to counter population management actions as long as recruitment from unhunted areas persists.

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Data accessibility

Data are available from the Dryad Digital Repository doi:10.5061/dryad.3mf68 (Minnie, Gaylard & Kerley 2015).

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