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SHORT COMMUNICATION

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Effects of humans and large carnivores on the survival of black-backed jackals

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1 | INTRODUCTION

The black-backed jackal (*Canis mesomelas*), hereafter referred to as jackal, is a common mesocarnivore throughout southern and eastern Africa. This species is a generalist omnivore, and research has shown it is very adaptable to different ecosystems, including both natural and anthropogenically modified habitats (Minnie, Avenant, et al., 2016). Historically, they occurred in ecosystems dominated by up to six species of large (>20 kg) carnivores, along with several other mesocarnivores. Under such natural conditions, jackals typically feed on prey ranging from small rodents to small antelope and scavenge on large carnivore kills (Minnie, Avenant, et al., 2016; Skinner & Chimimba, 2005). However, most of the arable land in South Africa has been transformed into agricultural farms and extensive livestock farms, and large carnivores have been extirpated over most of the country (van Sittert, 1998). Under such human-dominated conditions, jackals appear to thrive, and they have become the dominant predator on farmland throughout most of South Africa (Klare, Kamler, Stenkewitz, & Macdonald, 2010; Minnie, Avenant, Drouilly, & Samuels, 2018; Minnie, Avenant, et al., 2016). Consequently, jackals prey heavily on ungulates in game farms (Klare et al., 2010), and prey heavily on sheep on livestock farms (Kamler, Klare, & Macdonald, 2012; Minnie, Avenant, et al., 2018). In response, human persecution of jackals typically is high on farmland and game farms, and jackal control activities are a standard management practice on most farms (Drouilly, Nattrass, & O'Riain, 2018; Kamler, Stenkewitz, & Macdonald, 2013; Minnie, Avenant, et al., 2016; Minnie, Zalewski, Zalewska, & Kerley, 2018).

The high level of persecution of jackals in South Africa is controversial (Nattrass, Drouilly, & O'Riain, 2019). Although intensive jackal control can significantly reduce jackal densities on livestock farms compared to nearby reserves (Kamler et al., 2013), others believe persecution does not affect jackal densities due to compensatory mechanisms and immigration (Minnie, Gaylard, & Kerley, 2016; Minnie, Zalewski, et al., 2018). Nonetheless, under natural condition with large carnivores present, jackals might experience high mortality levels similar to those in human-hunted populations. For example, jackals have reportedly been killed or consumed by lions (*Panthera leo*; Schaller, 1972; Stander, 1992), spotted hyaenas (*Crocuta crocuta*; van Lawick & van Lawick-Goodall, 1970), brown hyaenas (*Hyaena brunnea*; Mills, 1982), leopards (*P. pardus*; Schaller, 1972; Estes, 1991), cheetahs (*Acinonyx jubatus*; Hayward, Hofmeyr, O'Brien, & Kerley, 2006) and African wild dogs (*Lycaon pictus*; Kamler, Davies-Mostert, Hunter, & Macdonald, 2007), yet the effects of these natural mortalities on jackal populations have never been quantified. Similarly, although the effects of human-caused mortalities on the genetic and population structure of jackals have been reported (Minnie, Gaylard, et al., 2016; Minnie, Zalewski, et al., 2018; Tensen, Drouilly, & van Vuuren, 2018), the effects of human-caused mortalities on the annual survival of a jackal population have never been determined.

This study aimed to compare the annual survival of two populations of jackals, which included a natural site with an intact large carnivore guild with no human hunting, and a game farm surrounded by small-livestock farms where large carnivores were absent and human hunting of mesopredators occurred. The goal was to compare the effects of natural top-down mortalities versus human-caused mortalities on the survival in these two jackal populations. To our knowledge, these are first estimates of annual survival for jackals, and therefore our results also provide a baseline for future studies in other jackal populations.

2 | METHODS

2.1 | Study sites

During 2006–2008, we conducted research on Benfontein Nature Reserve (BNR; 114 km^2), formerly Benfontein Game Farm, owned by De Beers Consolidated Mines, located ca. 10 km southeast of Kimberley on the border of the Free State and Northern Cape provinces, South Africa (28°50′S; 24°50′E). All large (>15 kg) carnivore species were extirpated from this area prior to 1900, and the largest remaining carnivores on BNR were jackals, caracals (*Caracal caracal*) and aardwolves (*Proteles cristatus*), although only the density of jackals was known (0.33 jackal/km^2; Kamler et al., 2013). There is relatively little human activity, aside from one or two annual culls for ungulates, which maintain a relatively high density of 20–25 springbok (*Antidorcas marsupialis*)/km^2 (Kamler, Stenkewitz, Gharajehdaghipour, & Macdonald, 2019). No carnivore species was heavily persecuted on BNR during the study, although jackals were occasionally shot (<3 jackal/yr) during culling operations for ungulates. However, most jackals frequently travelled throughout the year beyond the boundary of BNR and onto privately owned small-livestock farms (Kamler et al., 2019), where jackals were heavily persecuted and occurred at low densities (0.02 jackal/km^2; Kamler et al., 2013). Therefore, all jackals on BNR were vulnerable to human persecution either during culling operations on BNR, or when they travelled onto private lands surrounding BNR. Vegetation on BNR contained elements of three major biomes, Savanna, Nama Karoo and Grassland, although the most dominant was Nama Karoo vegetation. See Kamler, Stenkewitz, Klare, Jacobsen, and Macdonald (2012) for a more detailed description of the study site.

During 1995–1997, we conducted research on the Hwange estate (HWE; 1,000 km^2), an area containing state and private land bordering the northeastern side of Hwange National Park, Zimbabwe (18°45′S; 26°45′E). The HWE contains a self-regulated ecosystem with no human hunting, although safari tourism is allowed. There is no fence between HWE and Hwange National Park, so HWE contained the same fauna found in adjacent areas of the park. Thus, five species of large carnivores were present in HWE during the study, including lions, spotted hyaenas, leopards, cheetahs and African wild dogs (Loveridge, 1999). The only exception was brown hyaenas, which did not occur in the northern part of the park and adjacent areas at that time. The densities of jackals and large carnivores in HWE were unknown. Vegetation was predominately teak (*Baikiaea plurijuga*) woodland and false mopani (*Guibourtia coleosperma*) with some grassland and scrub areas. See Loveridge and Macdonald (2001) for a more detailed description of the study site.

2.2 | Capture and monitoring

On both sites, we captured jackals using padded foothold traps (Kamler, Jacobsen, & Macdonald, 2008) set along dirt roads where we encountered numerous jackal signs (e.g. scats and tracks). Trapping was undertaken only during the dry season to avoid capturing juveniles, and only fully grown individuals were collared. We fitted captured jackals with radio collars from Advanced Telemetry Systems (190 g) on BNR, and from Biotrack Ltd. (200 g) on HWE. Captured jackals were aged according to tooth wear and reproduction condition, and classified as alphas (breeding adults) or betas (non-breeding adults; Kamler et al., 2019). Jackals were captured in consecutive years during the study periods on both sites, for a total of 333 trap nights on BNR and 157 trap nights in HWE. The entire radio-tracking period consisted of 31 months on BNR and 22 months on HWE. However, only 4 jackals were collared during the first 11 months of the study on BNR, and these were biased towards jackals living near the research station at the centre of the reserve; thus, these data were excluded from the analyses. Consequently, we used 22 months of radio-tracking data for both sites. For BNR, our research and handling protocol (no. 0401/05) was approved by the Department of Tourism, Environment and Conservation, Kimberley, South Africa. For HWE, a research permit was not necessary at that time because the study occurred on private land. Our handling and care protocols were consistent with the guidelines provided by the University of Oxford, Biomedical Sciences, Animal Welfare and Ethical Review Body (AWERB).

On both sites, jackals were monitored on a weekly basis using triangulation with 4-element Yagi antennas. When jackals became stationary for >8 hr, we visually located jackals to confirm if they were dead. We classified causes of mortality as human hunting, leopard predation or indeterminate. Human hunting occurred on BNR and surrounding lands, and in all cases involved jackals being shot by humans. We classified mortality as leopard predation if carcasses were found hanging from tree limbs or beneath trees that leopards had used to feed on prey. In all cases, jackal carcasses were mostly or completely consumed by leopards, often with leopard tracks, claw marks and/or the burying of entrails at the feeding site. We classified mortality as indeterminate if carcasses had no visible evidence of cause of death.

Annual survival was calculated in the R package ‘survival’ using the Kaplan–Meier method with a staggered entry design (Pollock, Winterstein, Bunck, & Curtis, 1989) with site as a parameter. A log-rank test was used to compare annual survival curves between sites. Statistical analyses were carried out in R Studio version 2.38 (R Studio Team, 2016). Although data from 22 months of monitoring were used in the analysis, results were given as annual survival to standardise estimates among sites and studies.

3 | RESULTS

On BNR, we collected 4,684 radio-days from 12 jackals (7 males and 5 females) monitored from 1 May 2006 to 28 February 2008 (22 months). Of 6 confirmed deaths during the study on BNR, 5 were from human hunting and 1 was indeterminate. On HWE, we collected 4,380 radio-days from 12 jackals (3 males and 9 females) monitored from 1 July 1995 to 30 April 1997 (22 months). Of 6 confirmed deaths during the study on HWE, 4 were from leopard predation and 2 were indeterminate. Contact was lost from one jackal from each site due to probable dispersal. Annual survival of jackals was 0.56 (95% CI = 0.35–0.92) on BNR and 0.62 (0.42–0.91) on HWE, and there was no significant difference in the annual survival curves between sites ($p = 0.990$; Figure 1).

Jackals were killed by humans during both the wet (Sep-Feb; $n = 2$) and dry (Mar-Aug; $n = 3$) seasons, and jackals were killed by leopards during both the wet ($n = 2$) and dry ($n = 2$) seasons. Humans killed both alpha ($n = 2$) and beta ($n = 3$) jackals, and leopards killed both alpha ($n = 2$) and beta ($n = 2$) jackals. Humans killed both male ($n = 3$) and female ($n = 2$) jackals, whereas leopards killed only female jackals, although females comprised 9 of 12 collared jackals on HWE.

4 | DISCUSSION

Our results showed that mortality from human hunting can have similar effects on jackal survival as predation by large carnivores. On BNR, nearly half of all collared jackals died from human hunting. Most of these deaths (4 of 5) occurred when jackals took forays onto surrounding small-livestock farms (Kamler et al., 2019) where they inevitably came into contact with human hunters, whereas one death occurred on BNR during a culling operation for ungulates. On HWE, despite the lack of human hunters, jackals had survival that was similar to BNR, primarily because of 4 deaths to leopard predation. Jackals are likely to have evolved in ecosystems with high levels of mortalities from large carnivores and apparently compensate for increased mortality by having high reproductive rates, helping to explain why jackals can persist on private farmlands in South Africa despite high rates of human-caused mortalities (Minnie, Gaylard, et al., 2016). Major limitations of our research were that our two study sites occurred in different habitats with presumably different food resources, at different times, and in different countries. Nonetheless, we assume the top-down mortality factors (human or large carnivore) on each site overrode any potential differences that habitat, food resources, distance or year might have had on survival estimates. On both sites, top-down mortality factors were the largest cause of mortality and consequently had the greatest impact on jackal survival. Although sample sizes were too low for statistical comparisons, there did not appear to be any seasonal, sexual or social pattern of jackals killed by humans and leopards, suggesting the two major mortality factors had similar effects on jackal demographics. Although only 12 jackals were collared on each site, the collared jackals comprised 1–2 members of all 7 family groups that were known to occur on BNR (Kamler et al., 2019). Similarly, on HWE collared jackals comprised 1–3 members of all 5 family groups that were known to occur in the core of HWE (Loveridge, 1999). Therefore, we assume that the mortality and survival of the radio-collared jackals adequately represented the mortality and survival of the entire jackal population on both sites.

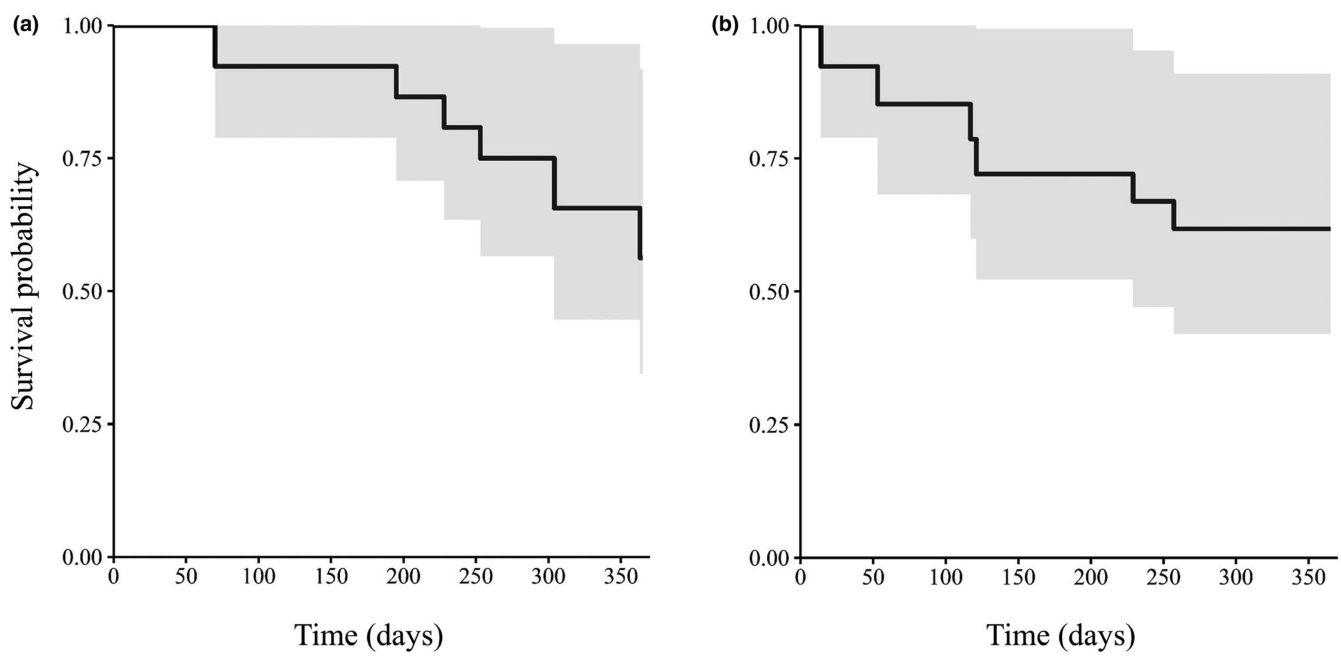

FIGURE 1 Annual survival curves for black-backed jackal populations on (a) Benfontein Nature Reserve (BNR), South Africa, and (b) Hwange Estate (HWE), Zimbabwe. Grey shading represents 95% confidence intervals

There is some uncertainty as to whether the presence of large carnivores is beneficial (via provisioning of carcasses) or detrimental (via increased competition or mortality) to populations of jackals. Some research has suggested that black-backed jackals benefit from large carnivores, because the proportion of large ungulates increased in jackal diets after lions were introduced into a site, presumably due to jackals scavenging on lion kills (Fourie, Tambling, Gaylard, & Kerley, 2015). In contrast, two other studies found that jackal diets did not differ based on the presence of large carnivores (Brassine & Parker, 2012;Yarnell et al., 2013), indicating jackals did not benefit from the presence of large carnivores. One study found that the presence of leopards and brown hyaenas did not affect the occupancy of jackals in South African Karoo (Drouilly, Clark, & O'Riain, 2018). In contrast, another study found that the density of jackals was 3 times higher at a site without lions and African wild dogs, compared to a neighbouring site where both large carnivores were present (Yarnell et al., 2013). Thus, it seems possible that different species and densities of large carnivores might have different impacts on jackal numbers, although future research in Africa is needed to test this hypothesis.

Although annual survival has never been previously determined for any jackal populations, several studies in North America have determined annual survival of coyote (*Canis latrans*) populations, an ecologically similar species. In general, annual survival of coyotes was 47%–64% in moderately to heavily hunted populations, 68%–74% in small protected areas or lightly hunted populations, and 87%–91% in large protected areas with no hunting (Kamler & Gipson, 2004). Thus, survival of jackals on BNR was comparable to those of coyotes in moderately to heavily hunted populations. Similar to jackals on BNR, research on coyotes showed that this species has such wide-ranging movements and that populations on small reserves are affected by human-caused mortality and other edge effects outside those reserves (Kamler, Ballard, Gilliland, & Mote, 2004; Kamler & Gipson, 2004; Kamler, Klare, Ballard, Wallace, & Gipson, 2014). Survival of jackals on HWE also was comparable to moderately to heavily hunted populations of coyotes, indicating that predation on jackals by large carnivores has similar effects on jackal survival as human hunting. Of course, caution should be used when extrapolating our results to other areas, because human hunting of jackals on livestock farms can be much higher than on BNR (Kamler et al., 2013; Minnie, Avenant, et al., 2016, 2018; Minnie, Zalewski, Zalewska, & Kerley, 2018), which likely would result in much lower survival of jackals on livestock farms compared to BNR and HWE. Nonetheless, our results provide a baseline for future studies of jackal survival in other populations.

Although five species of large carnivores were present on HWE, only leopards were found to prey upon jackals. Consumption or killing of jackals by leopards was reported in previous studies (Hayward, Henschel, et al., 2006; Loveridge & Nel, 2004). In fact, leopards might be the greatest natural predator of jackals, at least in some populations. In East Africa, early researchers stated that leopards preyed frequently on jackals (van Lawick & van Lawick-Goodall, 1970; Schaller, 1972), and Estes (1991) reported that over several weeks a leopard brought back 11 jackals and proceeded to eat them on a tree platform beside his cabin. The latter account suggests some individual leopards might even specialise on predating jackals (Balme, le Roex, Rogan, & Hunter, 2020). Several studies in both East and South Africa found jackals were part of leopard diets, usually in small amounts (2%–5% of scats or kills; Kruuk & Turner, 1967; Bothma & le Riche, 1984; Mills, 1984; Grimbeek, 1992), although one study in the Kalahari found jackal remains in 15% of leopard scats (Bothma & le Riche, 1994). Regardless of their importance in leopard diets, predation on jackals by leopards likely varies spatially (Drouilly, Clark, et al., 2018) and could be related to densities of leopard and prey, as well as differences in habitat types. For example, leopards did not prey on side-striped jackals (*Canis adustus*) in HWE, which used a different habitat type compared to black-backed jackals (Loveridge & Macdonald, 2002). Similarly, other research in South Africa has shown that impacts of large carnivores on subordinate carnivores are affected by habitat (Rostro-García, Kamler, & Hunter, 2015). Clearly, more research is needed about the impacts of leopards on jackal populations, particularly to better understand under what conditions leopards could affect jackal ecology.

Our study provides the first estimates of annual survival for any jackal population and showed that mortalities from both large carnivores and humans produced similar effects on jackal survival. We were unable to determine whether top-down mortalities were compensatory or additive, although that should be the focus of future research. We also recommend that research be carried out in jackal populations where both large carnivores and human hunting are absent, to gain a more complete understanding of the major factors that affect jackal survival under different conditions.

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DATA AVAILABILITY STATEMENT

Data are available on request.

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