Evidence that vulture restaurants increase the local abundance of mammalian carnivores in South Africa

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Abstract

Vulture restaurants are used worldwide as a conservation tool to provide threatened vultures with a source of supplementary carrion free from anthropogenic contaminants such as poisons and veterinary drugs. While the impacts of supplementary feeding sites on ecosystem and scavenging community dynamics have been investigated in Europe, no information is currently available for southern Africa. This study presents evidence that providing supplementary carrion for vultures stimulated an increase in local abundance of two species of mammalian carnivores, the brown hyaena (*Hyaena brunnea*) and the black-backed jackal (*Canis mesomelas*). These findings require that the wider impacts of providing supplementary carrion for conserving threatened species are fully investigated.

Keywords: supplementary feeding; numerical response; scavengers; African carnivores; vultures; conservation management

Introduction

As specialised obligate scavengers *Gyps* vultures provide valuable ecosystem services by contributing to nutrient cycling and potentially limiting the spread of disease (DeVault *et al.*, 2003; Sekercioglu, 2006). However, their populations are declining worldwide due to multiple threats including poisoning and reduced availability of the carrion supply upon which they depend (Ogada *et al.*, 2012a). These declines are expected to cause detrimental effects on environmental and human health. For example, it has been suggested that an increase in human cases of rabies caused by dog (*Canis familiaris*) bites in India could be linked to a considerable increase in feral dog numbers following the near-extinction of vulture populations that previously competed for carrion at carcass dumps (Pain *et al.*, 2003; Markandya *et al.*, 2008).

Supplementary feeding sites, often termed "vulture restaurants", are used as a conservation tool by providing vultures with a source of uncontaminated food in an effort to reduce mortality risks associated with low food availability and high rates of poisoning (Piper *et al.*, 1999; Gilbert *et al.*, 2007; Deygout *et al.*, 2010). While such schemes have been shown to reduce mortality rates in some vulture populations (Piper *et al.*, 1999; Gilbert *et al.*, 2007), the wider impacts of regular provisioning of carrion at fixed locations on avian and terrestrial scavenger community dynamics remain poorly understood (Cortes-Avizanda *et al.*, 2012). It is likely that changing the spatial and temporal predictability of a naturally ephemeral food supply will lead to changes in the foraging ecology and competitive interactions of the scavenging community (Robb *et al.*, 2008; Deygout *et al.*, 2009; Cortes-Avizanda *et al.*, 2012; Wilson and Wolkovich, 2011; Oro *et al.*, 2013). For example, hunting activity (Wilmers *et al.*, 2003; Mateo-Tomas and Olea, 2010), changes in livestock carcass disposal practices (Donazar *et al.*, 2010; Yirga *et al.*, 2012) and changes in abundance of dominant predators and scavengers (van Dijk *et al.*, 2008; Olson *et al.*, 2012) have been linked to alterations in carrion availability affecting scavenger community composition and dietary habits. Although increased carrion availability and predictability have benefitted some species of conservation concern (Piper *et al.*, 1999; van Dijk *et al.*, 2008), detrimental impacts on non-target species have also been recorded. For instance, predation of ground nesting birds by opportunist scavengers was higher in the vicinity of a vulture restaurant in Europe (Cortés-Avizanda *et al.*, 2009). There is also a risk that encouraging aggregations of large numbers of mammalian carnivores at supplementary feeding sites will increase the likelihood of the spread of certain diseases such as rabies (Pain *et al.*, 2003; Wright & Gompper, 2005; Monello & Gompper, 2011; Ogada *et al.*, 2012b). This has resulted in fencing being used at some sites to successfully exclude terrestrial scavengers (Moreno-Opo *et al.*, 2012).

Vulture restaurants are used widely in South Africa to provide safe feeding sites for vultures and also act as a focal point for population monitoring (Mundy *et al.*, 1992; Monadjem *et al.*, 2013; Phipps *et al.*, 2013a). To date, the wider effects of providing supplementary carrion for vultures on ecosystem dynamics are unknown in the region. Two mammalian carnivores that potentially exploit carrion at vulture restaurants in southern Africa are the brown hyaena (*Hyaena brunnea*) and the black-backed jackal (*Canis mesomelas*, hereafter referred to as jackal). Both species are opportunistic scavengers that interact competitively with each other and with vultures (Kruuk, 1967; Ogada *et al.*, 2012b). The brown hyaena ("near threatened" (Wiesel *et al.*, 2008)) occurs mainly in unprotected rangelands where high levels of human persecution (St John *et al.*, 2012; Thorn *et al.*, 2012) and limited access to scavenging opportunities provided by other large predators (Thorn *et al.*, 2010) have led to reduced population densities. The brown hyaena might therefore be a species of conservation concern that benefits locally from the provisioning of supplementary carrion for vultures. By contrast, the jackal ("least concern" (Loveridge and Nel, 2008)) is often perceived as a pest species capable of preying on young livestock and wild ungulates (St John *et al.*, 2012; Thorn *et al.*, 2012) that has the ability to suppress populations of prey species and sympatric mesocarnivores through lethal and sub-lethal effects (Blaum *et al.*, 2009; Kamler *et al.*, 2013). Exploitation of carrion by jackals at vulture restaurants may cause local increases in their density, which is likely to be an undesirable consequence for livestock and game ranch managers or conservation practitioners (St John *et al.*, 2012; Thorn *et al.*, 2012; Kamler *et al.*, 2013). In addition, when densities of mammalian scavengers are elevated to unusually high levels around locally abundant sources of carrion the risk of the development and spread of diseases such as rabies increases, posing a threat to environmental and human health (Zulu *et al.*, 2009; Monello & Gompper, 2011; Bellan *et al.*, 2012; Ogada *et al.*, 2012b).

The aim of this study was to investigate whether providing supplementary carrion for vultures induced an increased abundance in two species of mammalian carnivores on a private game reserve in the North West Province of South Africa. Based on our findings we discuss the implications of introducing supplementary carrion for vultures from an ecological and conservation management perspective.

Methods

The study took place at two sites, Pilanesberg National Park (PNP) (25°24’S; 27°08’E) and Mankwe Wildlife Reserve (MWR) (25°13’S; 27°18’E), which are located approximately 6 km apart in North West Province, South Africa. PNP (570 km^2) was established in 1978 to promote conservation and tourism and is enclosed by an electrified wire mesh fence designed to prevent the movement of animals, especially the park’s large carnivores (lion *Panthera leo*, leopard *P. pardus*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus* and brown hyaena *H. brunnea*) (Van Dyk & Slotow, 2003; Carruthers, 2011). MWR (47 km^2) is a private game reserve that has been managed for conservation and ecotourism since 1982 and is surrounded by an electrified wire fence that prevents the movements of large ungulates but through which smaller species, including brown hyaena and jackal, can pass (Yarnell *et al.*, 2013). Brown hyaena are the only large carnivores resident in MWR. The surrounding land is a mixture of low intensity communal and freehold livestock farms farmed mainly by members of the former Bophuthatswana community (Carruthers, 2011).

A vulture restaurant was established at MWR in March 2008 where carcasses of domestic livestock (e.g. cattle *Bos primigenius*) and wild ungulates (e.g. common wildebeest *Connochaetes taurinus*) were collected from local farms and deposited (Phipps *et al.*, 2013b). The carcass type and estimated biomass was recorded for all depositions. Total annual and mean monthly biomass (kg) per year of supplementary carrion was calculated. Provisioning of supplementary carrion at the vulture restaurant at MWR began in 2008 (total 2008 biomass = 7986 kg) and continued until August 2011 (total 2011 biomass = 1320 kg) with a peak biomass of 15490 kg being deposited in 2009 (Fig. 1). The mean (±SD) number of days per month when supplementary carrion was provided was 4.00±2.86 in 2008, 5.17±3.64 in 2009, 2.33±1.83 in 2010, and 0.88±0.83 days month^{-1} in 2011 (up to August 2011 when provisioning ceased). From March 2008 until August 2011 the mean (±SE) biomass of carrion provided at the restaurant each month was 797±124 kg. No supplementary carrion was provided at PNP throughout the study period.

We used a relative index of abundance (RIA) calculated from faecal scat transect surveys (RIA = scat count km^{-1}; Jhala, Qureshi & Gopal, 2011) to monitor brown hyaena and jackal relative abundance at both sites between 2007 and 2013. This provided a RIA value for both species before, during and after carrion supplementation at the MWR vulture restaurant. Scat transect surveys were conducted annually in August from 2007 to 2013 for monitoring purposes along tourist and management roads at both sites (Thorn *et al.*, 2010). Scats were identified to species level based on appearance and size (Stuart & Stuart, 2000), and only scats that were identified with a high degree of confidence were included (Thorn *et al.*, 2010). For both species accumulations of more than one scat within a 10 m radius (*sensu* hyaena latrines (Thorn *et al.* 2010)) were recorded as one individual scat for comparative purposes. A total of 28.82 km and 63.90 km of consistently surveyed scat transect routes were completed annually in PNP (mean±SD transect length = 4.80±1.67 km; n = 6) and MWR (mean±SD transect length = 12.78±1.73 km; n = 5), respectively. Although survey effort was consistent each year, data on jackal scats were not collected in PNP in 2008 due to logistical constraints.

ANOVA tests with a repeated-measures design were used to assess whether jackal and brown hyaena RIA values differed significantly between years (2007 – 2013) across individual transects on each site (individual year was the repeated-measures factor). To test whether changes in annual jackal and brown hyaena RIA values were related at and between both sites, Spearman's rank correlation coefficients were calculated. In order to investigate the relationship between annual carrion supplementation and mean RIA across transects at MWR, a linear regression was performed. A time-lag of one and two years was also incorporated into the regression analysis to allow time for the abundance of each species to respond to the supplementary food. Statistical analyses were performed in Minitab 16 and SPSS 21.

RESULTS

The relative index of abundance (RIA = scats km^{-1}) for brown hyaena and jackal both increased annually at MWR following the onset of supplementary feeding in 2008, reaching a peak in 2011, and then declining in 2012 and 2013 when supplementary feeding had ceased (Fig. 1). There was a significant difference between years in jackal ($F(6,24) = 6.264$, $P < 0.0005$) and brown hyaena ($F(6,24) = 16.320$, $P < 0.0005$) RIA values across transects in MWR, with the highest values for both species recorded in 2011 (Fig. S1). At MWR hyaena (RIA = 1.63 scats km^{-1}) and jackal (RIA = 3.35 scats km^{-1}) RIA across all transects in 2011 was 54.33 and 6.32 times higher, respectively, than hyaena (RIA = 0.03 scats km^{-1}) and jackal (RIA = 0.53 scats km^{-1}) RIA in 2007 before supplementary carrion was provided at the vulture restaurant (Figs. 1 and 2). The change in annual jackal RIA was highly significantly related to the change in annual brown hyaena RIA at MWR ($r_s = 1.00$, $P < 0.001$), indicating that the RIA for both species fluctuated concurrently.

In contrast brown hyaena and jackal RIA values for PNP showed only minor fluctuations between 2007 and 2013 (Fig. 1). Although there was no significant difference between years in brown hyaena RIA at PNP ($F(6,30) = 2.220$, $P = 0.069$), the difference was significant for jackal RIA ($F(5, 25) = 4.255$, $P = 0.003$), explained by outlying high and low values recorded in 2013 and 2010, respectively (Fig. S1). Annual jackal RIA was not significantly related to annual brown hyaena RIA in PNP ($r_s = -0.257$, $P = 0.623$). Annual jackal and brown hyaena RIA values at MWR were not significantly related to annual jackal ($r_s = -0.657$, $P = 0.156$) or brown hyaena ($r_s = 0.571$, $P = 0.180$) RIA values at PNP.

Linear regression between RIA and food supplementation (annual mean monthly biomass of supplementary carrion) in the corresponding year at MWR found no significant relationship for hyaena (r^2 = 0.00, F = 0.002, P = 0.894) or jackal (r^2 = 0.00, F = 0.001, P = 0.918). By adding a time lag of one year between food supplementation and RIA there was still no significant relationship for hyaena (r^2 = 0.21, F = 2.600, P = 0.168), however there was a significant relationship for jackal (r^2 = 0.57, F = 8.960, P = 0.03). With a time lag of two years there was a significant relationship for both hyaena (r^2 = 0.76, F = 20.140, P = 0.006), and jackal (r^2 = 0.75, F = 18.950, P = 0.007) (Fig. 3).

Discussion

Our findings suggest that increases in the scat survey derived relative index of abundance (RIA) of both jackal and brown hyaena at MWR were closely linked to the provision of supplementary carrion at the newly established vulture restaurant. Correspondingly the subsequent decrease in RIA of both species followed the decrease and eventual cessation of carcass supplementation at the end of 2011. At neighbouring PNP where no supplementary carrion was provided, brown hyaena RIA remained relatively consistent between years (Fig. S1). The difference in jackal RIA between years at PNP was due to unusually high and low values in 2013 and 2010, respectively, and did not follow a clear pattern or correspond with the changes at MWR (Fig. S1). It is credible, therefore, that the introduction of supplementary carcasses increased the abundance and spatial predictability of carrion at MWR and stimulated an increase in the local abundance of both jackals and brown hyaena (Wilson & Wolkovich, 2011). Although evidence for the exact mechanism of the increase in abundance is not available, it is likely that a combination of immigration, increased productivity and changes to the spatial organisation of both species played a part (Fuller & Sievert, 2001; Bino *et al.*, 2010; Wilson & Wolkovich 2011).

The peak in provision of supplementary carrion occurred in 2009 at MWR, and the jackal and brown hyaena RIA peaked two years later (2011), demonstrating a time-lag between carrion provisioning and numerical response in carnivore abundance (Fig. 3). The lag may be due to the time taken for the populations of both species to respond to the increased abundance of carrion, in terms of lower mortality rates, increased birth rates or higher survival of young. It is also likely that brown hyaena and jackals foraging in the wider area would have taken time to learn of and respond to the increase in carrion supply, resulting in a lag between the increased carrion abundance and immigration into the area, with consequent changes to the spatial organisation and composition of the scavenger community (Fuller and Sievert, 2001; Kortello *et al.*, 2007; Bino *et al.*, 2010). Further evidence that supplementary feeding was linked to carnivore abundance can be seen in the years where levels of carrion provisioning drop and then cease. This reduction in carrion supply, and therefore overall food abundance and predictability in MWR, appears to have resulted in a decrease of RIA for both jackal and brown hyaena at MWR. Similar patterns of fluctuations in the local abundance of carnivores following the introduction or removal of abundant and spatially predictable food sources have been recorded in spotted hyaena *Crocuta crocuta* (Kolowski & Holekamp, 2007) and red foxes *Vulpes vulpes* (Bino *et al.* 2010). Interestingly, the decrease in RIA after the cessation of supplementary feeding appears to be slower than the initial increase observed after supplementation began. This follows suggestions that reducing available anthropogenic resources might result in lagged decreases in carnivore abundance, sometimes due to a preceding overexploitation of other local resources (Fuller and Sievert, 2001; Bino *et al.*, 2010).

In July 2012, seven jackals and one brown hyaena were found dead at MWR within the space of two weeks. Two jackal and one brown hyaena specimen were sent for post-mortem at Onderstepoort Faculty of Veterinary Science, University of Pretoria, where the cause of death for all three individuals was confirmed as rabies. It is suspected that all individual carnivores that were found dead at MWR during this period possibly died from rabies. Although firm evidence is lacking, it is plausible that the provision of supplementary carrion stimulated local jackal densities to increase, resulting in a higher frequency of competitive interactions at the feeding site and potentially increasing the possibility of rabies infection and transmission between individuals (Monello and Gompper, 2011; Bellan *et al.*, 2012; Ogada *et al.*, 2012b). Subsequently, the cessation of carrion supplementation at the end of 2011 might have introduced nutritional stress into the jackal population and expedited the onset of clinical symptoms in infected individuals, ultimately causing their death (Altizer *et al.*, 2003; Bino *et al.*, 2010; Bellan *et al.*, 2012). Although this is speculative discussion, given the serious threat that rabies and other diseases carried by jackals pose to human health, economic stability and wildlife conservation (Craft *et al.*, 2009; Zulu *et al.*, 2009), this inadvertent effect of providing and then withdrawing supplementary carrion urgently requires further investigation.

Although further replicate studies are needed to determine whether the trends reported here are representative of other vulture restaurants in southern Africa, the wider potential impacts of providing supplementary carrion at vulture restaurants may present a paradox to reserve managers and conservation practitioners. While it is widely acknowledged that vultures play an important role in reducing the development and spread of disease by quickly locating and consuming carcasses (Sekercioglu, 2006; Markandya *et al.*, 2008; Ogada *et al.*, 2012a, 2012b), it is possible that establishing vulture restaurants might cause disruption to their natural ecological function, as well as impacting upon their mammalian counterparts. It has already been shown in Europe that providing carrion at fixed locations is likely to reduce vulture scavenging efficiency and disrupt the social organisation of the scavenger guild (Deygout *et al.*, 2009, 2010; Cortez-Avizanda *et al.*, 2012). Moreover, given the ability of opportunistic species such as jackals to suppress local populations of prey and sympatric carnivore species through competition and increased predation rates (Blaum *et al.*, 2009; Cortés-Avizanda *et al.*, 2009; Kamler *et al.*, 2013), as well as their potential to act as disease vectors (Zulu *et al.*, 2009), we urge further assessment of the wider impacts of providing supplementary carrion at fixed locations.

If providing supplementary carrion for vultures continues to be used as a conservation tool in southern Africa we recommend that fences could be erected around vulture restaurants to exclude terrestrial scavengers, as used successfully in Europe (Moreno-Opo *et al.*, 2012). We also support suggestions that the most effective and appropriate method of providing supplementary carrion for both avian and terrestrial scavengers is to irregularly deposit carcasses of varying types and sizes at random locations throughout the landscape in order to simulate a naturally ephemeral and unpredictable food source (Deygout *et al.*, 2009, 2010; Cortés-Avizanda *et al.*, 2009, 2012; Donazar *et al.*, 2010). Although we acknowledge that there are many practical issues to consider when implementing supplementary feeding schemes, we urge land managers and conservation practitioners to consider the wider impacts of introducing supplementary carrion to the local ecosystem, and to attempt to mitigate any negative impacts where possible. We also propose that a thorough assessment of the use and management of vulture restaurants for vulture conservation across southern Africa is required.

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Figure Legends

Figure 1. Relative changes in Log_{10} of standardised brown hyaena and jackal relative index of abundance (RIA = scats km^{-1}) at Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR) in relation to total annual biomass of supplementary carrion placed at MWR vulture restaurant, North West Province, South Africa between 2007 and 2013. Annual RIA values were divided by the 2007 values in order to give a value of change relative to the first year of data collection, 2007.

Figure 2. Maps showing the location of jackal (hollow squares) and brown hyaena scats (grey circles) at Mankwe Wildlife Reserve in (a) 2007 before carrion supplementation started, and in (b) 2011 three years after carrion supplementation started. The location of the vulture restaurant is shown by a black triangle. Survey routes are denoted by letters A – E.

Figure 3. The linear regression relationship between annual mean monthly carrion biomass (kg) deposited at the vulture restaurant, and the mean relative index of abundance (RIA = scats km^{-1}) of (a) jackals (r^2 = 0.75, F = 18.950, P = 0.007; y = 1.06 + 0.0019 x) and (b) brown hyaena (r^2 = 0.76, F = 20.140, P = 0.006; y = 1.43 + 0.001 x), with a two year time lag across 5 transects at Mankwe Wildlife Reserve, between 2007 and 2013. 95% confidence intervals for RIA values are provided in Figure S1.

Figure S1. Mean annual relative index of abundance (RIA = scats km^{-1}) for (a) black-backed jackal and (b) brown hyaena determined from scat surveys along annually repeated transects at Mankwe Wildlife Reserve (MWR = Site 1; n = 5 transects) and Pilanesberg National Park (PNP = Site 2; n = 6 transects) between 2007 and 2013. Error bars represent 95% confidence intervals. Jackal scat data were not collected in 2008 at Pilanesberg National Park due to logistical constraints. Supplementary carrion was only provided at MWR from 2008 – 2011, inclusive, and never at PNP.

FIGURE 1

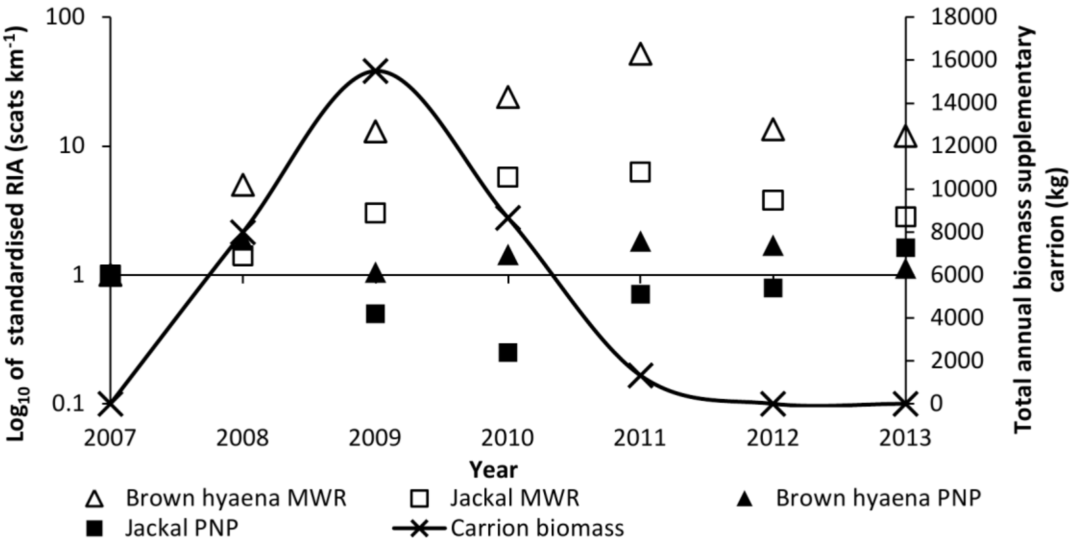

FIGURE 2

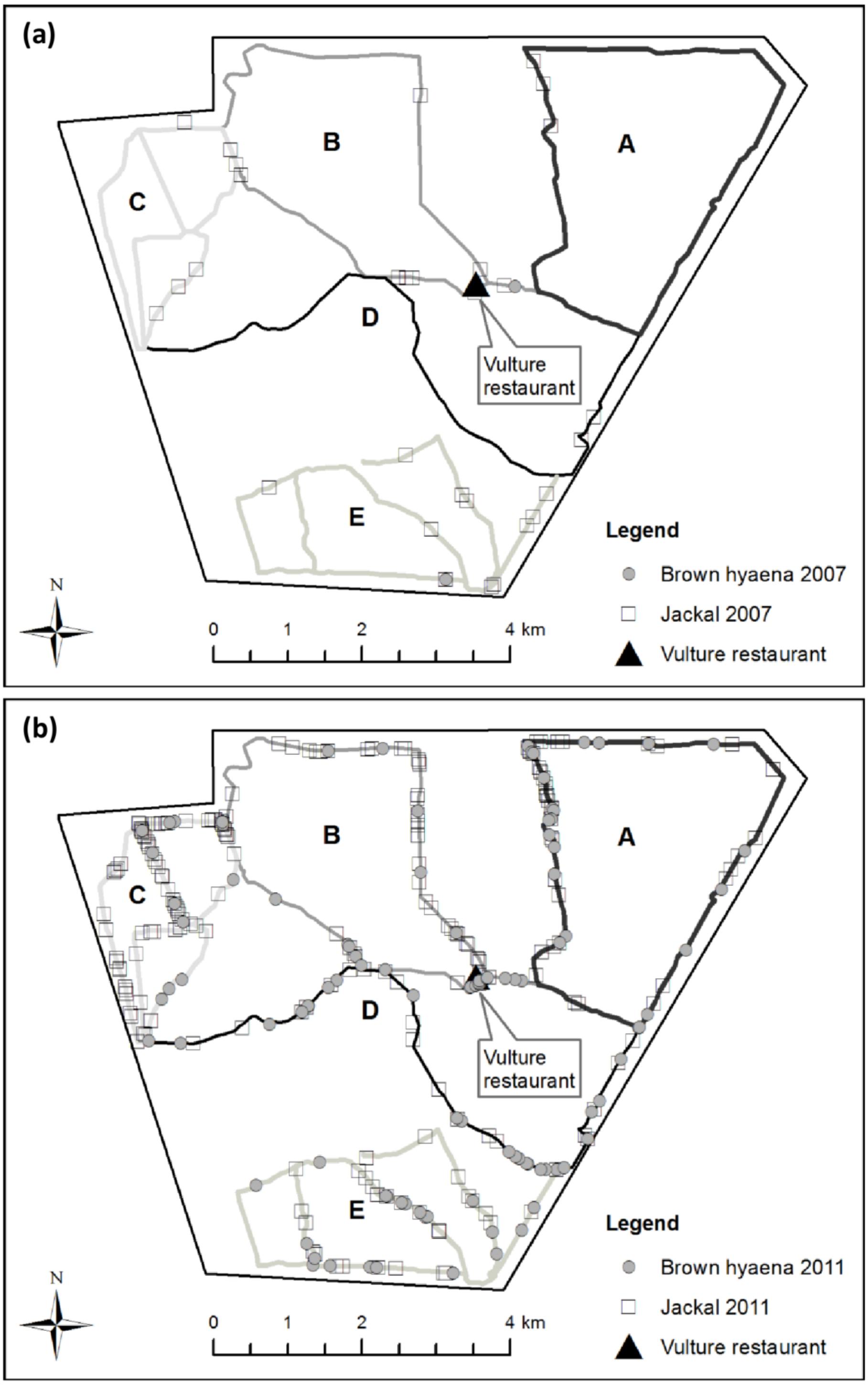
(a)
A
B
C
D
E
Vulture restaurant
Legend
Brown hyaena 2007
Jackal 2007
Vulture restaurant
N
0
1
2
4 km
(b)
A
B
C
D
E
Vulture restaurant
Legend
Brown hyaena 2011
Jackal 2011
Vulture restaurant
N
0
1
2
4 km

FIGURE 3

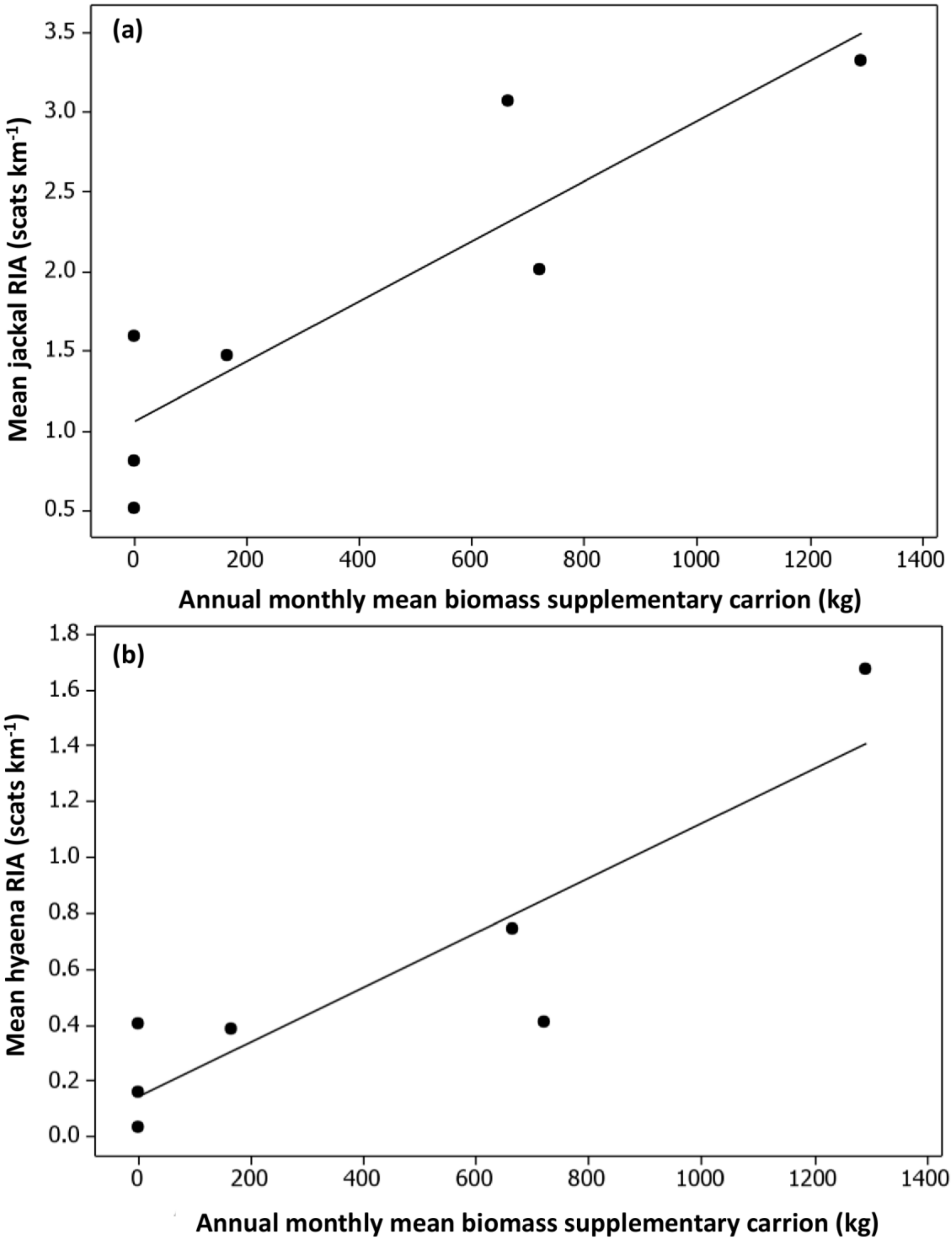
(a)
Mean jackal RIA (scats km-1)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
200
400
600
800
1000
1200
1400
Annual monthly mean biomass supplementary carrion (kg)
(b)
Mean hyaena RIA (scats km-1)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
200
400
600
800
1000
1200
1400
Annual monthly mean biomass supplementary carrion (kg)

FIGURE S1

Please see attached