Factors affecting the prey preferences of jackals (Canidae)

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Abstract

Prey selection by carnivores can be affected by top-down and bottom-up factors. For example, large carnivores may facilitate food resources for mesocarnivores by providing carcasses to scavenge, however mesocarnivores may hunt large prey themselves, and their diets might be affected by prey size and behaviour. We reviewed jackal diet studies and determined how the presence of large carnivores and various bottom-up factors affected jackal prey selection. We found 20 studies of black-backed jackals (*Canis mesomelas*) from 43 different times or places, and 13 studies of Eurasian golden jackals (*Canis aureus*) from 23 different times or places reporting on 3900 and 2440 dietary records (i.e. scats or stomach contents), respectively. Black-backed jackals significantly preferred small (< 30 kg) ungulate species that hide their young (duiker *Sylvicapra grimmia*, bushbuck *Tragelaphus scriptus* and springbok *Antidorcas marsupialis*), and avoided large (> 120 kg) hider species and follower species of any body size. They had a preferred and accessible prey weight range of 14-26 kg, and a predator to ideal prey mass ratio of 1:3.1. Eurasian golden jackal significantly prefer to prey on brown hare (*Lepus europaeus*; 4 kg), yielding a predator to preferred prey mass ratio of 1:0.6, and a preferred and accessible prey weight range of 0 – 4 kg and 0 – 15 kg, respectively. Prey preferences of jackals differed significantly in the presence of apex predators, but it was not entirely due to carrion availability of larger prey species. Our results show that jackal diets are affected by both top-down and bottom-up factors, because apex predators as well as prey size and birthing behaviour affected prey preferences of jackals. A better understanding of the factors affecting jackal prey preferences, as presented here, could lead to greater acceptance of mesocarnivores and reduced human-wildlife conflict.

Introduction

Adequate nutrition affects the fitness of an individual, and is crucial for its survival and reproductive success. Therefore, natural selection should theoretically select for behaviours that augment efficient feeding (Krebs, 1978). Optimal foraging theory states that animals forage in a way that maximizes their net rate of energy intake and subsequently their fitness; resulting in an optimal diet (Pyke, 1984; Pyke et al., 1977). While the evolutionary adaptations of large carnivores to optimal foraging via preferential predation are well studied (Clements et al., 2016; Hayward et al., 2016; Hayward et al., 2014; Krause and Godin, 1995), the optimal foraging strategies of mesocarnivores are poorly known. These might be affected by top-down factors, such as the presence of larger carnivores, as well as bottom-up factors, such as prey size, abundance, behaviour and habitat.

Larger carnivores can affect the prey selection of mesocarnivores through competition by: i) direct interference between individuals of the competing species or ii) exploitation of a shared food resource (Linnell and Strand, 2000). Yet, there are also commensal interactions between species where one benefits from the interaction while the other is not affected, such as the provisioning of carcasses for another species to scavenge from (Selva and Fortuna, 2007). Each of these top-down interactions may affect the prey preferences of mesocarnivores.

Jackals are typical mesocarnivores (5-15 kg) and generally are considered to be opportunistic generalist predators (Giannatos et al., 2010; McKenzie, 1997; Nowak, 1999; Van de Ven et al., 2013), or temporarily food specialists (Fourie et al., 2015; Lanszki et al., 2006) that perform valuable ecosystem services (Ćirović et al., 2016). However extensive research on predator prey preferences illustrates this generalisation is rarely the case, with bottom-up effects also influencing diet (Hayward et al., 2012; Hayward and Kerley, 2005). Side-striped jackals *Canis adustus* are considered omnivorous scavengers, while black-backed *C. mesomelas* and the golden jackals are thought to be more predatory but still omnivorous (scientific names of other species are in Table 1; Nowak, 1999). In Hwange, Zimbabwe, for example, side-striped and black-backed jackals had high dietary overlap (Loveridge and Macdonald, 2003). Jackal dietary flexibility enables them to respond to seasonal or other fluctuations in prey availability (Kaunda and Skinner, 2003). Rodents are a key component of the diets of jackals (Atkinson et al., 2002), but except for special cases (Klare et al., 2010; Lanszki et al., 2006), this reliable source of small packages of high energy yielding prey may not be sufficient for jackals to have evolved to optimally forage upon them as many prey may be required to satisfy the 168-240 g daily dietary requirements of jackals (Mukherjee et al., 2004). The slightly larger Ethiopian wolf's (*Canis simensis*) specialization on rodent prey is thought to reflect the abundance and reliability of these rodents in its

Afroalpine habitat, but may also lead to the restricted distribution and population size of this species (Sillero-Zubiri et al., 1995).

Foraging group size may affect the predation patterns of jackals as they live in pairs and family groups and have also been observed hunting and foraging in pairs or alone (Lamprecht, 1978; Macdonald, 1979). Similarly, different habitats may affect predation patterns due to different encounter rates. For example, small animals obtain more refuge in areas of dense vegetation, therefore encounter rates between them and jackals would be low (Stokes et al., 2004). Competition between sympatric black-backed and golden jackals (now considered African jackals; Koepfli et al., 2015) in Kenya was predicted to be low due to habitat and diet resource partitioning (Fuller et al., 1989). Similarly, in the Serengeti, black-backed jackals preferred areas of denser vegetation and around the perimeter of the plains whilst golden jackals mostly occurred in the open plains (Wyman, 1967). Black-backed jackals in Hwange displaced side-striped jackals from optimal grassland habitats through their higher levels of aggression, driving them into woodland and scrub (Loveridge and Macdonald, 2002). Prey communities, encounter rates and hunting efficiencies likely differ between habitats. Thus, habitat type is expected to affect jackal diets, although the extent is unknown.

Ungulate size and behaviour appears to have a large influence on jackal prey selection. On game farms in South Africa, black-backed jackals had a strong selection for hiders (Klare et al., 2010), ungulates in which the females give birth away from the herd and hide neonates in vegetation for the first weeks of their lives (Estes, 1999). In contrast, jackals avoided followers (Klare et al., 2010), whose neonates immediately follow the mother after birth, and are sheltered within the herd (Estes, 1999). Similar results were found in eastern Africa, where black-backed and golden jackals were considered to be major predators of gazelles, which are small, hider species, especially during birthing periods (Lamprecht, 1978;

Moehlman, 1983; Wyman, 1967). Among hiders, smaller species were more susceptible to jackal predation than larger species (Klare et al., 2010), indicating jackal predation is influenced by ungulate body size. Other factors, such as prey weaponry and aggressive nature, may also influence jackal prey selection due to the greater risk of injury, although this has never been studied in jackals, but is influential in other predators, like cheetahs *Acinonyx jubatus* (Clements et al., 2016; Hayward et al., 2006b). In general, the patterns of jackal prey preferences across their range are unknown, and additional factors, such as the presence of large carnivores, might alter the influence of ungulate behaviour on jackal prey preferences.

Livestock predation by both black-backed jackals and golden jackals induces conflict with humans, and patterns of such predation are uncertain (Lawson, 1989; McShane and Grettenberger, 1984; Rowe-Rowe, 1975; Yom-Tov et al., 1995). If predation on livestock by jackal occurs, it might be influenced by livestock type and behaviour. For example, the diet of black-backed jackals on small livestock farms in South Africa comprised 25-48% sheep *Ovis aries* across seasons, although jackals did not consume goat *Capra hircus* or cattle *Bos taurus* (Kamler et al., 2012). In contrast, golden jackals were found to predate on cattle calves in Israel (Yom-Tov et al., 1995). However, wild prey, including small mammals and ungulates, were consistently selected over sheep in South Africa, indicating that jackals do not preferentially prey upon livestock (Kamler et al., 2012).

This study aimed to determine the prey preferences of jackals. As jackals are below the 21.5 kg body mass threshold that dictates preferential predation on large body mass, vertebrate prey (Carbone et al., 1999; Macdonald et al., 2004a), we hypothesised that jackals will be small vertebrate specialists. We investigated the role that apex carnivores, a top-down factor, play in structuring jackal dietary preferences. We also investigated how various bottom-up factors, including prey size, prey behaviour, and habitat, as well as livestock type, affects jackal prey preferences. This provides the ability to predict the diet of jackals (following Hayward et al., 2007) is important due to their potential for human-wildlife conflict via predation on game animals and livestock and also due to their recent range expansion (Rutkowski et al., 2015; Trouwborst et al., 2015).

Materials and methods

We recognise that golden jackals have recently been split into a Eurasian *Canis aureus* and African *C. anthus* species (Koepfli et al., 2015; Rueness et al., 2011), however few studies are available for the African species. Similarly, there is insufficient dietary information on the side-striped jackal *C. adustus* coupled with prey availability to allow analysis (notwithstanding Atkinson et al., 2002; Loveridge and Macdonald, 2003). Hence, this study explores the prey preferences of black-backed and Eurasian golden jackals (golden jackals hereafter) only.

Simple dietary summaries reveal little about animal ecology. Species that occur more prominently in the diet could do so because they are the only species present or the most abundant in the area, or it may be a result of the carnivore selectively preying on that species (Hayward and Kerley, 2005). Hence, prey abundance data are crucial to interpret diet preferences. If a species is killed more frequently than expected based on its availability, it can be assumed that it is preferred, but if it is killed less than expected based on availability, that species is avoided.

We obtained data on jackal diet up until March 2015 by searching Google Scholar, Web of Science and grey literature, such as dissertations and reports, using keyword searches for *diet** OR *predation* OR *food* AND *jackal* OR *Canis*. Many studies had useful details on jackal diet yet were excluded from the analysis (Atkinson et al., 2002; Bothma, 1971; Giannatos et al., 2010; Loveridge and Macdonald, 2003; Macdonald et al., 2004b; Markov and Lanszki, 2012; McShane and Grettenberger, 1984; Van de Ven et al., 2013) due to; i) insufficient or no information on prey actual or relative abundance/densities or ii) inability to locate these data from other sources. Continuous observation is generally considered the superior method of determining the diet of predators (Mills, 1992). This type of data is particularly challenging to obtain for smaller predators, such as jackals, which are inherently evasive. Therefore, the studies featured herein relied on scat (n = 64) and stomach content analyses (n = 2; Supplementary Materials). In some cases, this could bias against larger prey species (Mills, 1992), but as studies on both species and sites with/without apex predators were dominated by scat analyses, we do not think this will affect our comparative results. Furthermore, the two stomach content studies were included because they may counter the biases associated with scat analysis (Mills, 1992).

There are many indices that researchers have used to define selectivity, however, none is without bias or increasing error with small sample sizes (Chesson, 1978). We used the Jacobs index, which minimizes these biases and relates actual or relative prey abundance to actual or relative diet (Jacobs, 1974), for this study. We used relative frequency of occurrence of prey items in scats as the measure of diet because we were focusing on the numerical preferences of jackals for prey species. We relied on the authors of the studies we used for their estimates of prey abundance, but we acknowledge that the methods used varied and this may be a source of error. Jacobs' index varies between +1 and -1, where +1 shows maximum preference and -1 shows maximum avoidance (Jacobs, 1974). The mean Jacobs index (*D*) for each prey species was calculated and these values were tested for significant avoidance or preference using *t*-tests against the mean of 0, where data were normally distributed, or a sign test if not. This type of analysis is not biased by results from one particular area because, for a species to be significantly preferred or avoided, several studies must have produced similar results (Lyngdoh et al., 2014). We determined whether sample size affected our prey preference estimates using regression models of Jacobs' index against sample size for all species with >4 studies where predation for a species was recorded.

Jackals are generally thought to eat small to medium-sized prey (Gittleman, 1985; Nowak, 1999) and particularly newborn ungulates (Klare et al., 2010), so we used ¾ of mean adult female body mass to account for juveniles and sub-adults killed following previous studies (Jooste et al., 2013; Table 1). Social organisation of prey species, their habitat use and their threat to predators can also affect a predator's ability to capture the prey and prey's ability to detect predators (Hayward and Kerley, 2005). We used a categorical variable of social organisation with 1 relating to solitary individuals, 2 relating to pairs, 3 to small family groups, 4 to small herds (10-50) and 5 to large herds (>50; Table 1). A categorical habitat variable was also used with 1 referring to open grasslands, 2 to savannah or open woodland and 3 to densely vegetated areas. Some species may occur in multiple habitats, in which case an average was used (Table 1). We estimated the likely threat of each prey species based on their possession of weaponry, aggressive nature and body size (where 0 = no likelihood of injury; 1 = potential for injury; 2 = potential for death; Table 1). Birthing strategies of ungulates can be classified into three types: 1) neonate hiders; 2) neonates followers; and 3) unknown (Estes, 1999). Because birthing strategy of ungulates was shown to affect prey preferences by black-backed jackals (Klare et al., 2010), this variable was included in the model for ungulates. Body mass, herd size, habitat use, potential threat and birthing strategy data were taken from Nowak (1999). Some prey species of golden jackal were grouped into categories because the species of cervids, birds or rodents consumed was not always stated. We tested whether these covariates influence jackal prey preferences using generalised linear models with Gaussian distributions and identity link functions on non-correlated variables. We evaluated all possible combinations of models derived from the covariates. Model selection occurred using Akaike's information criterion (AIC) within a maximum likelihood framework (Akaike, 1973, 1974). We used the sum of Akaike's weights (w_i) to determine the relative strength of each covariate with strongly supported models having ΔAIC of < 2 (Burnham and Anderson, 1998). We also presented model averaged parameter estimates using the full suite of models. Strongly supported relationships among individual variables were plotted using linear or loess best fit models.

At some sites, jackals occur sympatrically with larger carnivores, which may affect their diet via competition, intraguild predation risk or facilitation through jackals scavenging the carcasses of larger carnivore kills. It is difficult to distinguish kills from scavenging and, as were relied on studies using scat and stomach contents, whether they were scavenged or killed is unknown. To overcome this constraint, independent *t*-tests or Mann-Whitney U-tests were carried out on the Jacobs' index values of each prey species that occurred in sites with and without apex predators to determine whether apex carnivore presence had a significant affect. The presence of one or more of lion *Panthera leo*, leopard *P. pardus*, cheetah, African wild dog *Lycaon pictus*, spotted hyaena *Crocuta crocuta* and/or gray wolf *Canis lupus* was considered as the occurrence of an apex predator, notwithstanding the fact that sometimes jackals dominate interactions with some members of this guild. We used our knowledge of the study sites or the dietary publications themselves to define the presence or absence of apex predators at a site. We calculated the Shannon-Weiner diversity index (*H*) to compare the prey available at sites with and without apex predators for each jackal species. We also conducted an ANOVA to test whether Jacobs' index values for each species were affected by birthing strategy and the presence/absence of apex predators.

We identified the *accessible* prey weight range following the break point analysis using segmented models following Clements et al. (2014). The accessible prey weight range range refers to the size of prey potentially killed by a predator and is most likely to encompass the preferred weight range of earlier prey preference studies (Clements et al., 2014), which we estimated from loess smoothed plots of mean species Jacobs' index scores against body mass (Hayward et al., 2014). We calculated the *ideal* prey mass as the mean body mass of those species that were significantly preferred. We estimated the body mass of jackals as 7 kg, which was the lower range of adult female body mass (Nowak, 1999) and used this to determine the predator to prey mass ratio by dividing the ideal prey mass of prey by 7.

All analyses were conducted in R (Barton, 2013; R Core Development Team, 2008). Mean (± 1 S.E.) values are presented throughout.

Results

We found 20 studies of black-backed jackals from 43 different times or places over a total period of 56 years, and 13 studies of golden jackals from 23 different times or places over 47 years (Supplementary Materials). These reported on 3900 black-backed jackal scats and 2440 golden jackal scats or stomach contents (Supplementary Materials). There was spatial bias in the location of the studies we could use, with no records of black-backed jackal diet studies from the East African sub-population, and no records of golden jackal diets from west Asia and the Middle East (Fig. 1). We were unable to find any dietary studies of side-striped or African golden jackals that included prey abundance data.

Out of 23 prey species with >4 records, there was no effect of sample size on the prey preference estimates of black-backed jackals for 20 (Supplementary Material Fig. 1). Bushbuck ($r^2 = 0.16$, n = 27, $p = 0.001$) and steenbok ($r^2 = 0.11$, n = 19, $p = 0.0497$) exhibited negative relationships largely driven by no records of their predation at higher sample sizes, while common duiker prey preference increased with larger sample size ($r^2 = 0.09$, n = 20, $p = 0.046$). There was no effect of sample size on golden jackal prey preference estimates (Supplementary Material Fig. 2). The infrequency of these relationships, the low predictive power of these relationships, and the counterintuitive bias towards no records of predation events at larger sample size give us confidence that our results are not unduly biased by small sample size.

The most abundant prey at black-backed jackal study sites were rodents (relative abundance within the prey community = 0.91 ± 0.06 or 91% of the available prey community), impala (0.29 ± 0.06) and hares (0.24 ± 0.24); while small mammals (0.74 ± 0.10), chital (0.33 ± 0.09) and cattle (0.18 ±0.06) had the highest relative abundance at golden jackal study sites (Table 1). Black-backed jackals most frequently consumed birds (45.4 ± 11.8% of diet), sheep (42.7 ± 4.5%) and impala (26.3 ± 0.6%) where they were killed, while golden jackals primarily consumed small mammals (76.1 ± 6.7%), chital (33.4 ± 8.7%) and rodents (19.9 ± 13.3%; Table 1). Black-backed jackals consumed springhare, hares, birds, rodents, sheep, marine mammals and oribi; and golden jackals consumed sambar, roe and red deer, hares, nilgai, chital and rodents wherever they were sympatric (Table 1). The most frequently consumed items for black-backed jackals were kudu (consumed at 22 sites), bushbuck (18) and warthog (16), while golden jackals mainly consumed small mammals (11), wild boar (11) and pheasant (10; Table 1).

Jackal prey preferences

Black-backed jackals significantly prefer to consume birds, common duiker, bushbuck and springbok, and significantly avoid hares, blesbok, kudu, springhares, warthog, buffalo, small mammals, aardwolf, red hartebeest, eland, plains zebra, and wildebeest, and central tendency theory suggests that with a larger sample size they will significantly avoid giraffe, common reedbuck, ostrich, elephant, cattle, tsessebe, goats, sable, nyala, klipspringer and baboon (Table 1; Fig. 2). The mean mass of significantly preferred prey for black-backed jackal is 21.7 ± 3.5 kg (3/4 adult female body mass), yielding a predator to preferred prey mass ratio of 1:3.1.

European golden jackal significantly prefer to consume brown hare and significantly avoid cervids in general, and red deer specifically, langur monkeys, pheasant and small mammals (Table 1; Fig. 2). When small mammals and rodents are combined, they are consumed according to their availability ($D = -0.19 \pm 0.12$; $t_{15} = 1.52$, $p = 0.149$). The mean mass of golden jackal preferred prey (3/4 adult female brown hare body mass) is 4 kg, yielding a predator to preferred prey mass ratio of 1:0.6. There is no evidence for a preference for any livestock type by either jackal species (Table 1).

Black-backed jackals lived at sites with significantly more prey species present than did golden jackals (9.7 ± 0.8 cf 5.3 ± 0.3; $t_{22} = 8.31$, $p < 0.001$), but were more specific in preferentially consuming a significantly lower proportion of those available prey species (24 ± 4% cf 35 ± 4%; $t_{22} = 3.01$. $p = 0.013$). There was no difference in the number of species consumed or the number preferred between the jackal species (black-backed jackal species consumed = 4.6 ± 0.3, species preferred = 2.2 ± 0.2; golden jackal species consumed = 4.9 ± 0.3, preferred = 1.9 ± 0.2; Fig. 3). Nonetheless there were highly significant relationships between the number of prey at a site and the number of species consumed and preferred (Fig. 3).

Factors affecting jackal prey preferences

The generalised linear model of prey preferences by black-backed jackals revealed three models with strong support, and these consisted of prey body mass (twice) and threat (once) as the explanatory variables (Table 2; Fig. 4). These two variables were more than twice as influential in driving black-backed jackal prey preferences as herd size, prey abundance, habitat or prey birthing strategy (Table 2). The segmented model supported this and showed that black-backed jackals have a preferred and accessible prey weight range of 14 to 26 kg (Table 3; Fig. 5).

Black-backed jackals exhibited different diet preferences in the presence/absence of apex predators. Where apex predators were present, black-backed jackals had significantly greater preference for buffalo ($t_{10} = -2.27$, $p = 0.047$) and impala ($W_7 = 14$, $p = 0.045$), and significantly less for bushbuck ($t_{24} = 2.72$, $p = 0.012$; Fig. 6). This difference was not driven by differences in the relative abundance of prey species at sites with and without apex predators for any species except for impala ($W_7 = 10$, $p = 0.015$), which were significantly less common at sites with apex predators (14% of the available prey community) than without (50%). Despite this difference in dietary richness when apex predators are present, there is a greater dietary diversity at sites with apex predators ($H' = 0.70$) than without ($H' = 0.42$). Overall, there was a significant difference in Jacobs' index between birthing strategies with hiders preferred more than follower species, but there was no significant difference in Jacobs' index between the presence or absence of apex predators (Fig. 6). Black-backed jackals consume prey of similar size at sites with (32.3 ± 4.9 kg) and without apex predators (24.8 ± 7.7 kg; $t_{352} = 0.800$, $p = 0.423$).

The generalised linear model of diet preferences drivers of golden jackals revealed strong support for two models with body mass as the key explanatory variable (Table 2). Body mass was three-times as important in explaining golden jackal diet preferences as any other variable ($\Sigma w_i = 0.54$; Table 2). Jacobs' index values were highest at body masses below 4 to 5 kg (Fig. 4). This was confirmed by the segmented models showing strong support for three, four and five break points (Table 3) indicating a preferred prey weight range of 0 – 5 kg, and an accessible prey weight range of 0 – 15 kg (Fig. 5).

For golden jackals, wild boar were preferred at sites without apex predators and were significantly less preferred where apex predators were present (apex predators present Jacobs' index D = -0.25; absent D = 0.29; $t_{8.5}$ = 2.310, p = 0.048). Similarly, pheasants were significantly more avoided in the presence of apex predators (apex present D = -0.46, apex absent D = -0.27; $t_{1.4}$ = 0.001, p = 0.631). There was no difference in the relative abundance of these species at sites with and without apex predators (p > 0.05).

Discussion

Jackals are generally considered to be opportunistic, generalist predators – taking whatever prey is available - however our results show this is not the case as both focal species exhibit distinct preferences for specific species and particular body mass ranges. For black-backed jackals, this preference is not for small vertebrates (as predicted by their body mass being lower than the 21.5 kg limit for obligate large vertebrate predation; Carbone et al., 1999), but rather for smaller ungulates (< 30 kg) including springbok, common duiker and bushbuck, all of which are hider species. This adds weight to single site studies in South Africa that found black-backed jackals preferred species with such birthing behaviour (Klare et al., 2010). However, golden jackals follow predictions more closely with respect to their preference for hares. This optimal foraging on particular species is reinforced by the restriction and similarity in the number of prey species preferred by each jackal species – despite differences in the number available, both species target a limited number of them (Fig. 3). These preferences of jackals are driven mostly by prey body mass (Table 2), a bottom-up factor. The accessible and preferred prey weight range we determined was substantially larger than that reported from individual study sites (e.g., the Serengeti; Sinclair et al., 2003), however is likely to be reinforced if other studies were useable (e.g., Van de

Ven et al., 2013). The selection for ungulates may well be driven by predation on newborn young or sick individuals rather than healthy adults (McKenzie, 1997), although we did not find any evidence for this affecting prey preferences and observations of jackals hunting adult ungulates are not uncommon (Kamler et al., 2010; Macdonald, 1979).

The broader range of species killed by larger carnivores compared to smaller carnivores like jackal (Radloff and du Toit, 2004; Sinclair et al., 2003), is clear evidence that jackals compete with apex predators to exploit a shared resource. Furthermore, there are numerous records of jackals dying through intraguild predation (Palomares and Caro, 1999). It is therefore not surprising that the presence of apex predators has an impact on the prey preferences of jackals (Fig. 6, Fig. 7). Most researchers espouse the facilitation function of apex predators via provisioning of carcasses to jackals (Van de Ven et al., 2013), however our results illustrate that the situation is more complex. Black-backed jackals prefer buffalo and impala more where apex predators are present, and bushbuck, where they are absent (Fig. 6), however this does not appear to be driven by prey body mass as it is not solely large species that are more preferred when jackals are in sympatry with apex predators (Fig. 7). Similarly, wild boar and pheasant are more preferred by golden jackal in the absence of apex predators. This casts doubts on claims that jackals only scavenge larger species (Costa, 1995), as some larger species are consumed only at sites without apex predators present, although we cannot rule out these larger species being sourced from anthropogenic routes (Lanszki et al., 2015). Our results are consistent with previous research, which showed that in the absence of apex carnivores, jackals preyed mostly on small hider ungulates, both newborn and adults (Klare *et al*. 2010). Surprisingly, however, there does not appear to be a generalised provisioning function provided by apex predators related to prey body mass (or carcass mass; Fig. 7), as it is not solely larger prey species that are increasingly preferred in the presence of apex predators (that would indicate this was driven simply by the increased scavenging opportunities and that would be the mechanism). This provisioning service seems driven by the individual characteristics of each prey species and probably their vulnerability to each predator, such that scavenging may occur, but also individual species become increasingly targeted by jackals when they are no longer exploited by apex predators (as shown in Petrunenko et al., 2015). This may relate to a reduction in competition for carcasses arising from naturally occurring mortalities, increased hunting effort undertaken by jackals as solitary jackals can take down prey as larger as adult impala (Kamler et al., 2010), shifts in habitat use and behaviour (Tambling et al., 2015) by prey in the presence of apex predators, larger group sizes in the absence of apex predators (a potential driver of their flexible social systems; Macdonald, 1979), a reduction in offtake by apex predators of sick and injured individuals, ungulate social behaviour (solitary vs. herder), or the maternal behaviour of prey species with jackals killing juveniles that lose the protection of mothers killed by apex predators. Thus, while apex predators might fulfil a facilitation role by providing carcasses of large species for jackals to scavenge upon (commensalism), as indicated by the increased use of buffalo when apex predators are present, they may also facilitate jackal predation by removing the protection of adult individuals and thereby leave young vulnerable. The protection of adults does not necessarily have to be via direct aggression towards predators (which is rare), but rather through the increased vigilance they afford (Fitzgibbon, 1993). Alternatively, the presence of apex predators might induce behavioural changes to mesopredators that causes them to hunt different species (Moehrenschlager et al., 2007).

Although small mammals comprise the majority of jackal diet, their high relative abundance and low body mass means they are not preferentially preyed upon (Table 1). This is not an artefact of small sample size as over 20 studies reported on small mammals in the diet of jackals and included information on their relative abundance (Table 1). A key property of optimal foraging theory is that prey abundance does not solely control predator consumption of that species, so a predator will not specialize on a less preferred prey regardless of its availability (Pyke et al., 1977). Jackals appear to have evolved to optimally prey upon lagomorphs and small ungulates – indeed it is most likely that it is the young of these ungulates that are consumed rather than adults. Given this, the preferred prey weight range is probably inflated, particularly for black-backed jackals.

Although jackals are regularly persecuted for actual or perceived livestock depredation (Gusset et al., 2009; McShane and Grettenberger, 1984; Rowe-Rowe, 1976), we found no evidence that they preferentially preyed upon livestock. All livestock were killed as frequently as expected based on their relative abundance in the prey community (Table 1), suggesting that jackal-pastoralist conflict reduction strategies would be most effective if they concentrated on management strategies for increasing wild prey abundance, protecting livestock rather than persecuting jackals and/or adequately disposing of carcasses. Human persecution could influence the prey preferences of predators by means of increasing the risk-taking behaviour during predation when animals move into novel environments following a perturbation (Tuyttens et al., 2000) or by the need to satisfy increased energetic requirements associated with compensatory life history responses (Minnie et al., 2016).

The differences in the degree of study among the different jackal species are surprising. While black-backed and Eurasian golden jackals are relatively well studied, we found limited data on side-striped and, less surprisingly, on the newly described African golden jackal. That is not to say dietary studies on these species do not exist, because they do (Atkinson et al., 2002), but rather there were insufficient studies that linked diet to prey abundance to allow the analysis of prey preference. More research is needed on these species and scientists and funding agencies need to recognise that replicated studies are fundamental to our ability to draw broad inferences about the natural world.

The resilience of jackal prey preference estimates to the inclusion of small sample sizes is reassuring. We previously tested for differences between prey preference estimates for leopards, and found no effect (Hayward et al., 2006a), and this robustness is reinforced by 32 of 35 showing no effect of sample size (Supplementary materials Fig. 1 & 2). Two of the three species that did show an effect of sample size showed that larger sample size was more avoided, which was driven by no records of kills of those species, which seems less likely with larger sample sizes. All species where preference estimates were effected by sample size had sample sizes larger than 38. This has implications for single site and seasonal dietary studies more generally in that even relatively large sample sizes can be biased, however our use of several sites to estimate mean prey preference minimises the impact of a few studies with small sample sizes.

The determination of prey preferences of jackals identifies the key prey resources they have evolved to optimally forage upon, illustrates the ecological flexibility jackals exhibit in the absence of apex predators, and shows the diversity of facilitation services these larger species offer. Thus, we provide a more nuanced understanding of the interactions between apex and mesocarnivores and illustrate the behavioural flexibility of jackals where they can switch between wolf-like (ungulate) and fox-like (small mammal) predation patterns. The preference values for the prey of each jackal species can be used in many ways, including dietary or home range prediction (Hayward et al., 2009; Hayward et al., 2007). Finally, we show that both top-down and bottom-up forces affect jackal prey preferences. Undoubtedly, the effects of top-down and bottom-up forces on jackal prey preferences vary with intensity across sites, and probably are dependent on jackal density, large carnivore density and diversity, prey density and diversity, levels of human persecution, and habitat. Black-backed and golden jackals appear to have evolved to exploit different resources through their distinct feeding habitats. Future research should investigate how these specific factors influence jackal prey preferences under various conditions, thereby leading to a more comprehensive understanding of how top-down and bottom-up forces shape jackal prey preferences.

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Tables

Table 1. Preference status (P/A; where – denotes significantly avoided, + significantly preferred, and ~ killed in accordance with relative abundance), mean Jacobs's index value of each jackal prey species, number of studies recording it as potential prey ($n_{present}$) and actual prey (n_{kill}), preference test statistics via either *t*-tests or sign tests, mean proportional abundance and kills of each prey species, body mass (three-quarters of adult female), and categories of herd size, main habitat, potential threat to black-backed and Eurasian golden jackals, and ungulate birthing behaviour (H – hider; F – follower; O - other) of black-backed jackal prey. Scientific names are based on the IUCN Red List. Species names with (no kills) refers to data where studies with no kills of this species were reported. An asterisk (*) refers to species likely to be significantly avoided with a larger sample size.

Species	**Scientific name**	**P/A**	**Jacobs' index (+- S.E.)**	**$n_{present}$**	**n_{kill}**	**t/Sign test**	**d.f.**	***p***	**Abundance**	**Kills**	**Body mass (kg)**	**Herd size / Habitat / Threat / Birthing**
a) Black-backed jackal												
Aardwolf	*Proteles cristatus*	-	-0.78 +/- 0.22	9	1	1	9	0.04	0.01 +/- 0.00	0.01 +/- 0.01	6	2 / 2 / 0 / O
Baboon	*Papio* spp.		-1 +/- 0	2	0				0.01 +/- 0.01	0 +/- 0	12	5 / 2 / 2 / O
Birds		+	0.83 +/- 0.15	4	4	5.66	3	0.01	0.07 +/- 0.05	0.45 +/- 0.12	1	5 / 1 / 0 / O
Blesbok	*Damaliscus dorcas phillipsi*	-	-0.56 +/- 0.13	16	9	-4	15	0.001	0.04 +/- 0.01	0.01 +/- 0.00	53	3 / 1 / 1 / F
Bontebok	*Damaliscus dorcas dorcas*		-1	1	0				0.01	0 +/- 0		
Buffalo	*Syncerus caffer*	-	-0.74 +/- 0.12	16	5	-6.01	15	<0.001	0.05 +/- 0.01	0.02 +/- 0.01	432	5 / 2 / 2 / F
Bushbuck	*Tragelaphus scriptus*	~	-0.06 +/- 0.15	27	18	-0.403	26	0.69	0.04 +/- 0.01	0.13 +/- 0.04	23	1 / 3 / 1 / H
Bushbuck (no kills)		+	0.41 +/- 0.10	18	18	4.23	17	<0.001				
Bushpig	*Potamochoerus larvatus*	~	-0.06 +/- 0.55	4	2	2	4	1	0.01 +/- 0.01	0.02 +/- 0.02	46	3 / 3 / 1 / O

Cattle	*Bos taurus*	~*	-1 +/- 0	4	0	0	4	0.125	0.03	0 +/- 0	235	3 / 1.5 / 2 / H
Dogfish			-0.67 +/- 0.33	2	1				0.02 +/- 0.01	0.01 +/- 0.01	0.66	5 / 1 / 0 / O
Duiker, blue	*Cephalophus monticola*		-1	1	0				0.01	0		
Duiker, common	*Sylvicapra grimmia*	~	-0.09 +/- 0.18	20	12	12	20	0.503	0.02 +/- 0.01	0.05 +/- 0.02	16	1 / 2.5 / 1 / H
Duiker, common (no kills)		+	0.51 +/- 0.12	12	12	4.15	11	0.002	0.01	0		
Eland	*Tragelaphus oryx*	-	-0.82 +/- 0.09	24	5	5	24	0.007	0.11 +/- 0.02	0.02 +/- 0.02	345	5 / 2 / 2 / H
Elephant	*Loxodonta africana*	~*	-1	4	0	0	4	0.125	0.02	0 +/- 0		
Gemsbok	*Oryx gazella*	~	-0.36 +/- 0.15	14	9	9	14	0.424	0.04 +/- 0.01	0.04 +/- 0.01	158	4 / 1 / 2 / H
Giraffe	*Giraffa camelopardalis*	-	-1 +/- 0	12	0	0	12	<0.001	0.03 +/- 0.01	0 +/- 0	550	3 / 2 / 2 / H
Goat	*Capra hircus*	~*	-1 +/- 0	3	0	0	3	0.25	0.06	0 +/- 0	45	3 / 1.5 / 1 / H
Grysbok, Cape	*Raphicerus melanotis*		0 +- 1	2	1				0.01 +/- 0.01	0.01 +/- 0.01	7	1 / 2.5 / 0 / H
Grysbok, Sharpe's	*Raphicerus sharpei*		0.79	1	1				0.001	0.01		
Hare, Cape	*Lepus capensis*	-	-0.55 +/- 0.06	3	3	-6.161	2	0.025	0.18	0.06 +/- 0.01	4	1 / 1.5 / 0 / O
Hare, scrub	*Lepus saxatilis*		-0.63 +/- 0.37	2	1				0.07 +/- 0.04	0.01 +/- 0.01	4	1 / 1.5 / 0 / O
Hares		-	-0.42 +/- 0.13	8	8	-2.5351	7	0.039	0.24 +/- 0.03	0.12 +/- 0.02	4	1 / 1.5 / 0 / O
Hartebeest, red	*Alcephalus busephalus*	-	-0.78 +/- 0.10	21	5	2	21	<0.001	0.07 +/- 0.01	0.02 +/- 0.01	95	4 / 1.5 / 1 / H
Hippopotamus	*Hippopotamus amphibious*		-1	1	0				0	0		
Impala	*Aepyceros melampus*	~	-0.24 +/- 0.20	17	14	6	17	0.332	0.29 +/- 0.06	0.26 +/- 0.10	30	4 / 2 / 1 / H
Klipspringer	*Oreotragus oreotragus*		-1 +/- 0	2	0				0.01 +/- 0.01	0 +/- 0	10	2.5 / 3 / 0 / H
Kudu	*Tragelaphus strepsiceros*	-	-0.59 +/- 0.09	31	22	5	31	<0.001	0.23 +/- 0.04	0.07 +/- 0.02	135	3 / 2 / 2 / H
Lagomorphs		-	-0.48 +- 0.09			-5.28	12	<0.001				
Lechwe	*Kobus leche*		-1	1	0				0.001	0		
Livestock		~	-0.61 +- 0.20			1	10	0.343				
Mussels			-0.60	1	1				0.05	0.01		
Nyala	*Tragelaphus angasi*		-1 +/- 0	2	0				0.01 +/- 0.00	0 +/- 0	47	3 / 2 / 2 / H
Oribi	*Ourebia ourebi*		0.20 +/- 0.69	2	2				0.06 +/- 0.06	0.03 +/- 0.01	14	2 / 1 / 1 / H
Ostrich	*Struthio camelus*	~*	-1 +/- 0	4	0	0	4	0.125	0.01 +/- 0.00	0 +/- 0	70	3 / 1.5 / 2 / O

Reedbuck, common	*Redunca arundinum*	~*	-1 +/- 0	5	0				0.01 +/- 0.00	0 +/- 0	32	3 / 3 / 1 / H
Reedbuck, mountain	*Redunca fulvorifula*	~	-0.67 +/- 0.33	3	1	3	1	1	0.07 +/- 0.04	0.05 +/- 0.05	23	3 / 3 / 1 / H
Rhebuck, grey	*Pelea capreolus*		0.33	1	1				0.23	0.37		
Roan	*Hippotragus equinus*		-1	1	0				0.01	0		
Rodents		~*	-0.97 +/- 0.03	4	4	0	4	0.125	0.91 +/- 0.06	0.08 +/- 0.02	0.02	5 / 1.5 / 0 / O
Sable	*Hippotragus niger*		-1 +/- 0	2	0				0.01 +/- 0.00	0 +/- 0	180	4 / 2 / 2 / H
Seal/dolphin			0.85 +/- 0.05	2	2				0.02 +/- 0.00	0.20 +/- 0.06		
Sheep	*Ovis aries*	~	0.29 +/- 0.09	3	3	3.40	2	0.077	0.29	0.43 +/- 0.04	23	5 / 1.5 / 0 / F
Small mammals		-	-0.74 +- 0.06			-12	14	<0.001			0.03	
Springbok	*Antidorcas marsupialis*	~	-0.24 +/- 0.14	24	15	11	24	0.839	0.11 +/- 0.03	0.12 +/- 0.03	26	5 / 1 / 1 / H
Springbok (no kills)		+	0.22 +/- 0.09	15	15	2.34	14	0.035	0.17 +/- 0.04	0.20 +/- 0.04		
Springhare	*Pedetes capensis*	-	-0.65 +/- 0.07	11	11	-9.79	10	<0.001	0.22 +/- 0.03	0.06 +/- 0.01	2	1 / 2 / 0 / H
Steenbok	*Raphicerus campestris*	~	-0.14 +/- 0.18	19	14	7	19	0.359	0.10 +/- 0.03	0.04 +/- 0.01	8	1.5 / 1.5 / 0 / H
Suids		-	-0.64 +- 0.10			4	37	<0.001				
Tsessebe	*Damaliscus lunatus*	~*	-1 +/- 0	3	0				0.01 +/- 0.00	0 +/- 0	90	3 / 2 / 1 / H-F
Warthog	*Phacochoerus africanus*	-	-0.70 +/- 0.08	32	16	3	32	<0.001	0.14 +/- 0.03	0.03 +/- 0.01	45	3 / 2 / 2 / O
Waterbuck	*Kobus ellipsiprymnus*	~	-0.49 +/- 0.26	8	3	3	8	0.727	0.01 +/- 0.00	0.01 +/- 0.01	188	3.5 / 2 / 2 / H
Wildebeest, black	*Connochaetes gnou*	-	-1 +/- 0	13	0	0	13	<0.001	0.02 +/- 0.00	0 +/- 0	100	4 / 1 / 1 / F
Wildebeest, blue	*Connochaetes taurinus*	-	-0.92 +/- 0.06	11	2	0	11	<0.001	0.13 +/- 0.02	0.01 +/- 0.00	135	5 / 1 / 1 / F
Zebra, mountain	*Equus zebra*		-1	1	0				0	0		
Zebra, plains	*Equus quagga*	-	-0.88 +/- 0.05	17	6	0	17	<0.001	0.08 +/- 0.02	0.01 +/- 0.00	175	3 / 2 / 2 / F
b) *Eurasian golden jackal*												
Badger	*Meles meles*		-0.33 +- 0.50	3	1	-0.661	2	0.576	0.01 +- 0.01	0.01 +- 0.01	10	1 / 2
Birds			-0.41 +- 0.11									
Blackbuck	*Antilope cervicapra*		-0.02 +- 0.98	2	1				0.02 +- 0.01	0.19 +- 0.19	28	4 / 1
Cattle	*Bos taurus*		-0.34 +- 0.28	5	4	-1.233	4	0.285	0.28 +- 0.06	0.18 +- 0.06	235	3 / 1.5
Deer spp.		-	-0.57 +- 0.04	3	3	-13.84	2	0.005	0.21 +- 0.11	0.07 +- 0.05		
Deer, chital	*Axis axis*		-0.14 +- 0.14	5	5	-0.985	4	0.380	0.38 +- 0.08	0.33 +- 0.09	30	4 / 1.5

Deer, fallow/roe			-0.25 +- 0.10	3	3	-2.541	2	0.126	0.03 +- 0.01	0.02 +- 0.01	22.5	3 / 2
Deer, fallow/roe/red			0.20 +- 0.10	4	4	2.020	3	0.137	0.02 +- 0.01	0.03 +- 0.01		
Deer, red	*Cervus elaphus*	-	-0.76 +- 0.07	3	3	-11.26	3	0.001	0.02 +- 0.01	0.04 +- 0.02	130	3 / 3
Deer, roe	*Capreolus capreolus*		-0.39 +- 0.32	5	5	-1.200	4	0.296	0.03 +- 0.01	0.06 +- 0.01	15	3 / 2
Deer, sambar	*Rusa unicolor*		-0.31 +- 0.13	6	6	-2.368	5	0.064	0.11 +- 0.02	0.07 +- 0.03	200	3.5 / 2
Donkey	*Equus asinus*		-1 +- 0						0.08	0.01	160	3 / 1
Gaur	*Bos gaurus*		-0.92						0.15	0.01	650	3 / 3
Goat	*Capra hircus*		-0.44						0.08	0.03	24	4 / 1
Hare	*Lepus* spp.		0.29 +- 0.37	3	3	0.783	2	0.515	0.11 +- 0.09	0.09 +- 0.03	4	1 / 1
Hare, brown	*Lepus europaeus*	+	0.44 +- 0.12	5	5	3.516	4	0.025	0.01 +- 0.01	0.01 +- 0.01	4	1 / 1
Horse	*Equus ferus*		-1						0.02	0.01		
Invertebrates			-0.85									
Lagomorphs			0.38 +- 0.14				8	0.688				
Livestock			-0.49 +- 0.18				10	0.289				
Monkey, langur	*Semnopithecus entellus*	-	-0.66 +- 0.18	4	3	-3.742	3	0.033	0.17 +- 0.10	0.03 +- 0.01	5	5 / 2
Mule			-1 +- 0	1	0				0.02	0.01	190	1 / 1
Nilgai	*Boselaphus tragcamelus*		0.18 +- 0.32	5	5		5	1.000	0.09 +- 0.03	0.17 +- 0.10	169	4 / 2
Pheasant	*Chrysolophus* spp.	-	-0.58 +-0.10	13	10	-5.680	12	<0.001	0.04 +- 0.02	0.05 +- 0.02	5	2 / 2
Rodent			0.36 +- 0.13	3	3	2.880	2	0.103	0.09 +- 0.06	0.20 +- 0.13	0.3	1 / 2
Sheep	*Ovis aries*		-0.26						0.62	0.73		
Small mammals		-	-0.31 +- 0.12	13	11	-2.533	12	0.026	0.68 +- 0.07	0.76 +- 0.07	0.025	1 / 2
Tahr, Nilgiri	*Nilgiritragus hylocrius*		-0.99	1	1				0.74	0.01	80	4 / 2
Ungulates			-0.14 +-0.10			-1.419	30	0.166				
Wild boar	*Sus scrofa*		-0.06 +- 0.14	18	11	-0.390	17	0.701	0.06 +- 0.02	0.09 +- 0.03	47	3 / 2.5

Table 2. Model selection statistics for the top ten models of the drivers of prey selection in a) black-backed and b) Eurasian golden jackals.

Intercept	**Abundance**	**Body mass**	**Habitat**	**Herd size**	**Threat**	**Birthing strategy**	**d.f.**	**$\mathrm{AIC_c}$**	**$\Delta\mathrm{AIC_c}$**	**Akaike's weight**
Black-backed jackal										
-0.322					-0.215		3.0	57.757	0.000	0.149
-0.424		-0.001					3.0	58.043	0.285	0.130
-0.332		-0.001			-0.138		4.0	59.219	1.462	0.072
-0.271	-0.322				-0.233		4.0	59.839	2.082	0.053
-0.267				-0.021	-0.203		4.0	60.112	2.355	0.046
-0.306			-0.009		-0.214		4.0	60.242	2.485	0.043
-0.357		-0.001		-0.023			4.0	60.365	2.608	0.041
-0.542							2.0	60.382	2.625	0.040
-0.406	-0.151	-0.001					4.0	60.439	2.681	0.039
-0.366		-0.001	-0.032				4.0	60.465	2.708	0.039
Sum of Akaike's weights (w_i)	0.240	0.500	0.220	0.240	0.560	0.060				
Model-averaged parameter estimates	-0.052	-0.001	-0.006	-0.006	-0.110	0.446				
Eurasian golden jackal										
-0.091		-0.002					3.0	24.890	0.000	0.320
-0.246							2.0	25.516	0.626	0.234
-0.102				-0.056			3.0	27.937	3.047	0.070
0.062		-0.002	-0.086				4.0	27.978	3.088	0.068
-0.036		-0.002		-0.023			4.0	28.153	3.263	0.063
-0.067	-0.161	-0.002					4.0	28.155	3.265	0.063
-0.132			-0.065				3.0	28.300	3.410	0.058
-0.237	-0.071						3.0	28.415	3.525	0.055
-0.040			-0.041	-0.052			4.0	31.249	6.359	0.013
-0.089	-0.087			-0.056			4.0	31.275	6.385	0.013
Sum of Akaike's weights (w_i)	0.160	0.540	0.170	0.180						
Model-averaged parameter estimates	-0.019	-0.001	-0.013	-0.007						

Table 3. Model selection statistics for the segmented model to determine preferred and accessible prey weight ranges of a) black-backed and b) Eurasian golden jackals following Clements *et al.* (2014). Breakpoints refer to the number of slope changes within the segmented model and they are ranked according to Akaike's weights.

Breakpoints	**AIC_c**	**ΔAIC_c**
a) Black-backed jackal		
2	45.564	0
4	47.581	2.017
3	47.795	2.231
5	47.795	2.231
1	77.110	31.55
b) Eurasian golden jackal		
3	21.588	0
4	23.467	1.879
5	23.467	1.879
2	28.280	6.692
1	28.98	7.388

Figures

Fig. 1. Distribution map of the jackals with the locations of study sites that provided data on jackal diet and prey availability that were used in this study. Note that the distribution maps come from the IUCN Red List that have not yet been updated to reflect the two species of golden jackal (Jhala and Moehlman, 2008), however the African distribution of golden jackal reflects that of *Canis anthus* while the Eurasian distribution reflects that of *C. aureus.*

Fig. 2. Prey preferences of a) black-backed and b) golden jackals according to Jacobs' index. Black bars represent significantly preferred species and white bars significantly avoided species. Species in grey are consumed in accordance with their relative abundance.

Fig. 3. Relationships between the number of prey species present at a site and a) the number preferred and b) the number killed. There was no significant difference in the number of species killed or preferred between each jackal species ($t_{22} < 0.67$, $p > 0.40$ for both).

Fig. 4. Relationships between the most strongly supported variables explaining prey selection in a) black-backed jackals and b) Eurasian golden jackals based on the generalised linear modelling (Table 2). The insets show the loess smooth relationship over a subset of prey body masses. Grey shading represented the 95 percentile confidence interval.

Fig. 5. Segmented models of the preferred and accessible weight ranges of a) black-backed and b) Eurasian golden jackals. The x-axis shows the rank of species body mass and

the actual body mass this refers to the actual body mass at the segmented model breakpoints.

Fig. 6. The effect of the presence of apex predators on the prey selection by black-backed jackals. Stars show species with significant differences in prey selection (Jacobs' index) at sites with and without apex predators present. A two-way ANOVA revealed there was a significant difference in Jacobs' index values between birth strategies ($F_{1, 30}$ = 10.110, p = 0.003), but not in the effect of apex predators ($F_{1, 30}$ = 0.056, p = 0.815) or the interaction term ($F_{1, 30}$ = 0.129, p = 722).

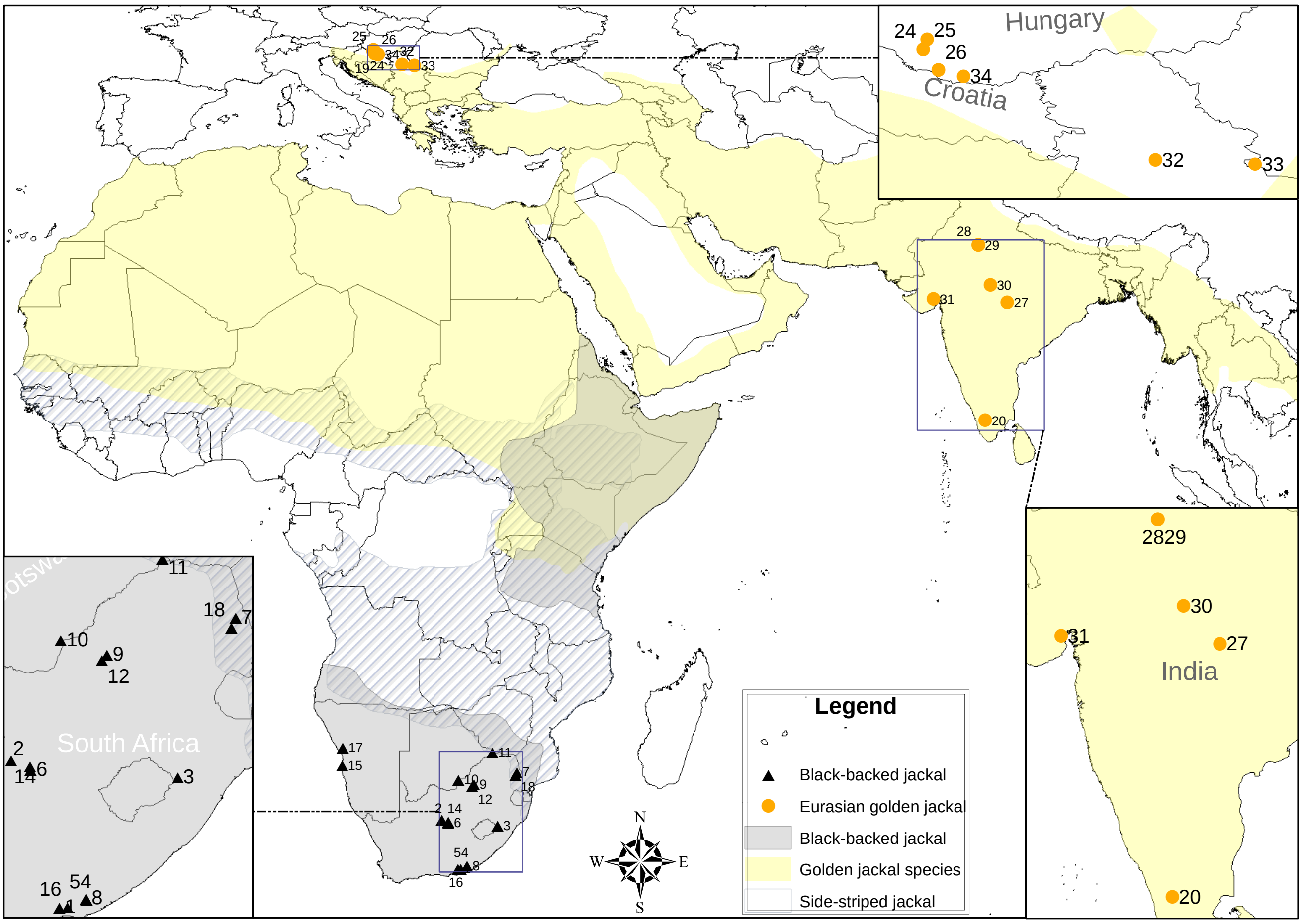

Legend
Black-backed jackal
Eurasian golden jackal
Black-backed jackal
Golden jackal species
Side-striped jackal
N
W
E
S
Hungary
Croatia
24
25
26
34
32
33
India
2829
30
31
27
20
28
29
South Africa
otswa
11
18
7
10
9
12
2
14
6
3
16
54
8
17
15
19

Fig. 1

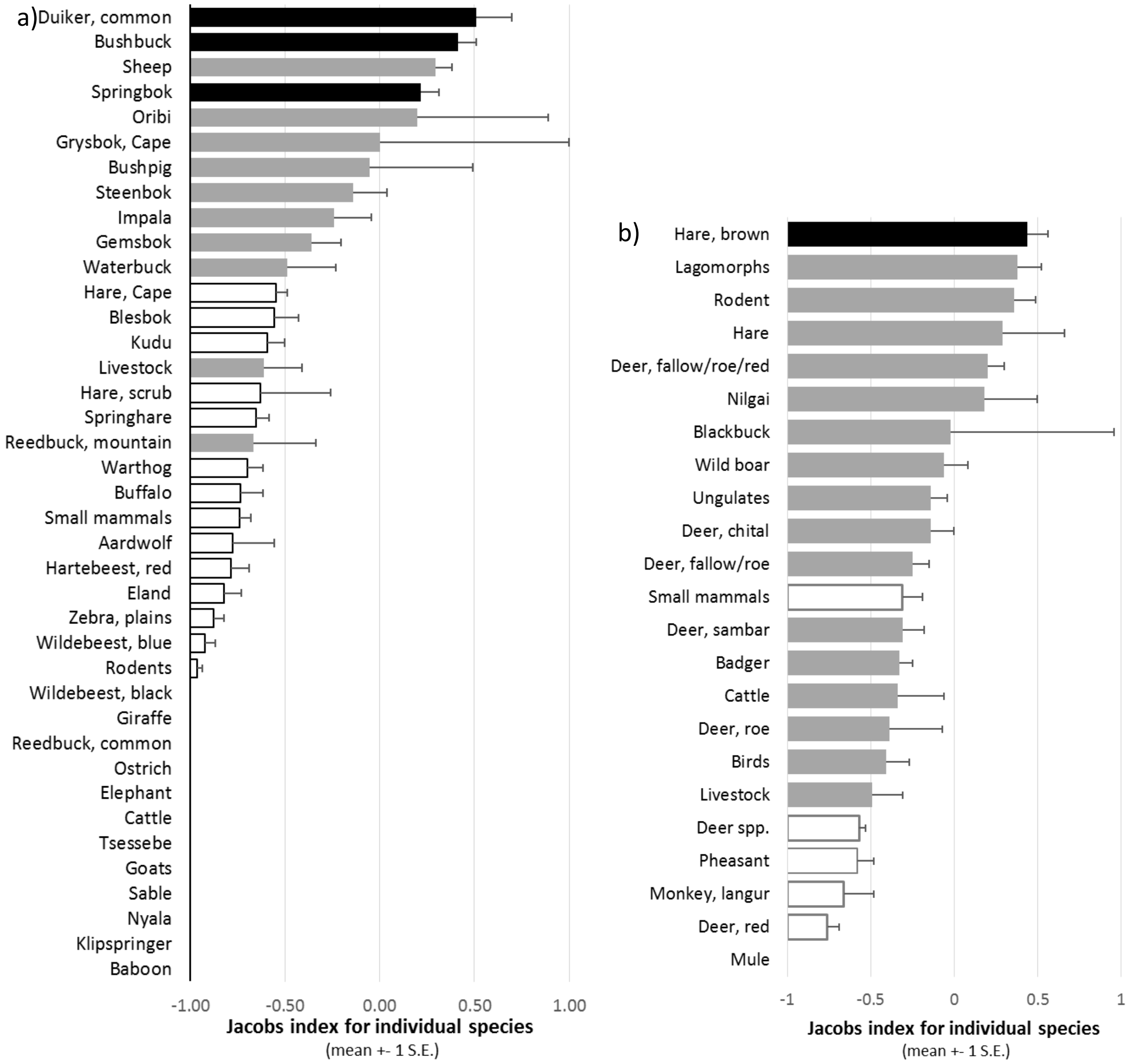

a)
Duiker, common
Bushbuck
Sheep
Springbok
Oribi
Grysbok, Cape
Bushpig
Steenbok
Impala
Gemsbok
Waterbuck
Hare, Cape
Blesbok
Kudu
Livestock
Hare, scrub
Springhare
Reedbuck, mountain
Warthog
Buffalo
Small mammals
Aardwolf
Hartebeest, red
Eland
Zebra, plains
Wildebeest, blue
Rodents
Wildebeest, black
Giraffe
Reedbuck, common
Ostrich
Elephant
Cattle
Tsessebe
Goats
Sable
Nyala
Klipspringer
Baboon
-1.00
-0.50
0.00
0.50
1.00
Jacobs index for individual species
(mean +- 1 S.E.)
b)
Hare, brown
Lagomorphs
Rodent
Hare
Deer, fallow/roe/red
Nilgai
Blackbuck
Wild boar
Ungulates
Deer, chital
Deer, fallow/roe
Small mammals
Deer, sambar
Badger
Cattle
Deer, roe
Birds
Livestock
Deer spp.
Pheasant
Monkey, langur
Deer, red
Mule
-1
-0.5
0
0.5
1
Jacobs index for individual species
(mean +- 1 S.E.)

Fig. 2

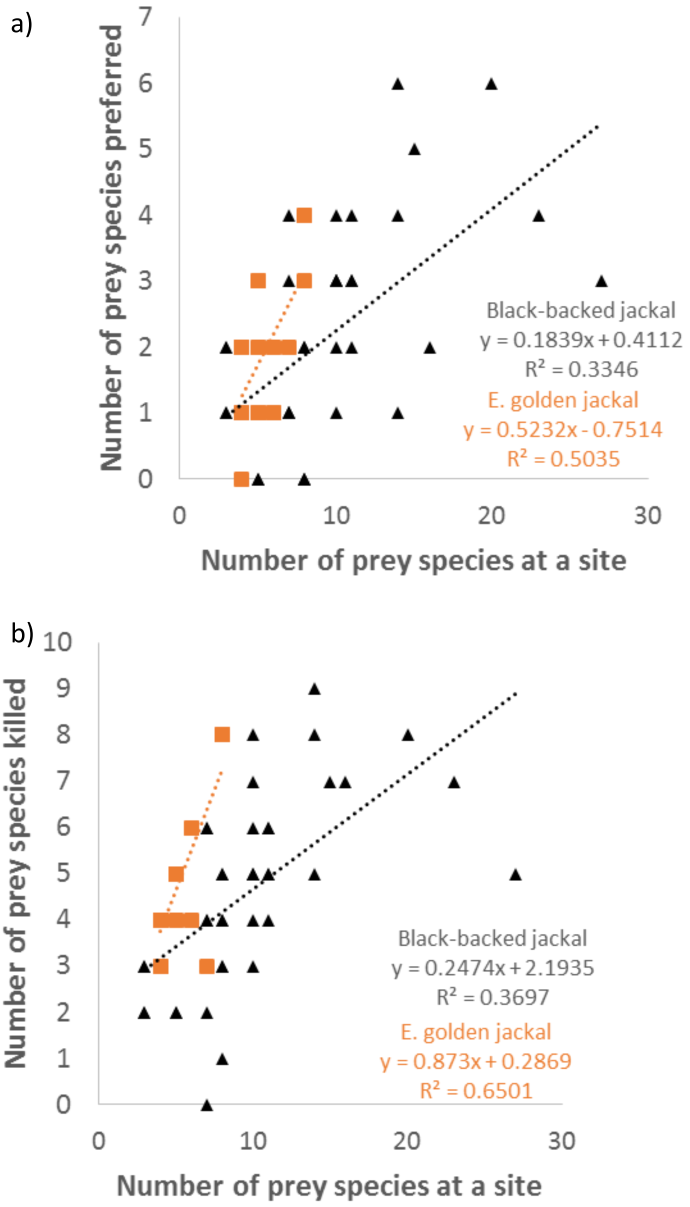
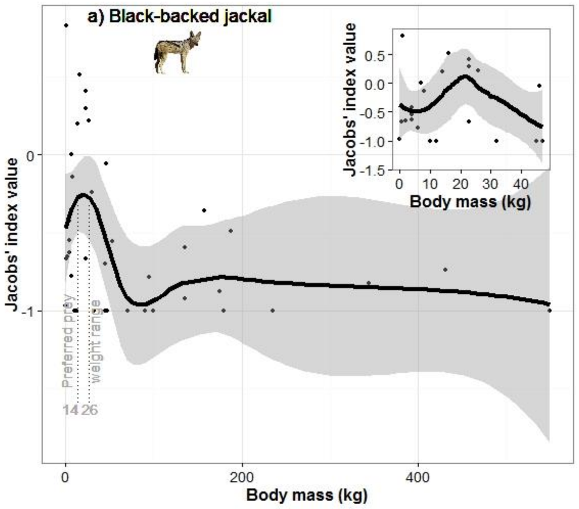
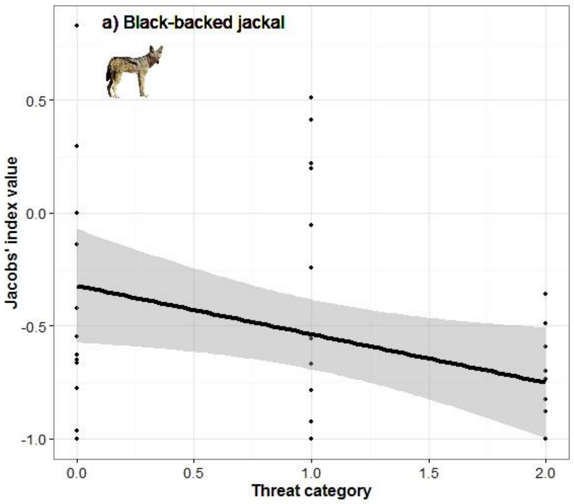

a)
Number of prey species preferred
0
1
2
3
4
5
6
7
0
10
20
30
Number of prey species at a site
Black-backed jackal
y = 0.1839x + 0.4112
R^2 = 0.3346
E. golden jackal
y = 0.5232x - 0.7514
R^2 = 0.5035
b)
Number of prey species killed
0
1
2
3
4
5
6
7
8
9
10
0
10
20
30
Number of prey species at a site
Black-backed jackal
y = 0.2474x + 2.1935
R^2 = 0.3697
E. golden jackal
y = 0.873x + 0.2869
R^2 = 0.6501

Fig. 3


a) Black-backed jackal
Jacobs' index value
0
-1
Preferred prey
weight range
14
26
0
200
400
Body mass (kg)
Jacobs' index value
0.5
0.0
-0.5
-1.0
-1.5
0
10
20
30
40
Body mass (kg)


a) Black-backed jackal
Jacobs' index value
0.5
0.0
-0.5
-1.0
0.0
0.5
1.0
1.5
2.0
Threat category

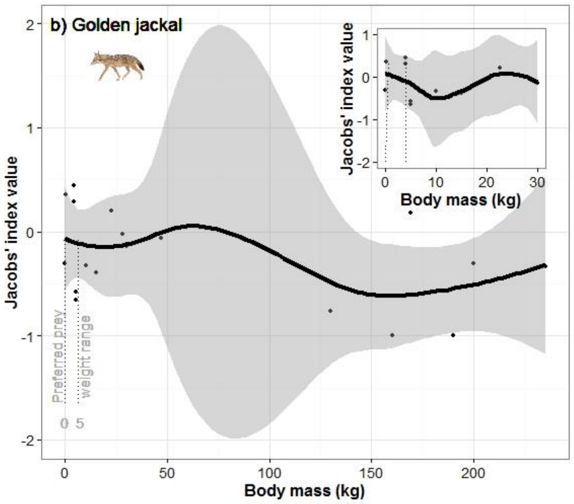

b) Golden jackal
Jacobs' index value
2
1
0
-1
-2
Preferred prey
weight range
0
5
0
50
100
150
200
Body mass (kg)
Jacobs' index value
1
0
-1
-2
0
10
20
30
Body mass (kg)

Fig. 4

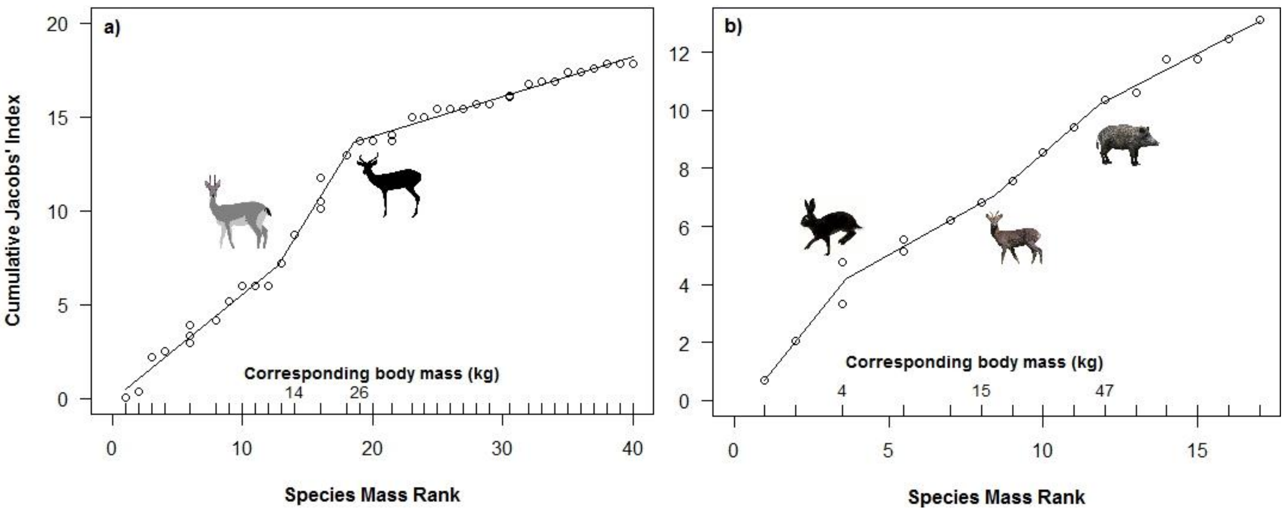

a)
Cumulative Jacobs' Index
20
15
10
5
0
Corresponding body mass (kg)
14
26
0
10
20
30
40
Species Mass Rank
b)
12
10
8
6
4
2
0
Corresponding body mass (kg)
4
15
47
0
5
10
15
Species Mass Rank

Fig. 5

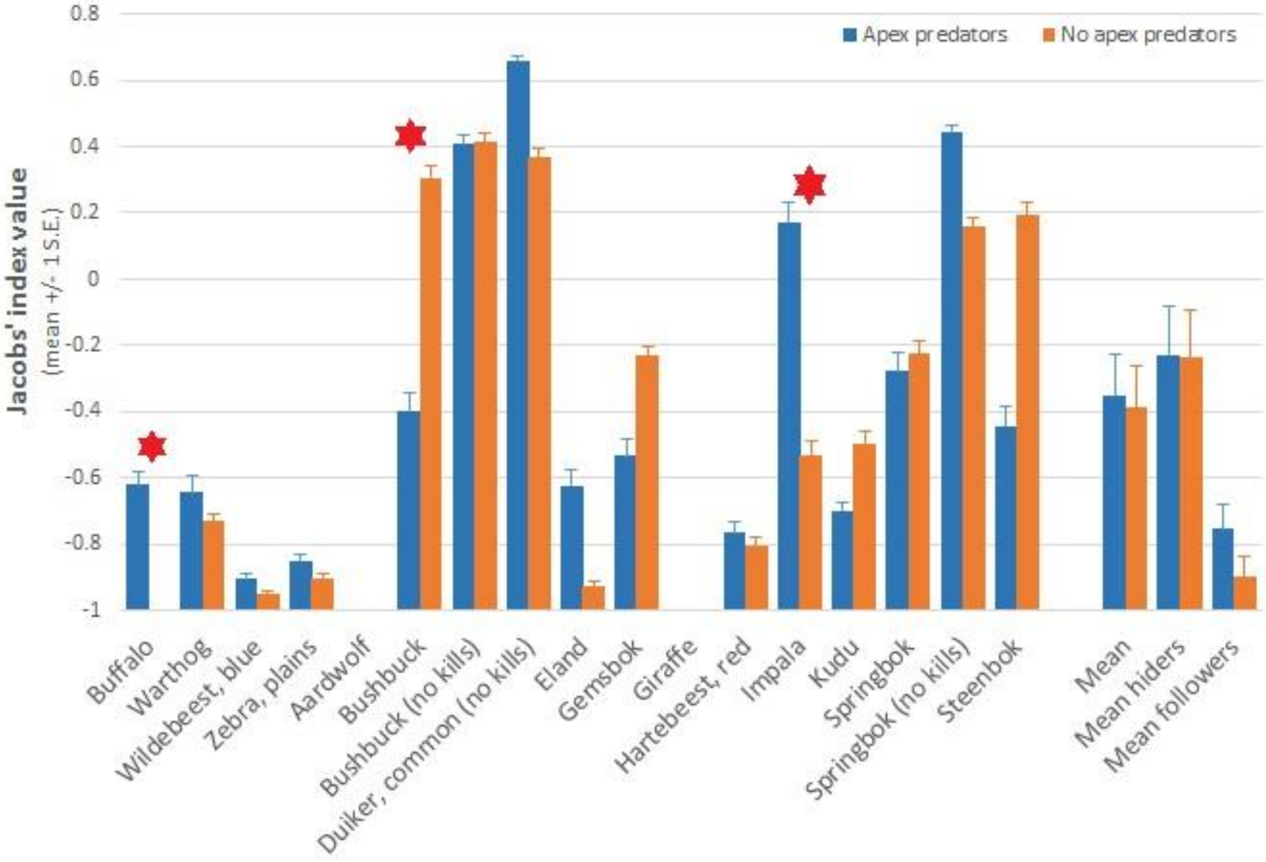

Apex predators
No apex predators
Jacobs' index value
(mean +/- 1 S.E.)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Buffalo
Warthog
Wildebeest, blue
Zebra, plains
Aardwolf
Bushbuck
Bushbuck (no kills)
Duiker, common (no kills)
Eland
Gemsbok
Giraffe
Hartebeest, red
Impala
Kudu
Springbok
Springbok (no kills)
Steenbok
Mean
Mean hiders
Mean followers

Fig. 6