



## Diet of the Golden Jackal (*Canis aureus*) and Silver-Backed Jackal (*Canis mesomelas*) in the Southern Part of the Serengeti Ecosystem, Tanzania: A Comparative Study

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### Abstract

Habitat and food resource partitioning are predicted to facilitate the coexistence of similar-sized carnivores. The golden jackal (*Canis aureus*) and silver-backed jackal (*Canis mesomelas*) are similar-sized canids that respectively inhabit grassland and woodland in the Serengeti ecosystem, Tanzania. As information on the diet and food-intake of these two species in this ecosystem is limited, we aimed to compare the diet and food-intake of these canids in the wet and dry seasons, using data from focal samples of foraging behaviour and scat analysis. We predicted dietary differences between these species, seasonal differences within species and peak food intake when breeding. Result of a logistic regression considering insect and small mammal remains in scats revealed dietary differences both between species and within-species seasonal differences. Results of a censored regression model on the estimated weigh of food intake by foraging individuals indicated that intake was highest during the breeding season of each species, which occurs in the wet season in golden jackals and the dry-season in silver-backed jackals. Our study provides new insights on differences in the foraging ecology of these two jackal species in the Serengeti ecosystem.

**Keywords:** *Canis aureus*, *Canis mesomelas*, diet, Serengeti ecosystem, seasons

### Introduction

Ecological theory (Putman and Wratten 1984, Johnson et al. 1996) predicts that interspecific competition for resources such as food should lead to the use of different habitats, foraging behaviour, and diet in similar-sized carnivore species, or the utilisation of different habitats by competing species within an ecosystem (Loveridge and Macdonald 2003). Thus, a degree of niche partitioning is expected for the coexistence of sympatric species within a given habitat (Putman and Wratten 1984, Johnson et al. 1996). Information on the diet of a species is

not only an important component of its ecology but is also essential for its conservation and management (Balestrieri et al. 2011).

The golden jackal (*Canis aureus*) and silver-backed jackal (*Canis mesomelas*) are similar-sized canids that respectively inhabit grassland and woodland in the Serengeti ecosystem, Tanzania. The African and Eurasian golden jackals have been considered one species (*Canis aureus*), but they may be genetically distinct and have independent lineages (Koepfli et al. 2015, Viranta et al. 2017). The African golden

jackal and Eurasian golden jackal are morphologically similar. A recent review of canid taxonomic uncertainties (Krofel et al. 2022) indicated that *Canis aureus* in Africa and Eurasia might be distinct taxa, but that further research is required (Kitchener et al. 2022). In this study, the name "*Canis aureus*" is applied to the African golden jackal which may be phylogenetically closer to grey wolves (*Canis lupus*) than to silver-backed and side-striped jackals. It has also been proposed that the silver-backed jackal (*C. mesomelas*) should be placed within *Lupulella* (Viranta et al. 2017). Due to the current lack of consensus on the taxonomy of these study species, in this study "*Canis mesomelas*" is used.

Golden and silver-backed jackals are roughly similar sized canids and their diets in protected areas in East Africa include broadly similar prey categories such as invertebrates, reptiles, birds, small and medium-sized mammals, carrion and plant material (Lamprecht 1978, Moehlman 1983, 1986, 1989, Fuller et al. 1989, Moehlman and Jhala 2013, Temu et al. 2016, 2017, Moehlman and Hayssen 2018). However, information on the ecological aspects including feeding habits of these jackals in East Africa is limited (Jhala and Moehlman 2004). Lamprecht (1978) provided information on diet and potential competition between golden and silver-backed jackals in the Seronera Area of the Serengeti National Park but available information on the current feeding habits of these two species in the southern portion of the Serengeti ecosystem is limited. Thus, there was a need for a more detailed investigation of the diet of both golden and silver-backed jackals in this part of the ecosystem to improve knowledge of the ecology of these sympatric carnivore species in the southern Serengeti ecosystem.

This study aimed to compare the diet of two similar-sized canid species, the silver-backed jackal and the golden jackal in the southern Serengeti ecosystem, Tanzania. Specifically, we aimed to: 1) determine the composition of food items consumed by silver-backed and golden jackals during focal follows of foraging animals, 2) estimate the

weight of food consumed by the two jackal species, in relation to distance travelled when foraging, time spent foraging and season.

Ecological theory predicts that the golden jackal and silver-backed jackal in the southern Serengeti ecosystem should inhabit different habitats, and this has previously been shown to be the case with silver-backed jackals primarily inhabiting *Acacia-Balanites* woodlands and golden jackals short grass areas (Moehlman 1983). In line with ecological theory we predict that the diet of these two canids should differ in terms of the categories of food items observed to be consumed. We also expect the estimated weight of food consumed to increase with both distance travelled and time spent when foraging and that seasonal changes in diet should reflect seasonal changes in the abundance of food categories present in golden or silver-backed jackal territories. Finally, we predict that the increased energetic cost of reproduction will cause food intake to peak during the season in which each species breeds, which is the wet season for golden jackals and the dry season for silver-backed jackals.

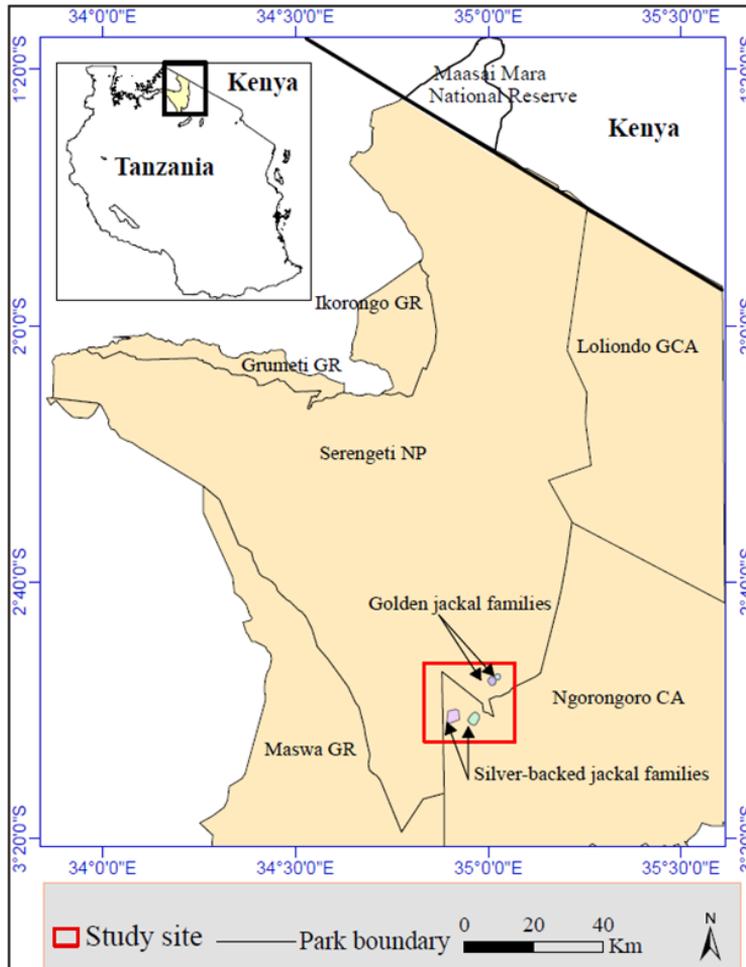
## Materials and Methods

### Study area

The study was conducted in the Serengeti ecosystem (34°–36 °E, 1°–3°30' S), which spans several protected areas including the Serengeti National Park (14,763 km<sup>2</sup>), and Ngorongoro Conservation Area (8,288 km<sup>2</sup>) (Metzger et al. 2015). The golden and silver-backed jackals observed in this study were part of an ongoing, long-term research project in the southern part of the Serengeti ecosystem (Moehlman 1987), where this study was conducted (Figure 1). Silver-backed jackals were studied in the *Acacia-Balanites* woodlands and golden jackals on short grass plains near Lake Ndutu in the southern part of the Serengeti National Park and the southwestern part of the Ngorongoro Conservation Area (Figure 1). Rainfall typically occurs in a bimodal pattern with the short rains during November–December and the long rains in March–May (Metzger et al. 2015). Data downloaded from the CHIRPS

satellite website (CHIRPS 2021) for the southern Serengeti ecosystem (2018–2020) indicated a mean ( $\pm$  SE) monthly rainfall of  $8.4 \pm 4.4$  mm in the dry season (July–October) and mean ( $\pm$  SE) monthly rainfall of  $114.1 \pm 28.9$  mm in the wet season (November–June). Temperatures in the

ecosystem vary with altitude, and are higher during the wet season (Metzger et al. 2015). Average daily temperatures in the southern Serengeti ecosystem (2000–2006) ranged between  $20.8$  °C (July) and  $23.5$  °C (February) (Metzger et al. 2015).



**Figure 1:** Map of the Serengeti ecosystem. GR = Game Reserve, NP = National Park, GCA = Game Controlled Area, CA = Conservation Area. *Source:* Department of Geography, University of Dar es Salaam, 2021.

The Serengeti ecosystem supports large herds of migrating ungulates, primarily wildebeest (*Connochaetes taurinus*) plains zebras (*Equus quagga*) and Thomson's gazelles (*Eudorcas thomsonii*). The seasonal migratory movements of these species result in substantial changes in their abundance in any given area (McNaughton 1990,

Wilmshurst et al. 1999). In addition to golden and silver-backed jackals, other carnivores in the ecosystem include the side-striped jackals (*C. adustus*), lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), bat-eared fox (*Otocyon megalotis*), leopard (*Panthera pardus*), serval (*Leptailurus serval*), caracal

(*Caracal caracal*) and African wild cat (*Felis lybica*) (Durant et al. 2011).

Data were collected between August 2018 and October 2020 during three dry seasons (August–November 2018, August–October 2019, and September–October 2020) and two wet seasons (March–June 2019 and January–June 2020). Typically, November is part of the wet season, but in 2018 when data collection ended on 18 November, dry season conditions persisted as no rain had occurred by this date.

## Methods

### Assessment of diet by focal samples of foraging behaviour

We quantified the diets of the golden jackal and silver-backed jackal using direct observations of foraging behaviour (e.g., Mills 1992, Temu et al. 2017). We used focal-animal sampling (Altmann 1974) of known individuals. In each focal follow, all behaviours performed by the individual were continuously recorded on a data sheet, together with the time, habitat, Geographical Positioning System (GPS) and odometer readings (Switalski et al. 2003, Temu et al. 2016). Individuals were observed using binoculars (Diamondback 8 x 42) and a spotting scope (Nikon Field Scope ED50) on a 12-h diurnal basis (usually from 0630 to 1930 hrs). Observations were made from a research vehicle. All focal animals had been habituated to the presence of vehicles as they were part of ongoing, long-term research project. One individual/pair was selected for focal observation per day. Binoculars and spotting scope were used to identify the food items being consumed by the focal animal. Food items large enough to be observed being consumed by focal animals were recorded in categories (e.g., rodent, beetle) when the species could not be identified.

Using data on the number of items in each food category consumed during focal observations per season, we computed the percentages each food category contributed to the total weight of food observed consumed per season for each study species. We also estimated the approximate weight of one prey item using known prey species and

types (e.g. insect) using published weights as follows: 5 g for dung beetles and other (flying) insects (Moehlman 1986); 3 kg for African hare (*Lepus capensis*) (Happold 2013); 100 g for small mammals (Happold 2013); 1 kg for helmeted guineafowl (*Numida meleagris*) (Urban et al. 1986); 80 g for superb starling (*Lamprolornis superbus*) (Fry et al. 2000); 150 g for white-browed coucal (*Centropus superciliosus*) (Fry et al. 1988); 150 g for crowned plover (*Vanellus coronatus*) (Urban et al. 1986); 60 g for lizards (all unidentified); and 750 g for one unidentified snake. Fruits from the desert date (*Balanites aegyptiaca*) were weighed in the field and the mean weight per fruit was 13 g (N = 30). Hares were the only species in the medium-sized mammal category and most small mammals recorded were rodents. We used these weights to compute the percentage each broad food category contributed to the total estimated weight of food observed consumed by each study species per season.

### Assessment of diet by scat analysis

Scats were collected for diet analyses from known individuals during focal follows, shortly after they were deposited in a manner that ensured that this procedure did not disturb the animals being followed. Entire scats were collected and each scat was placed in a paper bag on which the following details were recorded: collection date, GPS location, species name, sex, individual number and habitat type (Loveridge and Macdonald 2003). The laboratory analysis of scats was conducted by Steven E. Temu at the Department of Zoology and Wildlife Conservation at the University of Dar es Salaam using the procedures detailed by Lamprecht (1978) and Breuer (2005). Individual scat samples were soaked in water, the solid content was washed in a sieve, dietary items were separated and identified under a binocular microscope (Lamprecht 1978, Breuer 2005) using field guides to birds, mammals and insects, plus a reference collection of potential food items obtained from the study area. The key purpose of the scat analyses was to compare

the occurrence of “key components” in the scats, such as large insects and bones of small mammals, rather than detailed scat analyses of the hair structure of different mammalian species. Indigestible prey remains in the scats included insect exoskeletons, skeletal remains of small mammals, and plant seeds. Scats were collected in both the dry and wet season for determination of possible seasonal differences. Food items found in the scats were classified into broad food categories, such as insects, small mammals and plant materials, not to a species level. For each food category, we used a binary score to record whether a scat either contained (1) or did not contain (0) each food category.

## Data analyses

### a) Direct observations

We applied a censored regression model to estimate the total weight of food consumed by an individual during a focal observation period (g) as a function of species, season and distance travelled (km), and time spent foraging (hours). We assumed when an animal was active, it was foraging. The response variable was the estimated total weight of food consumed (g), and jackal species, season, time and distance travelled for foraging were explanatory variables. Interactions between these covariates were also included. The model was fitted in R (R

core Team 2018) using function ‘CensReg’ as follows:

Model = censReg [weight consumed (g) ~ species + season + species \* season + distance (km)]

Collinearity between distance travelled and time spent foraging was tested using Spearman rank correlation,  $r_s$ . There was a significant correlation between the two variables (Spearman rank correlation,  $r_s = 0.7$ ,  $p < 0.05$ ,  $N = 288$ ), therefore, only one variable (distance travelled for foraging) was included in the analysis. Mean values (weight consumed and distance) for all samples from each individual in the study were used in the censored regression model to avoid pseudo-replication.

### b) Scat analysis

Our scat analysis included 73 scats (45 in the dry season and 28 in the wet season) from individually known silver-backed jackals and 59 scats (35 in the dry season and 24 in the wet season) from individually known golden jackals. The data were recorded on a presence/absence basis, i.e., whether a particular food item was present in the scat or not. This was mainly based on the presence of exoskeleton for insects, bones for small mammals and seeds for plants. The frequency of occurrence of the food items present in the scats from silver-backed jackals and golden jackals were computed using the following formula:

Percentage frequency of occurrence of food items in scats

$$= \frac{\text{Number of scat samples containing particular food item}}{\text{Total number of scat samples collected}} \times 100$$

The likelihood of the two main food items (i.e., small mammals and insects) in the jackal scats was modelled as a function of jackal species and season (explanatory variables) using two logistic regression models as follows:

```
[logit_insects <- glm (Insects ~ Species + Season, family = "binomial")]
```

```
[logit_small_mammals <- glm (Small mammals ~ Species + Season, family = "binomial")]
```

The models were fitted in R version 3.5.1 (R core Team 2018).

## Results

In line with ecological theory, and despite a degree of overlap, we found that insects were the most common food item consumed by golden jackals, whereas the most common item consumed by silver-backed jackals was small mammals. However, contrary to our expectation that there would be a seasonal change in the food categories consumed in the wet and dry season, we found that the majority of food items (in terms of our broad food categories, see Table 1) consumed in both the wet and dry season by golden

jackals were insects and by silver-backed jackals were small mammals (Table 1). When considering the contribution of food categories to the estimated weight to food intake, small mammals contribute substantially to the weight of food intake by silver-backed jackals in the dry season (Table 2), whereas reptiles, small mammals and insects were key dietary categories in terms of their contribution to the weight of food consumed by golden jackals during the dry season. During the wet season, the largest amount of food in terms of weight consumed

by golden jackals was scavenged carrion from ungulate carcasses (63.4%) and placentas (14.25%, Table 3). By contrast, the largest amount of food in terms of weight consumed by silver-backed jackals in the wet season were small mammals (46.4%), and scavenged carrion 20.8%, Table 3). There was no significant difference in the estimated weight of small mammals and reptiles consumed by golden jackals in the dry season (Mann-Whitney U test, U = 1547, p > 0.05, N = 57).

**Table 1:** The percentage and total number (in bracket) of items consumed in food categories by silver-backed and golden jackals in the dry and wet seasons. The two highest values for each species in the wet and dry seasons are in bold type.

Food category	Dry season (%)		Wet season (%)	
	Silver-backed jackal	Golden jackal	Silver-backed jackal	Golden jackal
Insects	3.3 (8)	<b>81.5 (154)</b>	<b>56.9 (87)</b>	<b>83.5 (167)</b>
Small mammals	<b>33.8 (81)</b>	4.8 (9)	<b>34.6 (53)</b>	4.5 (9)
Carrion	2.5 (6)	1.1 (2)	3.3 (5)	<b>6.5 (13)</b>
Birds	2.1 (5)	0.5 (1)	2.6 (4)	0.0 (0)
Medium- sized mammals	0.8 (2)	0.0 (0)	0.0 (0)	1.0 (2)
Fruits	<b>57.5 (138)</b>	0.0 (0)	0.0 (0)	0.0 (0)
Reptiles	0.0 (0)	<b>12.2 (23)</b>	0.0 (0)	0.5 (1)
Placentas	0.0 (0)	0.0 (0)	2.6 (4)	4.0 (8)
<b>Total</b>	100 (240)	100 (189)	100 (153)	100 (200)

**Table 2:** Estimated consumption of food categories by golden and silver-backed jackals when foraging in the dry season, per km (g km<sup>-1</sup>), per hr (g hr<sup>-1</sup>) and as a percentage of the estimated total weight of food items (g) consumed per hr. Bold type indicates the two highest values in each column.

Food category	Estimated weight consumed (g km <sup>-1</sup> )		Estimated weight consumed (g hr <sup>-1</sup> )		Percentage of estimated total weight consumed per hr	
	Silver-backed jackal	Golden jackal	Silver-backed jackal	Golden jackal	Silver-backed jackal	Golden jackal
Insects	0.1	4.5	0.3	7.1	0.2	20.7
Small mammals	<b>35.3</b>	<b>5.0</b>	<b>68.7</b>	<b>7.9</b>	<b>50.6</b>	<b>23.1</b>
Carrion	2.0	3.3	3.9	5.2	2.9	15.2
Birds	5.2	0.8	10.2	1.3	7.5	3.8
Medium-sized mammals	<b>19.9</b>	0.0	<b>38.8</b>	0.0	<b>28.6</b>	0.0
Fruits	6.4	0.0	12.4	0.0	9.1	0.0
Reptiles	0.8	<b>8.1</b>	1.6	<b>12.8</b>	1.1	<b>37.3</b>
<b>Total</b>	<b>69.6</b>	<b>21.7</b>	<b>135.7</b>	<b>34.5</b>	<b>100.0</b>	<b>100.0</b>

**Table 3:** Estimated consumption of food categories by golden and silver-backed jackals when foraging in the wet season, per km ( $\text{g km}^{-1}$ ), per hr ( $\text{g hr}^{-1}$ ) and as a percentage of the estimated total weight of food items (g) consumed per hr. Bold type indicates the two highest values in each column.

Food category	Estimated weight consumed $\text{g km}^{-1}$		Estimated weight consumed per $\text{g hr}^{-1}$		Percentage of estimated total weight consumed per hr	
	Silver-backed jackal	Golden jackal	Silver-backed jackal	Golden jackal	Silver-backed jackal	Golden jackal
Insects	1.0	2.5	1.5	2.6	2.2	1.8
Small mammals	<b>20.1</b>	5.6	<b>31.0</b>	5.7	<b>46.4</b>	4.0
Carrion	<b>9.0</b>	<b>89.0</b>	<b>13.9</b>	<b>91.2</b>	<b>20.8</b>	<b>63.4</b>
Medium-sized mammals	5.9	0.0	9.1	0.0	0.0	13.3
Fruits	0.0	0.0	0.0	0.0	0.0	0.0
Reptiles	0.0	0.0	0.0	0.0	0.0	0.0
Birds	0.0	4.7	0.0	4.8	13.7	3.3
Placentas	7.3	<b>19.9</b>	11.3	<b>20.4</b>	16.9	<b>14.2</b>
<b>Total</b>	<b>43.3</b>	<b>121.6</b>	<b>66.8</b>	<b>124.7</b>	<b>100.0</b>	<b>100.0</b>

The energetic cost of reproduction should increase food intake in both jackal species; thus, food intake should be higher in the dry than wet season for silver-backed jackals, which breed in the dry season, and the reverse should be the case for golden jackals which breed in the wet season. The results of our censored regression model (Table 4) are

consistent with these expectations. Food intake was significantly higher for silver-backed jackals in the dry than wet season, whereas food intake by golden jackals was higher in the wet than dry season. Increased food intake was associated with an increase in foraging distance (Table 4).

**Table 4:** Censored regression model investigating the effects of study species, season, foraging distance and interaction between study species and season on the estimated weight of food consumed by the golden jackal and silver-backed jackal. Reference parameters are in italics. *P*-values in 'bold' indicate a significant relationship.

Parameters	Estimate	SE	T	P
Species- <i>golden jackal</i>	204.708	90.21	2.269	<b>0.020</b>
Season- <i>dry</i>	296.127	94.81	3.123	<b>0.002</b>
Distance (km)	37.351	12.55	2.976	<b>0.003</b>
Species- <i>golden jackal</i> : season- <i>dry</i>	-351.630	126.78	-2.774	<b>0.006</b>
Intercept	-91.662	89.86	-1.02	0.307

### Food items in scats

The remains of small mammals had the highest frequency of occurrence in silver-backed jackal scats in the dry (84%) and wet season (46%), followed by *Balanites* fruits (42%), which were only available in the dry season, and insects (16%). Insect remains were present in golden jackal scats in both

the dry (77%) and wet season (96%) followed by small mammals in the dry (40%) and wet season (21%). A small proportion of golden jackal scats (6%) collected in the dry season contained seeds that belonged to Cucurbitaceae family. The binary logistic regression model on insect remains in scats (likelihood ratio test,  $G = -58.775$ ,  $df = 2$ ,  $p$

= 0.00001, Table 5) indicated that insects were a more frequent items in the diet of golden jackals than silver-backed jackals. The binary logistic regression model on small mammal remains in scats (likelihood

ratio test,  $G = -73.423$ ,  $df = 2$ ,  $p = 0.00001$ , Table 5) indicates that small mammals were a more frequent item in the diet of silver-backed jackals than golden jackals.

**Table 5:** Logistic regression models investigating i) the presence/absence of insects and ii) the presence/absence of small mammals in jackal scats. The reference parameters are in italics. *P*-values in ‘bold’ indicate a significant relationship.

Model	Parameters	Estimate	SE	<i>z</i>	<i>P</i>
(i) Insects	Species: <i>golden</i>	-3.253	0.48	-6.81	< <b>0.001</b>
	<i>jackal</i>				
	Season: <i>dry season</i>	0.567	0.49	1.17	0.242
	Intercept	1.384	0.38	3.63	< <b>0.001</b>
(ii) Small mammals	Species: <i>golden</i>	1.863	0.42	4.43	< <b>0.001</b>
	<i>jackal</i>				
	Season: <i>dry season</i>	-1.579	0.43	-3.684	< <b>0.001</b>
	Intercept	-0.307	0.32	-0.972	0.331

### Discussion

Our study on the diet and foraging behaviour of silver-backed jackals in *Acacia-Balanites* woodland and golden jackals in short grassland in the southern Serengeti ecosystem found evidence indicating both a degree of dietary separation between these similar-sized carnivores, particularly in the dry season, and also dietary overlap, for example in the consumption of small mammals and insects (Table 1), which might lead to food competition in areas of the Serengeti ecosystem co-inhabited by both jackal species (Lamprecht 1978, Moehlman 1983, 1986). Consistent with previous studies (e.g., Moehlman 1983, 1986, 1989, Fuller et al. 1989, Loveridge and Macdonald 2003), we found evidence that both species exhibited seasonal shifts in their diets in terms of food categories consumed (Table 2-3) and the occurrence of the remains of food categories in scats (Table 5).

Our estimates of the contribution of different food categories to the estimated total weight of food ingested during focal follows indicated that food intake (in g) by silver-backed jackal was dominated by small mammals during both the dry (Table 2) and wet season (Table 3). Reptiles and small mammals were estimated to contribute the most to food intake by golden jackals in the dry season and carrion and ungulate

placentas during the wet season (Table 2 and Table 3 respectively). As the estimated weight of small mammals and reptiles consumed by golden jackals was similar in the dry season, reptiles and small mammals appear to be similarly important dietary items for this species particularly in the dry season. The dietary importance of small mammals and ungulate placentas to both jackal species suggest that this might result in feeding competition between golden and silver-backed jackals in areas of habitat overlap in the ecosystem, as previously reported by Lamprecht (1978).

Silver-backed jackals mostly capture live prey and scavenged only 15% of the total weight of food consumed. In contrast, our results indicate that scavenging is a more important mode of foraging for golden jackals, particularly in the wet season (Tables 3) when the majority (63%) of the total weight of food consumed was carrion obtained from carcasses of seasonally available wildebeests, zebras and Thomson gazelles usually killed by spotted hyenas and lions (Temu, pers. observ.). A large proportion of the diet of golden jackals in the dry season, in terms of the percentage of total weight (Table 2) was from vertebrates (reptiles and small mammals) plus insects. In the wet season, the importance of vertebrate food to the total weight of food consumed by

golden jackals substantially increased (Table 3). The diet of silver-backed jackal diet by weight was predominantly obtained from vertebrates in both the dry and wet seasons (Tables 2 and 3).

The results of our censored regression model (Table 4) showed that silver-backed jackals consumed a larger amount of food in the dry than the wet season whereas golden jackals consumed a larger amount of food in the wet season than the dry season (Table 4). In line with our prediction, this finding probably reflects the increased energetic costs (e.g., gestation and lactation for breeding females and the provisioning of pups with solid food by both parents) associated with reproduction, as in the Serengeti ecosystem, silver-backed jackals mainly breed in the dry season and golden jackals in the wet season (Moehlman 1983, 1986, 1987, Moehlman and Hofer 1997). The model also showed that the amount of food consumed by both study species increased with the distance travelled (Table 4), which is what might be expected for species considered opportunistic, generalist foragers.

Results from a logistic regression model investigating the occurrence/absence of prey remains in scats (Table 5) indicated that insects formed a more important item in the diet of golden jackals than silver-backed jackals, and small mammals were a more important item in the diet of silver-backed jackals than golden jackals (Table 5). These findings may be associated with the relative abundance of insects in short grassland (de Visser et al. 2015) and small mammals in woodland as was found by Senzota (1982), who reported that the abundance of small mammals such as *Arvicanthis niloticus* can be high (3,125–32,083 rodents km<sup>2</sup>) in the Ndutu woodlands.

The occurrence of small mammal remains in silver-backed jackal scats was lower in the wet than dry season. This seasonal shift in diet may be a response to the increased availability in the wet season of more profitable food sources (e.g., carrion from the carcasses of large migratory ungulates and ungulate placentas) linked to birth peaks in migratory ungulates during the wet season

(see McNaughton 1990, Wilmshurst et al. 1999). These herds and associated large carnivores (lions, spotted hyenas and cheetah) were abundant in the study area during the wet season and virtually absent during the dry season (Hofer and East 1993, Durant et al. 2011). Although golden jackals are known to capture and consume Thomson's gazelle fawns in the wet season in Serengeti National Park (Lamprecht 1978, Moehlman, pers. comm.), predation and consumption of Thomson gazelle's fawns was not observed during the current study.

As previously reported (Moehlman 1983, 1986, 1989, Fuller et al. 1989, Loveridge and Macdonald 2003), our results indicate that silver-backed jackals and golden jackals are opportunistic foragers that exploit relatively abundant and seasonal food resources. Silver-backed jackals consumed *Balanites* fruits and small mammals, including *A. niloticus*, during the dry season, and were observed hunting helmeted guineafowl and hares in their woodland habitat. Both canid species fed on ungulate carcasses and placentas when migratory ungulates were present in the wet season (see Mduma 1996), and golden jackals obtained food by scavenging from kills of spotted hyenas and lions in the wet season (see Moehlman 1983, 1986).

In anthropogenic landscapes, these canids might eat discarded food from human households, discarded remains from slaughtered animals and may prey on livestock (Fuller et al. 1989, Kalyahe et al. 2022). In South Africa, in protected areas and farmlands, the diet of silver-backed jackals includes antelopes, carrion, hares, hoofed domestic stock (particularly sheep), insects, and rodents (Walton and Joly 2003, Klare et al. 2010, Kamler et al. 2012). As both study species feed at night (Craft et al. 2015), future studies should include nocturnal observations on prey availability and selection by the two canids to better understand their feeding ecology and potential resource partitioning between these species.

## Conclusion

Similar to previous findings, our study of golden and silver-backed jackals revealed both species employed opportunistic, generalist foraging strategies and seasonal variations in diet and food consumption. Important food items for silver-backed jackals were small mammals in both the dry season and wet season and *Balanites* fruits in the dry season. Reptiles (mostly lizards) were important food items for golden jackals in the dry season and they relied on carrion from large migratory herbivores in the wet season. As predicted, food intake increased with distance travelled and time spent foraging and food consumption was highest during the breeding season of each jackal species. The co-occurrence of the two similar sized canid species in the southern Serengeti ecosystem may be explained by their habitat segregation.

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