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REVIEW

Diet composition of the golden jackal *Canis aureus* in south-east Europe – a review

Pauline N. A. M. J. G. LANGE *Department of Environmental Sciences, Subdivision Wildlife Ecology and Conservation, Wageningen University and Research, Postbus 47, Wageningen, 6700AA, the Netherlands. Email: pauline.lange@hotmail.com*
Glenn LELIEVELD* *Zoogdiervereniging, Postbus 6531, Nijmegen, GA, 6503, the Netherlands. Email: glenn.lelieveld@zoogdiervereniging.nl*
Henjo J. DE KNEGT *Department of Environmental Sciences, Subdivision Wildlife Ecology and Conservation, Wageningen University and Research, Postbus 47, Wageningen, 6700AA, the Netherlands. Email: henjo.deknegt@wur.nl*

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*Correspondence.

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ABSTRACT

1. The golden jackal *Canis aureus* is spreading throughout Europe and settling in countries where it has never been found before. Understanding its trophic ecology is increasingly important as it colonises new areas and ecosystems.
2. This paper aims to review the diet studies that have been performed on the golden jackal in Europe and provide a complete overview of its food intake, feeding behaviour and strategy.
3. Golden jackals were found to eat mainly small mammals (54% biomass), followed by domestic animals, ungulates and plants; together, these items make up 90% of the golden jackal's diet. Birds and lagomorphs were also often found in the diet. Domestic animals and ungulates were primarily consumed as carcasses, and not hunted or killed by golden jackals.
4. The diet composition differs greatly between areas and seasons, which points towards the golden jackal as a highly adaptive opportunistic omnivore, and demonstrates its ability to use many available food resources. The golden jackal provides regulating and maintenance ecosystem services as a scavenger and consumer of crop pests.

INTRODUCTION

The golden jackal *Canis aureus* is a widespread mesocarnivore (a carnivore weighing less than 15 kg), native to Asia and Europe, that has been expanding its geographical range throughout Europe for well over a decade (Arnold et al. 2012, Trouwborst et al. 2015). While it was previously most abundant in south-east Europe, progressively more records are found of sightings in the west, notably Germany (Klärner 2017), and of reproduction in Poland (Kowalczyk et al. 2020). The expansion of the golden jackal throughout Europe is thought to be driven by multiple factors, e.g. climate change (Arnold et al. 2012) and the intensive persecution of grey wolves *Canis lupus* in Eastern Europe, which eliminated top-down control of golden jackal populations (Krofel et al. 2017). Due to the range expansion of the golden jackal, scientists have raised concerns about their behaviour and ecology in newly colonised areas. As a result, the last decade has seen an increase in studies published on this species and its diet.

While apex predators such as the Eurasian lynx *Lynx lynx* and the grey wolf are known for their influence in the habitats they occupy (e.g. Kuijper et al. 2013), mesocarnivores such as the golden jackal and the coyote *Canis latrans* are rarely recognised for the ecological functions they exert (Roemer et al. 2009). However, especially in the absence of apex predators, mesocarnivores have been found to remove large numbers of rodent crop pests and favour plant biodiversity (Norrdahl et al. 2002, Hambäck et al. 2004, Ćirović et al. 2016).

This paper aims to review the diet studies that have been performed on the golden jackal in Europe and provide an overview of its dietary intake.

Species profile

The golden jackal is an opportunistic generalist canid predator, classified as a mesocarnivore, with a body weight of 8 to 14 kg (Lanszki et al. 2015). This means it is larger than the red fox *Vulpes vulpes* (4–7 kg; Lanszki et al. 2006) but smaller than the grey wolf (35–50 kg; Głowaciński & Profus 1997). Despite its name, studies have shown that it is more closely related to the coyote and the grey wolf than to other jackal species (Lindblad-Toh et al. 2005). Furthermore, the African relatives of the golden jackal that were identified as *Canis aureus* are now classified as golden wolves *Canis anthus* (Rueness et al. 2011).

The golden jackal's diet consists primarily of animals, but is complemented for a significant part with plants, arguably classifying the species as an omnivore (Markov & Lanszki 2012, Bošković et al. 2013, Penezić & Ćirović 2015). A study has shown that golden jackals can also provide regulating and maintenance ecosystem services; they function as 'cleaners' in human-dominated landscapes by consuming discarded animal waste in areas with insufficient animal waste regulations and rodent crop pests (Ćirović et al. 2016).

Golden jackals live in packs consisting of one monogamous pair and their young (usually 2–4) from the current year. Some packs include the young from the previous year, one of which then assists in the hunt and refrains from finding its own mate (Nowak 2005). The size of a pack's territory varies from 1 km^2 in high-quality habitats to 12 km^2 in low-quality habitats (Nowak 2005, Wennink et al. 2019).

METHODS

To find the studies used in this review, Scopus was the main search engine with the search terms: *Canis aureus*, golden jackal, diet, food, nutrition, faeces, excrement, scat, predation behaviour, feeding behaviour, and stomach content. Various operators and wildcards were included to maximise the search efficiency, resulting in the following search term: "*Canis aureus*" OR "golden jackal") AND ("diet*" OR "food" OR "nutrition*" OR "faeces" OR "excrement" OR "scat" OR "predation behaviour" OR "feeding behaviour" OR "stomach content". All results were scanned for relevance to the subject of this research and, if found to be relevant, read thoroughly. Relevance was considered minimal if the article either did not cover the subject of golden jackal diet, or if the research area was outside Europe. The datasets of publications that provided exact or relative amounts of food making up the diet were compiled into a spreadsheet. Distinctions between frequency of occurrence (indicated as 'O') and biomass (indicated as 'B') were kept intact and, whenever possible, both datasets were saved. Because some articles did specify the exact prey species, while others only gave the general taxa, all diet datasets were regrouped into 11 functional groups: birds, carnivores, domestic animals, fish, indigestible materials, invertebrates, lagomorphs, plants, reptiles & amphibians, small mammals and ungulates. If an article did not include one or more of these functional groups, it was assumed that group was not found in the diet. The data from the separate studies were combined into one overall dataset. From the overall dataset, a mean relative frequency of occurrence (%O) and percentage biomass consumed (%B) per functional group was calculated. However, in the results section, only percentage biomass consumed is presented, as this was found to be the method with the most ecological significance and the best approximation of a species' diet (Klare et al. 2011). Golden jackals were found to have a 168–240 g daily dietary requirement in the wild (Mukherjee et al. 2004), which amounts to 61.3–87.6 kg of food per golden jackal each year. These numbers were combined with the results of the mean percentage biomass consumed per functional group to give an indication of the mass required per diet group per year per golden jackal.

RESULTS

The search resulted in a total of 20 articles with relevant data, of which ten contained a dataset complete enough to use in an averaging overview. See Appendix S1 for a complete list of the articles and data, and Fig. 1 for an overview of the study areas.

Most studies point towards scavenging of improperly discarded (e.g. illegally dumped at the side of the road or left in the fields or woods) carcasses of livestock as the main component of the golden jackal's diet, varying between 62%B (percentage of biomass consumed) and 78%B of the total diet (Giannatos et al. 2010, Lanszki et al. 2010, Bošković et al. 2013, Raichev et al. 2013, Ćirović et al. 2014, Penezić & Ćirović 2015, Ćirović et al. 2016). Despite these high percentages, there seem to be no documented cases in the literature of golden jackals hunting domestic animals. Lanszki et al. (2015) also found that, in an area of intensive big game management, golden jackals primarily feed on viscera and carrion left behind by hunters and do not cause considerable losses to the wild boar *Sus scrofa* and cervid populations themselves. In a follow-up study, the big game viscera were removed from the area to measure the response of the golden jackal to a reduction in this anthropogenic food source. Although no statistically significant decrease in ungulate consumption was found, the reduction was still observably large: 55%B of the diet consisted of viscera before removal; the percentage was 29%B after removal (Lanszki et al. 2018).

In areas where animal livestock are rare or fully absent, the main food source for the golden jackal is often found to be small mammals, such as rodents, varying from 37%B to 78%B of the total diet (Lanszki & Heltai 2002, Lanszki

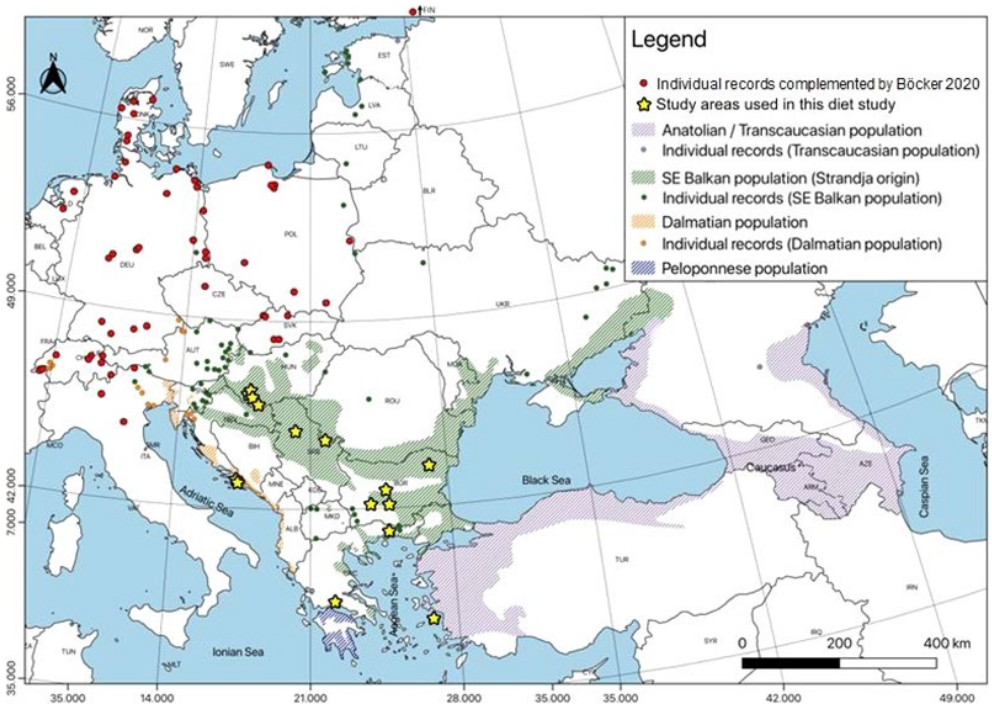

Fig. 1. Locations of diet studies used in this study (marked by stars) plotted on a map of golden jackal distribution in Europe (from Spassov & Acosta-Pankov 2019) and complemented by confirmed golden jackal sightings up to March 2020 by F. Böcker (personal communication).

et al. 2006, 2010, Markov & Lanszki 2012, Penezić & Ćirović 2015, Lanszki et al. 2016, Vlasseva et al. 2017).

Where arable agricultural plains are absent – and therefore small mammals less abundant – jackals are found to consume mainly large to medium-sized mammals, notably mouflon *Ovis gmelini*, wild boar and lagomorphs. Fruits and vegetables are a secondary food source (Radović & Kovačić 2010).

Figure 2 shows the results of the mean percentage of biomass consumed. The diet, subdivided into the ecological functional groups, is as follows: small mammals (mean percentage biomass ± standard deviation: 54 ± 32%B), domestic animals (17 ± 28%B), ungulates (11 ± 12%B), plants (10 ± 11%B), birds (3.8 ± 8.1%B), lagomorphs (1.4 ± 3.9%B), carnivores (0.8 ± 1.5%B), invertebrates (0.6 ± 0.7%B), reptiles & amphibians (0.06 ± 0.12%B) and fish (0.3 ± 0.5%B).

Five articles differentiated the small mammals into different taxa (Appendix S2): voles *Microtus* spp. (46 ± 20%B), mice *Apodemus* sp. (25 ± 14%B), coypu *Myocastor coypus* (22 ± 27%B), bank voles *Myodes glareolus* (12 ± 5.5%B), other rodents (9.1 ± 13%B), European water voles *Arvicola amphibius* (6.6 ± 6.3%B), European moles *Talpa europaea* (2.8 ± 3.4%B), dormice *Gliridae* sp. (2.5 ± 3.2%B), shrews *Soricidae* sp. (2.1 ± 4.2%B), rats *Rattus* spp. (1.2 ± 1.1%B) and muskats *Ondatra zibethicus* (0.4 ± 0.2%B). The results of this composition are shown in Fig. 3. Mice and voles comprise most of the diet. Coypu were found in only two areas, but make up a large part of the winter diet of the jackal in Serbia (Ćirović et al. 2014, Penezić & Ćirović 2015). According to a preference analysis considering the relative small mammal densities, golden jackals appear to prefer open-field-living voles *Microtus* spp. and to avoid forest-living bank voles *Myodes glareolus*, mice and shrews (Lanszki & Heltai 2010).

There are seasonal differences in the golden jackal's diet. Plant material (especially fruits) is mostly consumed in summer and autumn, when it is most abundant and when unharvested, ripe fruits lie easily available on the ground. Small mammals are most abundant in the diet in autumn. Plant material and small mammals are consumed less frequently in winter. Ungulates are most often consumed in winter and spring. Domestic animal consumption increases in winter, when other food sources are less readily available (Fig. 3).

To give an indication of the mass consumed per functional group per year, the percentages shown in Fig. 2 were used to calculate the estimated yearly intakes shown in Table 1.

DISCUSSION

Multiple aspects point towards the golden jackal being an opportunistic forager rather than a specialist hunter. The

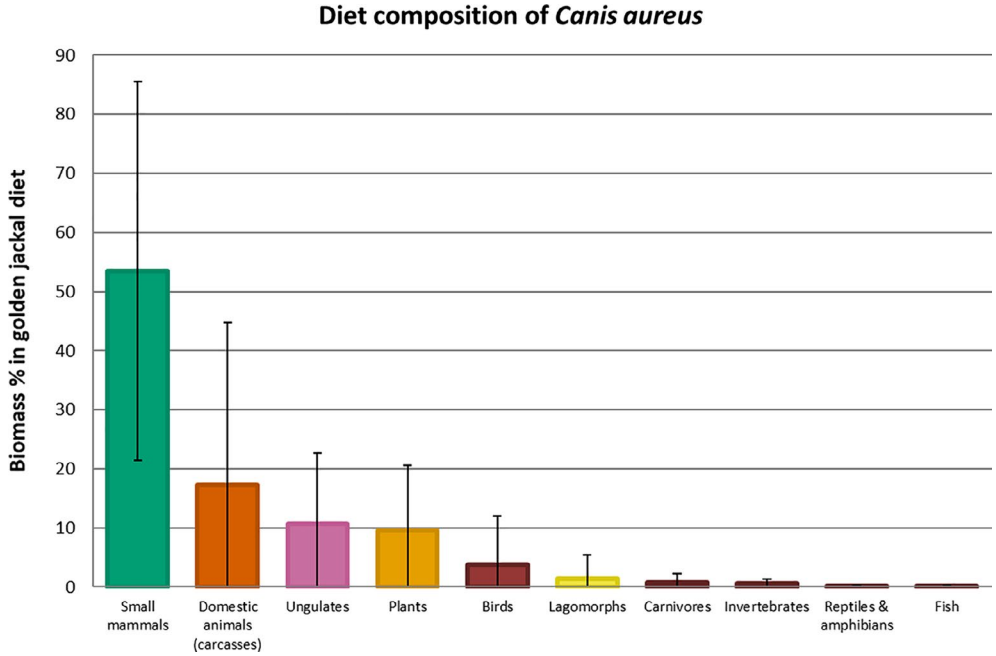

Fig. 2. Bar graph showing the diet composition of the golden jackal in mean percentage of biomass consumed of a diet group, with the groups being small mammals, domestic animals (mainly carcasses), (wild) ungulates, plants, birds, lagomorphs, carnivores, invertebrates, reptiles & amphibians, and fish. Standard deviations are shown. This analysis was based on ten datasets from published articles, both scat and stomach content analyses. Appendix S1 contains the full dataset.

wide variety of prey species, ranging from carcasses lying around to small animals weighing less than 50 g and even fruits, show that the canid eats whichever food source is most readily available and can be considered an omnivore rather than a true predator. The standard deviations in Figs 2 and 3, and Appendix S3 (data shown in Fig. 4), which are more often than not as large as the mean values themselves, point to a high adaptability and flexibility related to the area the golden jackal finds itself in. In areas where slaughter waste is improperly discarded, the bulk of the diet consists of viscera of domestic animals (e.g. Penezić & Ćirović 2015); when anthropogenic food sources are removed, golden jackals quickly adapt and consume more small mammals, invertebrates and plant materials

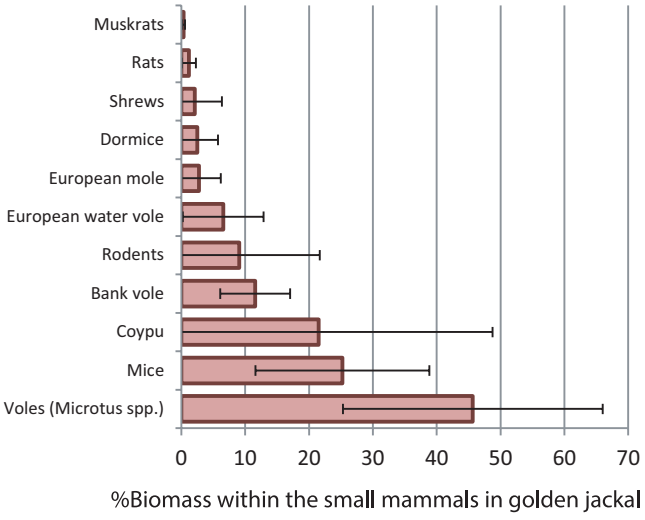

Fig. 3. Bar graph showing the mean contribution of different taxa (for scientific names, see the text) to the small mammal group in the golden jackal diet. Standard deviations are shown. Numbers are based on the data retrieved from five articles. Appendix S2 contains the full dataset.

Table 1. Estimation of the yearly intake per golden jackal of the functional groups in golden jackal diet

Functional group	Estimated yearly intake (kg) per golden jackal
Small mammals	32.8–46.8
Domestic animals	10.5–15.0
Ungulates	6.5–9.3
Plants	5.8–8.3
Birds	2.3–3.4
Lagomorphs	0.87–1.2
Carnivores	0.49–0.71
Invertebrates	0.36–0.52
Reptiles & amphibians	0.04–0.05
Fish	0.02–0.03

(Lanszki et al. 2018); when the majority of the area consists of cultivated lands, small mammals make up most of the golden jackal's diet (e.g. Lanszki & Heltai 2002); in more mountainous areas without livestock and without arable agriculture to house rodents, the canid adapts by scavenging on mouflon and wild boar and by consuming fruits as a secondary food source (Radović & Kovačić 2010).

Seasonality in the diet composition of the golden jackal further indicates that it eats whatever is plentifully available, as more plants and small mammals are consumed in summer and autumn when fruits fall from the trees and small mammals are plentiful. In one instance, wild boar piglets were present in the spring diet (Lanszki et al. 2006), which could point to hunting of young ungulates. However, Ćirović et al. (2016) found no muscle fibres of ungulates in the stomachs of golden jackals, which indicates that they do not kill the animals themselves but scavenge viscera left in the field by hunters or discarded domestic animal carcasses, and there are no recorded cases of golden jackals hunting domestic ungulates. Therefore, aside from the hunting of small mammals and the occasional piglet, the golden jackal can be considered a forager rather than a hunter, mainly searching for carcasses and fruits. It is possible that, in areas where apex predators such as Eurasian lynx are present, the golden jackal is able to consume leftovers from their hunted prey. Carcasses left by grey wolves are, however, unlikely to be used, as wolves actively drive golden jackals from their territories (Krofel et al. 2017, Trbojević et al. 2018), and there is a recorded case of a grey wolf killing a golden jackal (Mohammadi et al. 2017).

Figure 2 suggests that small mammals are a main component of the golden jackal's diet. The numbers provided in Table 1 on the mass contributed by the functional groups to one golden jackal's yearly diet show that 32.8–46.8 kg of small mammals is required, amounting to around a thousand individuals, as most small mammals weigh less than 50 g (Hayward et al. 2017), whereas one single ungulate is enough to provide the 6.5–9.3 kg yearly food intake. This again enunciates the importance of small mammals to the golden jackal. Whether they have a preference for certain species over others remains unclear. Lanszki and Heltai (2010) found that golden jackals prefer open-field-living small mammal species, but Lanszki et al. (2016) stated that they consume higher numbers of forest-living species. The apparent contradiction in these two statements is especially interesting as both studies were performed in the same area. It is possible that, in the latter study, despite jackals having a preference for open-field-living species, forest-living species were more abundant and were therefore consumed more.

In the golden jackal diet preference factor analysis done by Hayward et al. (2017), the body mass of prey was found to be three times as important a variable in explaining diet preferences as other variables (threat level, herd size, prey abundance, habitat and prey birthing strategy). The study concluded that golden jackals actively prefer

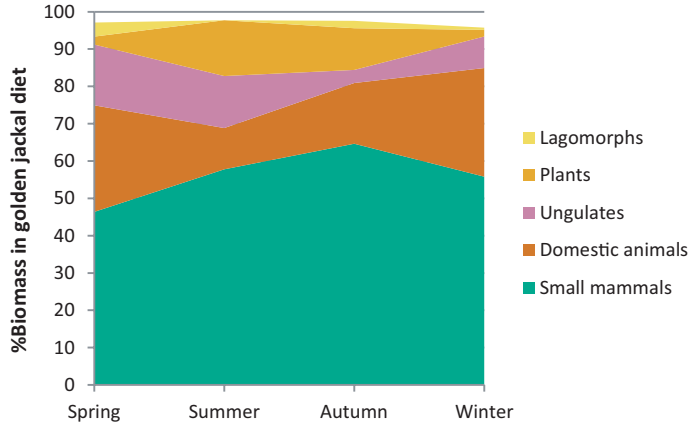

Fig. 4. Area graph showing the seasonal differences of the main diet groups in golden jackal diet, expressed in %biomass. Standard deviations were left out to conserve the comprehensibility of this figure. See Appendix S3 for the full dataset, including standard deviations.

lagomorphs and rodents, but seem to avoid all domestic animals and cervids. Haywood et al. (2017) describe a preferred prey weight range of 0–5 kg. Lanszki et al. (2010) had previously found a preferred weight of < 50 g.

Opportunistic predators rarely disrupt the diversity of ecosystems, but rather create a balance through their ability to switch between prey species in accordance with their fluctuating relative abundances (Miller et al. 2001). An opportunist could not bring a species to extinction, as it would change to a different prey species when the first became scarcer; but neither can a prey species dominate easily, as that would enhance the predation pressure from the opportunistic predator. Due to this, opportunist predators are able to control prey species abundances to a relatively stable level, avoiding the cyclic prey population fluctuations often associated with specialist predators (Erlinge et al. 1984). The control to stability is especially interesting, considering that many of the small mammals the golden jackal consumes are considered to be crop pest species. The intake of these small mammals (e.g. the common vole *Microtus arvalis*, one of the main prey species) can go up to over 20 kg per golden jackal per year (or 400 voles) in a territory of 1 to 12 km^2, so that golden jackals could play a significant role in natural crop pest control. This enunciates the importance of golden jackals as ecosystem service providers ('cleaners') in human-dominated landscapes.

In conclusion, golden jackals have a high degree of flexibility in their diet and can be classified as opportunistic omnivores with diets dominated by animal-derived foods. Excluding livestock carcasses, which vary in abundance due to sanitation regulations varying between countries, the most important components of the golden jackal's natural diet appear to be small mammals. Jackals scavenge on the carcases of wild and domestic animals whenever possible and complement their diet seasonally with fruits. If they reside in an area where any of those components are absent, they have no problem adapting to the situation by changing their diet composition. Golden jackals can act as providers of regulating and maintenance ecosystem services ('cleaners') in human-dominated landscapes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. The complete dataset used for the diet analysis, compiled from ten different articles.
Appendix S2. The complete dataset used for the small mammal specifications of the diet analysis, compiled from five different articles.
Appendix S3. The data on seasonality in golden jackal diet, derived from the data shown in Appendix S1.