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Variations in the trophic niches of the golden jackal *Canis aureus* across the Eurasian continent associated with biogeographic and anthropogenic factors

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Abstract. Our aim was to determine biogeographical patterns in the food habits of golden jackals by first reviewing their dietary patterns at the continental scale and then analysing associations between the food items in their diets and geographical, regional productivity and land-use variables, using multivariate analyses. Our findings indicated that jackals generally consume small mammals as a staple food but shift to consume plant materials or the carcasses of larger mammals when food resources are scarce owing to changes in the regional climate and productivity, as well as anthropogenic habitat modifications. Disruption of natural food resources (specifically small mammals) due to anthropogenic landscape modifications provokes dietary shifts in golden jackals, potentially increasing their reliance on anthropogenic resources. Consequently, conservation of their habitat in combination with waste management to decrease the accessibility to anthropogenic resources is required to resolve human-jackal conflicts.

Key words: anthropogenic food sources, Carnivora, diets, landscape modification, mesopredator, scavenging

Introduction

The trophic niches of animal species often diversify among their populations according to the effects of regional climate and environment. For example, milder climatic conditions in a region generally drive higher productivity and biodiversity, enabling predatory animals at higher trophic levels to use a wide variety of foods, whereas harsher climatic conditions result in predators relying on specific food sources and, thus, expressing narrower trophic niches (Korslund & Steen 2006, Zhou et al. 2011, Bojarska & Selva 2012). Consequently, biogeographical patterns in the trophic niches of an animal species provide a good indication of its adaptability.

Anthropogenic activities can also alter resource conditions and thereby affect biogeographical patterns in the niches of wild animals in the Anthropocene (Newsome et al. 2015). Human population growth is accelerating anthropogenic landscape modification globally through urbanisation, road networks and industrial farming, which are major drivers of wildlife habitat destruction and ecological and behavioural modifications in animals (Fischer & Lindenmayer 2007). However, some wild animals are tolerant of

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human activities and are able to adapt, allowing them to establish populations in human-modified landscapes, with higher survival and fecundity rates due to the presence of nutrient-rich human-subsidised resources (Adams & Lindsey 2010, Gehrt et al. 2010).

Mesocarnivores (order Carnivora, class Mammalia, with a body mass of < 15 kg; Roemer et al. 2009) generally exhibit trophic niche flexibility in association with environmental and climatic factors that affect the availabilities of regional food resources (Zhou et al. 2011, Diaz-Ruiz et al. 2013, Soe et al. 2017), and can even expand their ranges into human-modified landscapes (Gehrt et al. 2010, Bateman & Fleming 2012). Their successful establishment and population growth in human-dominated landscapes may be facilitated by their greater reliance on human-subsidised foods (e.g. trash, domestic animals, and cultivated fruits, vegetables and cereals) (Fedriani et al. 2001, Prange et al. 2004, Bino et al. 2010, Newsome et al. 2015), suggesting that anthropogenic factors may also affect their trophic niches (Soe et al. 2017). Mesocarnivores can cause declines in populations of small animals and may have an impact on regional biodiversity through predation and competition (Prugh et al. 2009, Roemer et al. 2009). These animals may also come into conflict with humans through activities such as the depredation of crops and domestic animals (including companion animals such as dogs and cats), intrusion into houses, and zoonotic transmissions (Curtis & Hadidian 2010, Bateman & Fleming 2012), raising concerns for their management in human-dominated landscapes.

The golden jackal *Canis aureus* (Canidae) is a mesocarnivore that has a wide distribution across the Eurasian continent, from tropical to cooler temperate zones (Jhala & Moehlman 2004). This species is tolerant of anthropogenic disturbance, which has allowed populations to become established in human-modified habitats (Šálek et al. 2014, Sign et al. 2016), where they show high utilisation of human-subsidised foods (Borkowski et al. 2011, Ćirović et al. 2014b). For example, its range in Europe has rapidly expanded from the Balkan Peninsula to central and western countries (Arnold et al. 2012, Rutkowski et al. 2015) in which the dominant competitor, the wolf *Canis lupus*, is absent (Krofel et al. 2017, Newsome et al. 2017). This range expansion has increased concerns about zoonotic disease transmissions (Ćirović et al. 2014a) and depredations on domestic animals (Yom-Tov et al. 1995) in the newly colonised areas, but as a primary scavenger this species also provides ecosystem services by removing discarded animal remains and facilitating detritus food chains (Ćirović et al. 2016). Thus, knowledge of the trophic ecology of the golden jackal at a wider geographical scale is fundamental to understanding its success in human-modified landscapes and planning strategic management. However, while several qualitative reviews of jackal diets (Borkowski et al. 2011, Singh et al. 2016) and meta-analyses of their prey preferences (Hayward et al. 2017) have been published, biogeographical patterns in their diets have not yet been assessed.

To address this gap, we undertook a comprehensive review of the food habits of golden jackal populations across the Eurasian continent with the aim of determining biogeographical patterns in their trophic niches. Specifically, we assessed four main hypotheses: *H1*, major foods in the diets of jackals are negatively correlated with each other and several dietary patterns are present, e.g. feeding on small- and medium-sized animals or scavenging large-mammal carcasses, according to previous reviews on jackal diets (Borkowski et al. 2011, Singh et al. 2016, Hayward et al. 2017); *H2*, the dietary patterns of jackals vary along geographical (i.e. latitudinal, longitudinal and/or altitudinal) gradients, with consuming mammalian remains being more commonly observed in higher latitudinal and/or altitudinal sites owing to the cooler climates, according to previous meta-analyses of other generalist mesocarnivores (Zhou et al. 2011, Diaz-Ruiz et al. 2013, Soe et al. 2017); *H3*, the diversity of food items in the jackal diet increases with increasing regional primary productivity due to enhanced regional diversity and an abundance of wild prey, such as rodents, birds and insects (Pettorelli et al. 2011); and *H4*, the reliance of jackals on anthropogenic foods increases in human-altered environments due to landscape modifications as a result of anthropogenic drivers (e.g. urbanisation or monocultural industrial farming) decreasing the availability of natural food resources while increasing the availability of anthropogenic resources (e.g. domestic animals and trash; Fischer & Lindenmayer 2007, Bateman & Fleming 2012). To assess these four hypotheses, we first reviewed the dietary patterns of jackals and then used multivariate analyses to examine the associations between food items in their diets and geographical gradients, regional productivities and landscape modifications.

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Material and Methods

Literature review

We undertook a comprehensive review of published literature by searching academic information sources (i.e. ISI Web of Science and Google Scholar) between March 2016 and May 2017 using the following keywords: "golden jackal" or "*Canis aureus*" and "diets" or "food habits". We also reviewed some of the available literature that had been written in non-English languages (e.g. Russian, Croatian, Hungarian and Romanian) cited by some of the English articles (e.g. Geptner & Naumov 1967, Borkowski et al. 2011, Bošković et al. 2013, Farkas et al. 2017; see Table S1). We translated the information in the non-English literature using dictionaries and online language translation tools (Google translation: https://translate.google.co.jp/).

This review process resulted in the compilation of a total of 45 reports that had been published between 1967 and 2016 and investigated the food habits of golden jackals from Eurasia and Africa (see Fig. S1A). These studies were then further refined as follows. The African golden jackal has recently been identified as a new species, the African golden wolf (*Canis anthus* or *Canis lupaster*), based on genetic and systematic studies (Koepfli et al. 2015, Viranta et al. 2017, Álvares et al. 2019), being potentially ecomorphologically divergent in trophic niches from the Eurasian golden jackal. Therefore, we excluded all African studies ($n = 3$) from the compiled reports, owing to knowledge gaps and uncertainties in eco-behavioural differences between the two canids (Álvares et al. 2019). We selected only those datasets that met the following criteria: 1) stomach or scat samples were randomly sampled from a local population; 2) sample sizes were > 15 stomachs/scats for seasonal studies or > 30 stomachs/scats for annual studies (Soe et al. 2017); 3) the number (n) or proportion (%) of the frequency of occurrence (FO) of each food item was reported; 4) recognised food items or categories were fully recorded; and 5) both the geographical location (or at least name of the study area) and sample season/month were described. Where a study included data from two or more different study areas or populations within a single season (Raichev et al. 2013, Ćirović et al. 2014b, Lanszki et al. 2016), or data from two or more seasons within a single area (e.g. Lanszki et al. 2006, Aleksandra & Duško 2015), we treated each of these as individual datasets. This refinement resulted in a total of 50 datasets from 31 published articles being included in the final analysis, which together assessed a total of 1097 stomachs and 4439 scats from different localities or seasons (Fig. 1 and Table S1).

Data acquisition and standardisation

The food items in jackal diets were divided into 10 categories based on the findings of previous

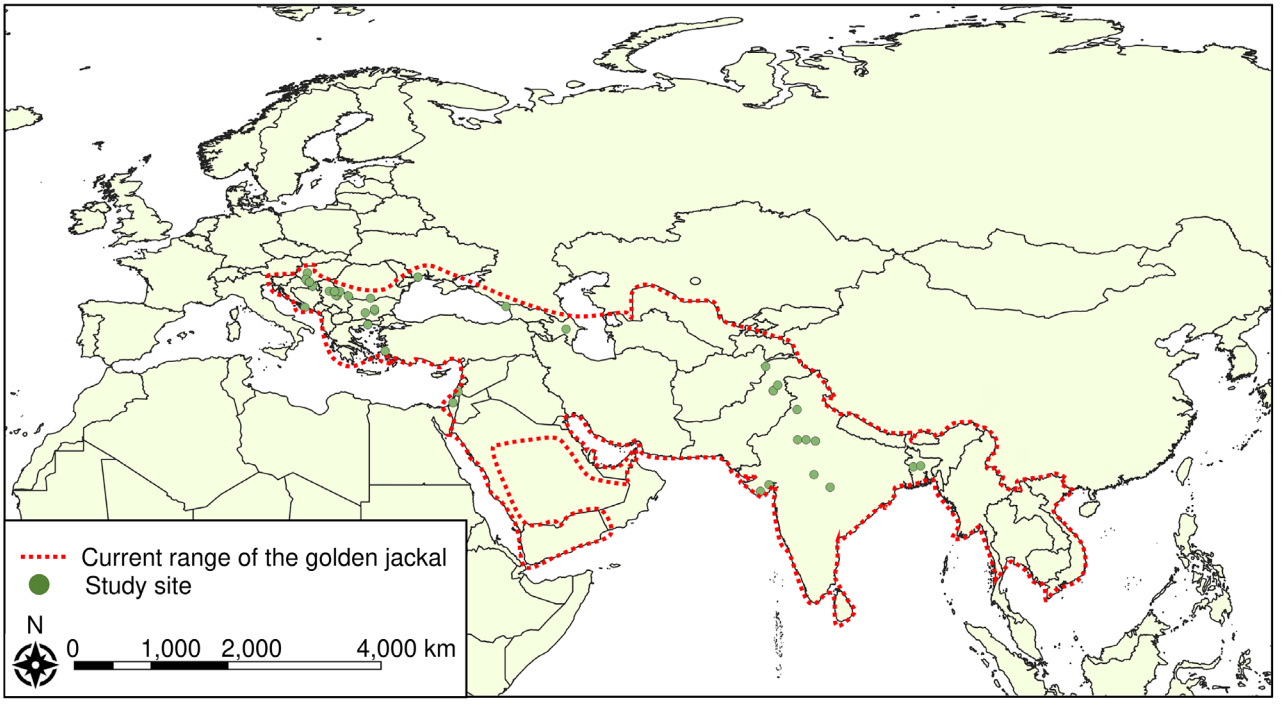


Fig. 1. Locations of the study areas that were used in the reviewed articles to investigate the food habits of the golden jackal *Canis aureus* in the Eurasian continent.

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studies (Lanszki et al. 2006, Raichev et al. 2013) and excluding contaminants (e.g. sand and gravel) and any unidentified items: 1) small mammals (mainly rodents and shrews, < 1 kg body mass); 2) medium-sized mammals (e.g. hares, mesocarnivores, primates and coypu *Myocastor coypus*, mostly < 15 kg body mass); 3) wild ungulates (e.g. cervids, bovids and wild boar *Sus scrofa*; 4) domestic mammals (e.g. pig, sheep, cow, goat, donkey and horse, as well as feral cats and dogs); 5) wild birds (including game species); 6) poultry; 7) other vertebrates (i.e. reptiles, amphibians and fishes); 8) invertebrates (e.g. insects, molluscs and earthworms); 9) plant materials (fruits, seeds, cereals and leaves) and 10) trash (e.g. envelopes or wrappers consumed with leftovers of human meals). We then estimated the relative frequency of occurrence (RFO; %) for each of these food categories using the following equations:

RFO (%) = number of occurrences of the food category/total number of food categories × 100.

In instances where the numbers of occurrences of food items were not shown in the published literature, we back-calculated from the FO and then estimated the RFO. Although use of the RFO is not the most comprehensive technique for evaluating absolute carnivore diets (Klare et al. 2011), previous studies have demonstrated that it is suitable for making inter-population dietary comparisons in meta-analyses, such as the present study (Clavero et al. 2003, Lozano et al. 2006, Zhou et al. 2011).

Geographical and environmental factors

For each published study, we obtained the latitude, longitude and altitude of the centre of each study area as geographical factors and the normalised difference vegetation index (NDVI) and proportions of agricultural and urban areas within a 10-km radius of the centre of each study area as environmental factors. To obtain altitudes, we used the global version elevation data of the Geospatial Information Authority of Japan (version 1, https://globalmaps.github.io/el.html), which covers the whole world at 1-m intervals, and log-transformed the values obtained for analysis. NDVI was obtained by extracting monthly vegetation index data for 2001 from a global dataset (0.25-degree resolution) provided by the National Aeronautics and Space Administration (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD_NDVI_M) and calculating an annual mean value. The proportions of agricultural and urban areas within a 10-km radius were calculated from a land-use map reclassified by the Global Land Cover by National Mapping Organizations (GLCNMO version 1, https://globalmaps.github.io/glcnmo.html: Tateishi et al. 2011), which was created from Moderate Resolution Imaging Spectroradiometer data from 2003 at a resolution of 30 seconds (approximately 1 km). We had to use recently measured values of the NDVI and land covers, owing to the difficulties with data availability and accessibility in the past. Although our compiled datasets on jackal diets covered 50 years (from 1967 to 2016; Table S1), more than 90% of them were published within the last two decades (Fig. S1).

Statistical analyses

To test hypothesis *H1*, we first performed Pearson's correlation analysis for all possible pairs of the 10 food categories (i.e. a total of 45 pairs) using the "corr.test" function in the "psych" package for R (Revelle 2019). To test hypotheses *H2-4*, we performed multivariate analyses using generalised linear mixed effects models (GLMMs) using the "glmer" function in the "lme4" package for R (Bates et al. 2015). Prior to GLMM analyses, we assessed the effects of methodological differences among the studies by performing permutational multivariate analysis of variance (PERMANOVA) using the "adonis" function (with the Bray-Curtis distance and 9999 permutations) in the "vegan" package for R (Oksanen et al. 2019), in which sample size (i.e. total number of sampled stomachs/scats), sample type (i.e. stomachs or scats) and sample season were included as explanatory variables, following the procedures used in previous studies (Diaz-Ruiz et al. 2013, Doherty et al. 2015). Any methodological parameters that were found to be statistically significant were then included as random effects in the GLMM analyses. In addition, we performed Pearson's correlation analysis for all possible pairs of geographical (latitude, longitude and altitude) and environmental (NDVI, proportion of agricultural areas and proportion of urban areas) parameters to test for multicollinearity. This analysis showed that there was a significant negative correlation with a relatively high variance inflation factor (VIF) between latitude and longitude ($r = -0.913$, $P < 0.001$, VIF = 6.02; see Table S2), indicating a strong multicollinearity between these variables. Therefore, we summarised these parameters into a single variable using principal component analysis (PCA) (see "Results").

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Table 1. Pearson's correlation coefficients (lower left corner) and statistical significances (upper right corner) for all possible pairs of relative frequencies of occurrence for 10 food categories in the diets of the golden jackal *Canis aureus*.

Food category	Small mammals	Medium-sized mammals	Wild ungulates	Domestic mammals	Wild birds	Poultry	Other vertebrates	Invertebrates	Plant materials	Trash
Small mammals			< 0.05	< 0.05					< 0.01	< 0.05
Medium-sized mammals	–0.177				< 0.01				< 0.05	
Wild ungulates	–0.287	–0.005			< 0.001					
Domestic mammals	–0.317	–0.105	–0.111			< 0.001			< 0.05	
Wild birds	–0.008	0.430	–0.462	–0.255						
Poultry	–0.232	–0.073	–0.176	0.503	–0.255					
Other vertebrates	0.035	–0.119	–0.027	–0.254	0.189	–0.204		< 0.05		
Invertebrates	–0.198	–0.115	–0.077	–0.274	0.132	–0.135	0.311			
Plant materials	–0.373	–0.341	0.021	–0.316	–0.183	–0.130	–0.070	0.164		
Trash	–0.282	–0.040	–0.005	0.151	0.030	0.021	0.087	–0.133	–0.014	

After completing these procedures, we developed models to explain the RFO, which included the five explanatory variables as fixed effects and two methodological parameters as random effects (see "Results"), which were fitted with a binomial error distribution with a logit link function. To adopt models with higher explanatory power and fewer variables, we performed a best-subset selection

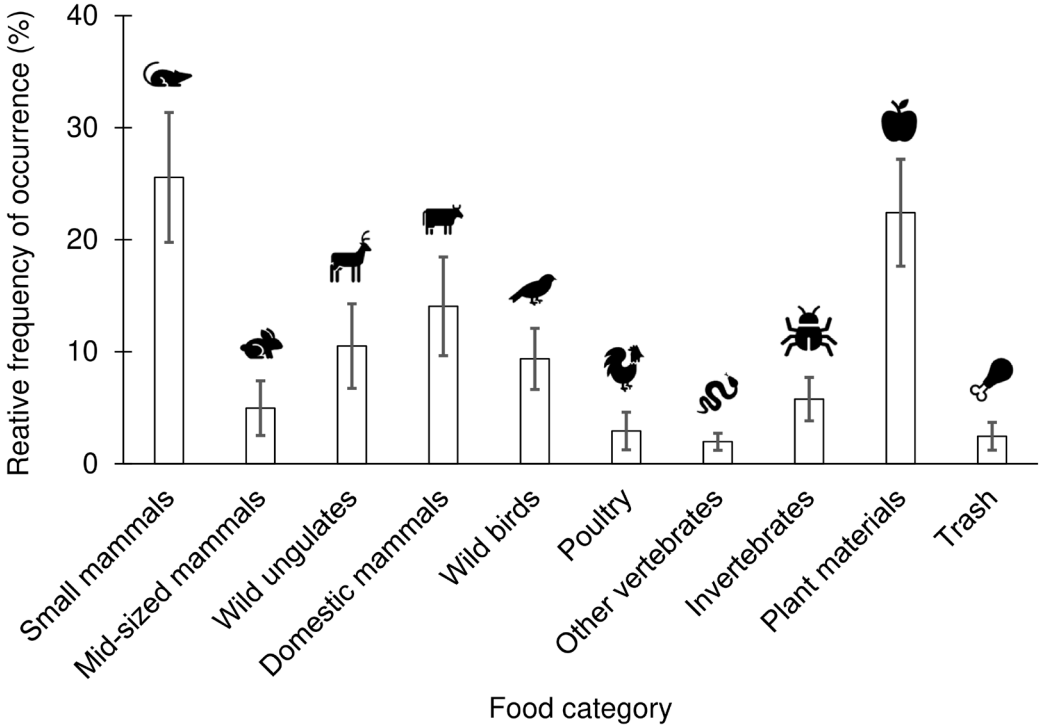


Fig. 2. Mean and 95% confidence intervals (horizontal bars) of the relative frequencies of occurrence (%) of 10 food categories in the diets of the golden jackal *Canis aureus*.

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Table 2. Results of the permutational multivariate analysis of variance (PERMANOVA) examining the effects of sample season, sample size and sample type on the overall diets of the golden jackal *Canis aureus*.

Variable	*d.f.*	*F*	R^2	*P*
Season_spring	1	4.197	0.071	0.002
Season_summer	1	1.022	0.017	0.398
Season_autumn	1	1.126	0.019	0.349
Season_winter	1	2.992	0.051	0.014
Sample sizes	1	1.393	0.024	0.220
Sample materials	1	5.218	0.089	< 0.001
Residuals	43		0.729	

procedure using all possible combinations of the five explanatory variables and chose the model with the lowest Akaike's information criterion score using the "dredge" function in the "MuMIn" package for R (Bartoń 2015).

Results

With respect to *H1* (dietary patterns), the primary food category that was taken by golden jackals across the reviewed datasets was small mammals [mean RFO ± 95% confidence interval (CI) = 25.6 ± 5.8%; predominant in 17/50 datasets], followed by vegetable materials (22.4 ± 4.8%; 15/50 datasets), domestic mammals (14.1 ± 4.4%; 10/50 datasets) and wild ungulates (10.5 ± 2.4%; 6/50 datasets) (Fig. 2). The RFO of small mammals in the jackal diet was significantly negatively correlated with the RFOs of wild ungulates (P = 0.046), domestic mammals (P = 0.025) and plant materials (P = 0.008) (Table 1). For the major food categories (i.e. those with a mean RFO > 10%), there were also significant negative correlations between small mammals and trash (P = 0.047), wild ungulates and wild birds (P < 0.001) and domestic mammals and plant materials (P = 0.025), while there was a significant positive correlation between domestic mammals and poultry (P < 0.001) (Table 1).

PERMANOVA revealed that the overall diets of jackals were significantly related to sample type (P < 0.001) and sample season, particularly winter (P < 0.05) and spring (P < 0.01), but not sample size (Table 2). Therefore, both sample type and

Table 3. Results of the generalised linear mixed model (GLMM) analyses examining biogeographical patterns in the consumption of 10 food categories in the diet of the golden jackal *Canis aureus* across the Eurasian continent (blanks represent a non-selected variable in the best-fitting model).

Food category		(Intercept)	Principal component on longitude-latitude	Altitude	NDVI	Agricultural lands	Urbanized area
Small mammals	β	−1.435	−0.620	0.156	0.522	0.951	−0.691
	P	0.211	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Medium-sized mammals	β	−3.804	0.556		−0.176	−0.816	−0.546
	P	< 0.001	< 0.001		0.011	< 0.001	< 0.001
Wild ungulates	β	−3.417	−0.117		−0.127		0.310
	P	< 0.001	0.012		0.010		< 0.001
Domestic mammals	β	−1.398	0.354	−0.307	−0.643	−0.519	−0.378
	P	0.153	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Wild birds	β	−2.421	0.624	−0.228	0.266	−0.387	
	P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
Poultry	β	−4.851		0.672	−0.716	−0.406	−0.443
	P	< 0.001		< 0.001	< 0.001	< 0.001	0.130
Other vertebrates	β	−3.782	0.272			0.296	
	P	< 0.001	0.016			0.024	
Invertebrates	β	−2.444	0.103	−0.444		−0.738	−0.859
	P	< 0.001	0.147	< 0.001		< 0.001	< 0.001
Plant materials	β	−1.738	0.099	0.056	−0.179	−0.096	0.787
	P	0.002	0.010	0.101	< 0.001	0.007	< 0.001
Trash	β	−5.916	−0.602	1.911	−0.880	0.694	1.781
	P	< 0.001	0.062	< 0.001	< 0.001	0.016	< 0.001

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season were included as random effects in the following GLMM analyses. The PCA for latitude and longitude showed that the first principal component (PC) explained 95.6% of the variance and indicated a positive interaction with longitude and a negative interaction with latitude (see Table S3). Therefore, we included the first PC score as an explanatory variable in the following GLMM analyses.

With respect to *H2* (geographical patterns in jackal diets), the GLMM analysis with model selection showed that the summarised latitudinal-longitudinal variable was significantly positively associated with the RFOs of medium-sized mammals ($P < 0.001$), domestic mammals ($P < 0.001$), wild birds ($P < 0.001$), vertebrate prey ($P = 0.016$) and plant materials ($P = 0.010$), and significantly negatively associated with the RFOs of small mammals ($P < 0.001$) and wild ungulates ($P = 0.012$) (Table 3). In addition, altitude was significantly positively associated with the RFOs of small mammals ($P < 0.001$), poultry ($P < 0.001$) and trash ($P < 0.001$) and significantly negatively associated with the RFOs of domestic mammals ($P < 0.001$), wild birds ($P < 0.001$) and invertebrates ($P < 0.001$) (Table 3).

With respect to *H3* (effects of regional primary productivity), NDVI was significantly positively associated with the RFOs of small mammals ($P < 0.001$) and wild birds ($P < 0.001$) and significantly negatively associated with the RFOs of medium-sized mammals ($P = 0.011$), wild ungulates ($P = 0.010$), domestic mammals ($P < 0.001$), poultry ($P < 0.001$), plant materials ($P < 0.001$) and trash ($P < 0.001$) (Table 3).

With respect to *H4* (effects of anthropogenic landscape modifications), the proportion of agricultural areas was significantly positively associated with the RFOs of small mammals ($P < 0.001$), other vertebrate prey ($P = 0.024$) and trash ($P = 0.016$), and significantly negatively associated with the RFOs of medium-sized mammals ($P < 0.001$), domestic mammals ($P < 0.001$), wild birds ($P < 0.001$), poultry ($P < 0.001$), invertebrates ($P < 0.001$) and plant materials ($P = 0.007$) (Table 3). In addition, the proportion of urban areas was significantly positively associated with the RFOs of wild ungulates ($P < 0.001$), plant materials ($P < 0.001$) and trash ($P < 0.001$), and significantly negatively associated with the RFOs of small mammals ($P < 0.001$), medium-sized mammals ($P < 0.001$), domestic mammals ($P < 0.010$) and invertebrates ($P < 0.010$) (Table 3).

Discussion

This review revealed that small mammals are a staple food for golden jackals on the Eurasian continent, while plant materials, domestic mammals and wild ungulates are also major food items in their diets (i.e. mean RFOs > 10%; Fig. 2 and Table S1). There were significant negative correlations between the RFOs of small mammals and the other three categories, as well as between plant materials and domestic mammals (Table 1), supporting hypothesis *H1*. It has previously been reported that the extent to which jackals consume rodents corresponds functionally to the prey availability in their habitat (Lanszki et al. 2006), and our findings indicated that golden jackals switch their staple food from small mammals to alternative foods, probably according to regional resource availability (see below), as observed in other European mesocarnivores (e.g. Lozano et al. 2006, Diaz-Ruiz et al. 2013). Our findings also indicated that the dietary patterns of Eurasian jackals can be divided into three main groups: feeding on small mammals; consuming fruits or grains (e.g. Nadeem et al. 2012, Penezić & Ćirović 2015, Tsunoda et al. 2019) and scavenging the carcasses of domestic animals or wild ungulates (Giannatos et al. 2010, Borkowski et al. 2011, Raichev et al. 2013, Ćirović et al. 2014b). Food categories that make up a relatively smaller proportion of the jackal diet (i.e. mean RFO < 10%) may serve as supplementary prey/foods when there are seasonal or temporal shortages of the staple food resources (Newsome et al. 2016).

Two of the staple food categories (i.e. small mammals and wild ungulates) were significantly negatively associated with the summarised longitudinal-latitudinal parameter, indicating that they were more frequently observed in the diet in more north-western regions (i.e. from Asia to Europe), and the consumption of small mammals also increased with altitude, supporting hypothesis *H2*. These geographical patterns in the diet of jackals may result from resource availabilities being affected by regional climates, which are milder in Asia (ranging from tropical to temperate zones) than in Europe (dominated by temperate zones). Mammalian prey may be the main available resource in cooler temperate zones (i.e. higher latitudes or highlands) owing

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to the scarcity of vegetative resources (e.g. fruits or grains), poikilothermic vertebrates and invertebrate prey, particularly in the cold season, so jackal populations inhabiting higher latitudinal and/or altitudinal zones may rely more on mammalian foods. However, contrary to our prediction, the consumption of other mammalian categories (i.e. medium-sized mammals and domestic mammals) increased at lower latitudes (with increasing longitude) and altitudes. Medium-sized mammals were a regionally predominant foods for some jackal populations, possibly owing to regional resource diversity (e.g. in Asia; Shabbir et al. 2013), or region-specific prey abundances (e.g. jackals specifically rely on coypu in the Caucasus; Geptner & Naumov 1967), whereas those prey items generally make up a lower proportion of the diet of European populations (mostly RFO < 10%; see Table S1). The consumption of domestic mammals, which are often scavenged as carcasses (Giannatos et al. 2010, Borkowski et al. 2011, Nadeem et al. 2012, Raichev et al. 2013, Ćirović et al. 2014b, Singh et al. 2016), may also be associated with their regional availability, which will depend on the disposal method for the remains of slaughtered or dead animals (Bino et al. 2010), rather than the numbers of animals raised.

The consumption of both small mammals and wild birds increased with NDVI as an indicator of regional productivity, which is typically associated with the increased regional abundance and diversity of these small animals (Pettorelli et al. 2011), supporting hypothesis *H3*. Since NDVI is an indicator of vegetation cover and herbaceous biomass on the land surface as measured by satellite sensors, it is also typically positively associated with the abundance or diversity of various herbivorous animals, e.g. insects and wild ungulates (Pettorelli et al. 2011). However, the RFOs of these food categories in the diet of jackals were negatively or non-significantly associated with NDVI (Table 3). This finding may be due to dietary shifts from preferred foods, i.e. small mammals, to alternative foods during times when resources are scarce due to lower productivity, as discussed above in terms of hypothesis *H1*.

While the consumption of trash by golden jackals was positively associated with both agricultural land use and urbanisation, the consumption of domestic mammals and poultry was not associated with either factor, which was inconsistent with hypothesis *H4*. These findings indicate that landscape modifications at a relatively large geographical scale (e.g. 10-km radius in the present study) are unlikely to respond to the availability of carcasses of domestic animals, which may depend on regional waste management legislation (i.e. piled up in the open or buried in landfill; e.g. Bino et al. 2010) or the cultural norms of local communities (e.g. the illegal dumping of slaughtered remains in Bulgarian rural hamlets; Raichev et al. 2013). Furthermore, in general, the disposal sites may be located away from human settlements for sanitation purposes – indeed, we recently observed that jackals in montane secondary forests predominantly consume the carcasses of domestic mammals, while those in agricultural lowlands mainly preyed on rodents (Markov & Lanszki 2012, Raichev et al. 2020).

In contrast to anthropogenic resources, the consumption of small mammals was positively associated with the proportion of agricultural land and negatively associated with the extent of urbanisation. This finding may be explained by regional differences in prey availability, which is consistent with our prediction, as it has previously been shown that the richness and diversity of small rodents is elevated in agricultural landscapes (Delattre et al. 1996, Alain et al. 2006, Panazacchi et al. 2010) and reduced in urban areas (Cavia et al. 2009, Łopucki & Kitowski 2017). However, we could not find any similar patterns in the consumption of other natural foods, despite faunal and floral richness and diversity generally showing similar responses to landscape modification (e.g. Saito & Koike 2013, Aronson et al. 2014, French et al. 2018).

The consumption of plant materials was found to increase in urban areas but decrease in agricultural areas. One potential explanation for this pattern is as an artefact of the designation of land as agricultural in the study. In general, floral biodiversity in agricultural ecosystems is richer in small mosaics of agricultural land with heterogenous environments (e.g. agro-forest landscapes) than in relatively large and homogenous agricultural land under intensive cultivation (Sodhi et al. 2010, Vrdoljak & Samways 2013, Plieninger et al. 2015). In support of this idea, jackals that inhabit mosaic agricultural landscapes were found to consume a relatively higher proportion of fruit (Lanszki et al. 2009, 2010). It should also be noted that there was a methodological issue with the plant materials food category, as this included both wild

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and cultivated species in many of the reviewed articles and consequently these were categorised into a single item in the study. Cultivated plants may be available in urban areas, originating from ornamental and roadside plants (Johnson & Swan 2014) or might represent the leftovers from human meals, and may represent a staple food resource for carnivores that have shifted their diets to be more omnivorous (Fedriani et al. 2001, Hisano et al. 2016). Therefore, jackals may shift their foraging strategies from feeding on small mammals to consuming rich vegetative resources in urban areas.

The consumption of wild ungulates was significantly positively associated with urbanisation, which is surprising given that wild ungulates are generally vulnerable to landscape modification and thus their potential availability is predicted to be negatively affected by urbanisation (Saito & Koike 2013). However, wild ungulates are mainly consumed by jackals through scavenging rather than predation (Raichev et al. 2013, Lanszki et al. 2015) and urbanisation generally increases the number of vehicle collisions with ungulate species (Adams & Lindsey 2010, Riley et al. 2014, Rodewald & Gehrt 2014). Thus, the availabilities of wild ungulate carcasses for jackals may be higher in urban areas.

Golden jackals have expanded northward in Europe (Arnold et al. 2012), as evidenced by their establishment and potential reproduction in the Baltic region (Kowalczyk et al. 2020), which has raised concerns for their management in newly colonised countries (Trouwborst et al. 2015). Our finding that jackals consume small mammals to a greater extent at higher latitudes indicates potential food resource competition with other rodentivorous carnivores, such as the red fox *Vulpes vulpes*; previous studies have demonstrated food competition between these two canids in southern European and Mediterranean regions (Scheinin et al. 2006, Farkas et al. 2017, Tsunoda et al. 2017). Furthermore, disruption to the availability of the staple food of jackals (i.e. small mammals) due to anthropogenic landscape modification (specifically urbanisation) has facilitated dietary shifts and potentially an increased reliance on anthropogenic resources. However, we should note a caveat to our results in assessing environmental associations (e.g. NDVI) and anthropogenic impacts (e.g. urbanisation) on resource use patterns in some jackal populations sampled before the 1980s (e.g. in the Caucasus and some Asian areas; Fig. 1 and Fig. S1 and Table S1), due to the lack of historical geographic data (see "Material and Methods").

In conclusion, biogeographical patterns and anthropogenic impacts of jackals trophic niches observed in our meta-analytical study at a continental scale are probably best supported in the European and Asian populations that have been studied in recent years (i.e. after the 2000s). For the last several decades, land transformation from forests to croplands have increased through Asian regions (Ramankutty & Foley 1999), while farmland abandonment has extended in Central and Eastern Europe (Alcantara et al. 2013). Further meta-analytical studies in each region (i.e. Europe or Asia) might be helpful in explaining patterns in the trophic niches associated with these regional landscape changes in golden jackals. We propose that a fundamental approach for solving human-jackal conflicts may be through the conservation of their habitat to maintain their natural food resources, in combination with appropriate waste management to decrease the accessibility of anthropogenic resources (Bino et al. 2010) rather than lethal population control (Treves & Naughton-Treves 2005).

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Literature

Adams C.E. & Lindsey K.J. 2010: Urban wildlife management, 2nd ed. *CRC Press, Boca Raton, Florida, USA.*

Alain B., Gilles P. & Yannick D. 2006: Factors driving small rodents assemblages from field boundaries in agricultural landscapes of western France. *Landsc. Ecol. 21: 449–461.*

Alcantara C., Kuemmerle T., Baumann M. et al. 2013: Mapping the extent of abandoned farmland in Central and Eastern Europe using MODIS time series satellite data. *Environ. Res. Lett. 8: 035035.*

Aleksandra P. & Duško C. 2015: Seasonal variation in diet of the golden jackal (*Canis aureus*) in Serbia. *Mammal Res. 60: 309–317.*

Álvares F., Bogdanowicz W., Campbell L.A.D. et al. 2019: Old World *Canis* spp. with taxonomic ambiguity: workshop conclusions and recommendations. *Canid Biology & Conservation, CIBIO, Vairão, Portugal. http://www.canids. org/Old_world_canis_taxonomy_workshop.pdf*

Arnold J., Humer A., Heltai M. et al. 2012: Current status and distribution of golden jackal *Canis aureus* in Europe. *Mammal Rev. 42: 1–11.*

Aronson M.F.J., La Sorte F.A., Nilon C.H. et al. 2014: A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. Lond. B 281: 2013.3330.*

Bartoń K. 2015: MuMIn: multi-model Inference. R package version 1.15.1. *https://cran.r-project.org/web/packages/MuMIn/index.html*

Bateman P.W. & Fleming P.A. 2012: Big city life: carnivores in urban environments. *J. Zool. Lond. 287: 1–23.*

Bates D., Maechler M., Bolker B. & Walker S. 2015: Fitting linear mixed-effects models using lme4. *J. Stat. Softw. 67: 1–48.*

Bino G., Dolev A., Yosha D. et al. 2010: Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *J. Appl. Ecol. 47: 1262–1271.*

Bojarska K. & Selva N. 2012: Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Rev. 42: 120–143.*

Borkowski J., Zalewski A. & Manor R. 2011: Diet composition of golden jackals in Israel. *Ann. Zool. Fenn. 48: 108–118.*

Bošković I., Šperanda M., Florijančić T. et al. 2013: Dietary habits of the golden jackal (*Canis aureus* L.) in the eastern Croatia. *Agric. Conspec. Sci. 78: 245–248.*

Cavia R., Cueto G.R. & Suarez O.V. 2009: Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landsc. Urban Plan. 90: 11–19.*

Ćirović D., Chochlakis D., Tomanović S. et al. 2014a: Presence of *Leishmania* and *Brucella* species in the golden jackal *Canis aureus* in Serbia. *BioMed Res. Int. 2014: 728516.*

Ćirović D., Penezić A., Milenković M. & Paunović M. 2014b: Winter diet composition of the golden jackal (*Canis aureus* L., 1758) in Serbia. *Mamm. Biol. 79: 132–137.*

Ćirović D., Penezić A. & Krofel M. 2016: Jackals as cleaners: ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biol. Conserv. 199: 51–55.*

Clavero M., Prenda J. & Delibes M. 2003: Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. *J. Biogeogr. 30: 761–769.*

Curtis P.D. & Hadidian J. 2010: Responding to human-carnivore conflicts in urban areas. In: Gehrt S.D., Riley S.P.D. & Cypher B.L. (eds.), Urban carnivores: ecology, conflict, and conservation. *Johns Hopkins University Press, Baltimore, Maryland, USA: 201–211.*

Delattre P., Giraudoux P., Baudry J. et al. 1996: Effect of landscape structure on common vole (*Microtus arvalis*) distribution and abundance at several space scales. *Landsc. Ecol. 11: 279–288.*

Diaz-Ruiz F., Delibes-Mateos M., Garcia-Moreno J.L. et al. 2013: Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. *Mammal Rev. 43: 59–70.*

Doherty T.S., Davis R.A., van Etten E.J.B. et al. 2015: A continental-scale analysis of feral cat diet in Australia. *J. Biogeogr. 42: 964–975.*

Farkas A., Janoska F., Fodor J.T. & Nahlik A. 2017: The high level of nutritional niche overlap between red fox (*Vulpes vulpes*) and sympatric golden jackal (*Canis aureus*) affects the body weight of juvenile foxes. *Eur. J. Wildl. Res. 63: 46.*

Fedriani J., Fuller T. & Sauvajot R. 2001: Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography 24: 325–331.*

Fischer J. & Lindenmayer D.B. 2007: Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr. 16: 265–280.*

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French S.S., Webb A.C., Hudson S.B. & Virgin E.E. 2018: Town and country reptiles: a review of reptilian responses to urbanization. *Integr. Comp. Biol. 58: 948–966.*

Gehrt S.D., Riley S.P. & Cypher B.L. 2010: Urban carnivores: ecology, conflict, and conservation. *Johns Hopkins University Press, Baltimore, Maryland, USA.*

Geptner V.G. & Naumov N.P. 1967: Mammals of the Soviet Union. *Vysshaya Shkola Publishers, Moscow, Russia. (in Russian)*

Giannatos G., Karypidou A., Legakis A. & Polymeni R. 2010: Golden jackal (*Canis aureus* L.) diet in southern Greece. *Mamm. Biol. 75: 227–232.*

Hayward M.W., Porter L., Lanszki J. et al. 2017: Factors affecting the prey preferences of jackals (Canidae). *Mamm. Biol. 85: 70–82.*

Hisano M., Raichev E.G., Peeva S. et al. 2016: Comparing the summer diet of stone martens (*Martes foina*) in urban and natural landscape in Central Bulgaria. *Ethol. Ecol. Evol. 28: 295–311.*

Jhala Y.V. & Moehlman P. 2004: Golden jackal (*Canis aureus*). In: Sillero-Zubiri C., Hoffman M. & Macdonald D.W. (eds.), Canids: foxes, wolves, jackals and dogs. *IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, UK: 156–161.*

Johnson A.L. & Swan C.M. 2014: Drivers of vegetation species diversity and composition in urban ecosystems. In: McCleery R.A., Moorman C.E. & Peterson M.N. (eds.), Urban wildlife conservation: theory and practice. *Springer US, New York, USA: 75–90.*

Klare U., Kamler J.F. & Macdonald D.W. 2011: A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Rev. 41: 294–312.*

Koepfli K.-P., Pollinger J., Godinho R. et al. 2015: Genome-wide evidence reveals that African and Eurasian golden jackals are distinct species. *Curr. Biol. 25: 2158–2165.*

Korslund L. & Steen H. 2006: Small rodents winter survival: snow conditions limit access to food resources. *J. Anim. Ecol. 75: 156–166.*

Kowalczyk R., Wudarczyk M., Wójcik J.M. & Okarma H. 2020: Northernmost record of reproduction of the expanding golden jackal population. *Mamm. Biol. 99: 107–111.*

Krofel M., Giannatos G., Ćirović D. et al. 2017: Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? *Hystrix 28: 9–15.*

Lanszki J., Giannatos G., Dolev A. et al. 2010: Late autumn trophic flexibility of the golden jackal *Canis aureus*. *Acta Theriol. 55: 361–370.*

Lanszki J., Giannatos G., Heltai M. & Legakis A. 2009: Diet composition of golden jackals during cub-rearing season in Mediterranean marshland in Greece. *Mamm. Biol. 74: 72–75.*

Lanszki J., Heltai M. & Szabó L. 2006: Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannoninan ecoregion (Hungary). *Can. J. Zool. 84: 1647–1656.*

Lanszki J., Kurys A., Heltai M. et al. 2015: Diet composition of the golden jackal in an area of intensive big game management. *Ann. Zool. Fenn. 52: 243–255.*

Lanszki J., Kurys A., Szabó L. et al. 2016: Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary). *Folia Zool. 65: 310–322.*

Łopucki R. & Kitowski I. 2017: How small cities affect the biodiversity of ground-dwelling mammals and the relevance of this knowledge in planning urban land expansion in terms of urban wildlife. *Urban Ecosyst. 20: 933–943.*

Lozano J., Moleon M. & Virgos E. 2006: Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *J. Biogeogr. 33: 1076–1085.*

Markov G. & Lanszki J. 2012: Diet composition of the golden jackal, *Canis aureus* in an agricultural environment. *Folia Zool. 61: 44–48.*

Nadeem M.S., Naz R., Shah S.I. et al. 2012: Season- and locality-related changes in the diet of Asiatic jackal (*Canis aureus*) in Potohar, Pakistan. *Turk. J. Zool. 36: 798–805.*

Newsome T.M., Boitani L., Chapron G. et al. 2016: Food habits of the world's grey wolves. *Mammal Rev. 46: 255–269.*

Newsome T.M., Dellinger J.A., Pavey C.R. et al. 2015: The ecological effects of providing resource subsidies to predators. *Glob. Ecol. Biogeogr. 24: 1–11.*

Newsome T.M., Greenville A.C., Ćirović D. et al. 2017: Top predators constrain mesopredator distributions. *Nat. Commun. 8: 15469.*

Oksanen J., Blanchet F.G., Friendly M. et al. 2019: vegan: community ecology package, version 2.5-5. *https://CRAN.R-project.org/package=vegan*

Panazacchi M., Linnell J.D.C., Melis C. et al. 2010: Effect of land-use on small mammal abundance and diversity in a forest–farmland

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mosaic landscape in south-eastern Norway. *For. Ecol. Manag. 259: 1536–1545.*

Penezić A. & Ćirović D. 2015: Diet of adult and juvenile golden jackals (*Canis aureus*) during cubs' dependency stage. *Balkan J. Wildl. Res. 2: 27–32.*

Pettorelli N., Ryan S., Mueller T. et al. 2011: The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Clim. Res. 46: 15–27.*

Plieninger T., Hartel T., Martin-Lopez B. et al. 2015: Wood-pastures of Europe: geographic coverage, social-ecological values, conservation management, and policy implications. *Biol. Conserv. 190: 70–79.*

Prange S., Gehrt S. & Wiggers E. 2004: Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J. Mammal. 85: 483–490.*

Prugh L.R., Stoner C.J., Epps C.W. et al. 2009: The rise of the mesopredator. *BioScience 59: 779–791.*

Raichev E.G., Peeva S., Kirilov K.B. et al. 2020: Autumn-winter dietary adaptability of the golden jackal (*Canis aureus*) with respect to type and intensity of human activities in three areas (Central Bulgaria). *Acta Zool. Bulg. 72: 413–420.*

Raichev E.G., Tsunoda H., Newman C. et al. 2013: The reliance of the golden jackal (*Canis aureus*) on anthropogenic foods in winter in central Bulgaria. *Mamm. Study 38: 9–27.*

Ramankutty N. & Foley J.A. 1999: Estimating historical changes in global land cover: croplands from 1700 to 1992. *Glob. Biogeochem. Cycles 13: 997–1027.*

Revelle W. 2019: psych: procedures for psychological, psychometric, and personality research. R package version 1.9.12. *Northwestern University, Evanston, Illinoi, USA. https://CRAN.R-project.org/package=psych*

Riley S.P.D., Brown J.L., Sikich J.A. et al. 2014: Wildlife friendly roads: the impacts of roads on wildlife in urban areas and potential remedies. In: McCleery R.A., Moorman C.E. & Peterson M.N. (eds.), Urban wildlife conservation: theory and practice. *Springer US, New York, USA: 323–360.*

Rodewald A.D. & Gehrt S.D. 2014: Wildlife population dynamics in urban landscapes. In: McCleery R.A., Moorman C.E. & Peterson M.N. (eds.), Urban wildlife conservation: theory and practice. *Springer US, New York, USA: 117–147.*

Roemer G.W., Gompper M.E. & Van Valkenburgh B. 2009: The ecological role of the mammalian mesocarnivore. *BioScience 59: 165–173.*

Rutkowski R., Krofel M., Giannatos G. et al. 2015: A European concern? Genetic structure and expansion of golden jackals (*Canis aureus*) in Europe and the Caucasus. *PLOS ONE 10: e0141236.*

Saito M. & Koike F. 2013: Distribution of wild mammal assemblages along an urban-rural-forest landscape gradient in warm-temperate East Asia. *PLOS ONE 8: e65464.*

Šálek M., Červinka J., Banea O.C. et al. 2014: Population densities and habitat use of the golden jackal (*Canis aureus*) in farmlands across the Balkan Peninsula. *Eur. J. Wildl. Res. 60: 193–200.*

Scheinin S., Yom-Tov Y., Motro U. & Geffen E. 2006: Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment. *Anim. Behav. 71: 577–584.*

Shabbir S., Anwar M., Hussain I. & Nawaz M.A. 2013: Food habits and diet overlap of two sympatric carnivore species in Chitral, Pakistan. *J. Anim. Plant Sci. 23: 100–107.*

Singh A., Mukherjee A., Dookia S. & Kumara H.N. 2016: High resource availability and lack of competition have increased population of a meso-carnivore – a case study of golden jackal in Keoladeo National Park, India. *Mammal Res. 61: 209–219.*

Sodhi N.S., Koh L.P., Clements R. et al. 2010: Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv. 143: 2375–2384.*

Soe E., Davison J., Suld K. et al. 2017: Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. *Mammal Rev. 47: 198–211.*

Tateishi R., Uriyangqai B., Al-Bilbisi H. et al. 2011: Production of global land cover data – GLCNMO. *Int. J. Digit. Earth 4: 22–49.*

Treves A. & Naughton-Treves L. 2005: Evaluating lethal control in the management of human-wildlife conflict. In: Woodroffe R., Thirgood S. & Rabinowitz A. (eds.), People and wildlife: conflict or coexistence? *Cambridge University Press, Cambridge, UK: 86–106.*

Trouwborst A., Krofe M. & Linnell J.D.C. 2015: Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (*Canis aureus*) in Europe. *Biodivers. Conserv. 24: 2593–2610.*

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Tsunoda H., Peeva S., Raichev E. et al. 2019: Autumn dietary overlaps among three sympatric mesocarnivores in the central part of Stara Planina Mountain, Bulgaria. *Mamm. Study 44: 275–281.*

Tsunoda H., Raichev E.G., Newman C. et al. 2017: Food niche segregation between sympatric golden jackals and red foxes in central Bulgaria. *J. Zool. Lond. 303: 64–71.*

Viranta S., Atickem A., Werdelin L. & Stenseth N.C. 2017: Rediscovering a forgotten canid species. *BMC Zool. 2: 6.*

Vrdoljak S.M. & Samways M.J. 2013: Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodivers. Conserv. 23: 133–148.*

Yom-Tov Y., Ashkenazi S. & Viner O. 1995: Cattle predation by the golden jackal *Canis aureus* in the Golan Heights, Israel. *Biol. Conserv. 73: 19–22.*

Zhou Y.B., Newman C., Buesching C.D. et al. 2011: Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *J. Biogeogr. 38: 137–147.*

Supplementary online material

Fig. S1. Yearly distributions of (A) the reviewed studies (n = 45; solid and open bars represent the studies compiled and not-compiled for meta-analyses, respectively) and (B) the compiled datasets for meta-analyses from the 31 studies.

Table S1. List of the studies that were compiled for review and meta-analyses in this study.

Table S2. Pearson's correlation coefficients (lower left corner) and variance inflation factors (VIFs; upper right corner) among the explanatory variables used in the generalised linear mixed model (GLMM) analyses.

Table S3. Results of the principal component analysis (PCA) of latitudes and longitude of the study areas used in the articles reviewed in this study.

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