Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes

Duško Ćirović[1,*,‡], Aleksandra Penezić[1], and Miha Krofel[2,‡]

[1] Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia

[2] Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia

[*]Corresponding author. Tel.: +381 11 2637024; fax: +381 11 2638500. E mail address: dcirovic@bio.bg.ac.rs (D. Ćirović)

[‡] Both authors contributed equally to this work

ABSTRACT

Ecosystem services are receiving increasing attention among researchers and managers, due to emerging recognition of their global extent and contribution towards human welfare. Obligatory scavengers have been identified as important providers of these services, namely waste management, but their populations are declining worldwide and mesocarnivores are taking on the role of dominant scavengers in many regions. However, mesocarnivores are rarely appreciated for their services of waste removal, and are mostly cited in negative contexts in the literature. Here we explored the widely neglected potential of mesocarnivores as providers of ecosystem services. We used the golden jackal (*Canis aureus*) as a model species and evaluated its provision of ecosystem services in a developing country in the Balkans, where waste management creates numerous challenges. Based on contents of 606 jackal stomachs, food intake and population size, we estimate that in Serbia jackal population annually removes >3 700 tonnes of animal waste and 13.2 million crop pest rodents. We estimate the monetary value of animal waste removal at >0.5 million € per year. We scaled this result up to evaluate ecosystem services at the continental-scale, and these results indicate that jackals remove substantial amounts of discarded animal waste (> 13 000 tonnes) as well as potential crop pests (> 158 million crop pest rodents) across human-dominated landscapes of Europe. These results are the first to demonstrate the value of ecosystem services provided by mesocarnivores as facultative scavengers, and show that they are of great value for local communities in the modern world. We emphasize the importance of recognizing ecosystem services provided by species with predominantly negative public images, in consideration of their conservation.

HIGHLIGHTS

- We evaluated ecosystem services provided by a mesocarnivore in a developing country
- Jackals removed substantial amounts of discarded animal waste and crop pests
- Benefits from mesocarnivores for local communities appear higher than costs
- Re-evaluation of mesocarnivore role in ecosystem services is called for

KEYWORDS

waste management, anthropogenic food subsidies, scavenging, golden jackal, *Canis aureus*, Serbia

INTRODUCTION

Large mammalian carnivores are regularly recognized as keystone species with important roles in maintaining biodiversity and stability of ecosystems (Estes et al. 2011; Ripple et al. 2014). There is also ample literature documenting their provision of ecosystem services (Brashares et al. 2010; Duffield et al. 2008; Krofel et al. 2014; Ripple et al. 2014). In contrast, mesocarnivores (i.e. carnivores with body weight <15 kg such as coyotes [*Canis latrans*] and badgers [*Meles meles*]) are rarely appreciated for their ecological role or the ecosystem services they provide (Roemer et al. 2009). In fact, most literature reports only their negative ecological effects, including killing of endangered species or monopolizing vital resources (DeVault et al. 2011; Prugh et al. 2009; Ripple et al. 2014). Due to real or perceived losses caused by mesocarnivores on livestock or valuable hunted species, they are often considered to be vermin or agricultural pests (Roemer et al. 2009). Consequently, the general public and various interest groups often express negative attitudes towards them (Kellert 1985; Mihelič & Krofel 2012) and they are subject to intensive lethal control programs (Berger 2006). At present, it is difficult to assess whether the deficiency of literature on ecosystem services provided by mesocarnivores is due to a lack of research or if is it a genuine indication that mesocarnivores have a limited role in providing such services.

Ecosystem services are receiving increasing attention among researchers and managers (Millennium Ecosystem Assessment 2005, Posner et al. 2016) and waste management has been identified as one of the most globally important ecosystem services (Costanza et al. 1997). Every year, human societies discard substantial quantities of livestock carcasses and other animal waste (Mateo-Tomás et al. 2015; Oro et al. 2013). Obligate vertebrate scavengers, such as vultures, have been recognized as important agents of carcass removal and related ecosystem services (Markandya et al. 2008; Moleón et al. 2014b). However, especially in human-dominated landscapes, obligate scavengers have suffered dramatic declines (Ogada et al. 2012). On the other hand, facultative scavengers, including mesocarnivores, have been rarely considered as providers of waste management services, and have even been regarded as detrimental to endangered scavengers through competition for carrion (DeVault et al. 2011; Moleón et al. 2014a). In contrast to vultures, mesocarnivores are highly adaptable to human-caused habitat modifications and often thrive in human-dominated landscapes, including urban and rural areas (Šálek et al. 2013). Therefore, there is potential for mesocarnivores to have an important impact by removing animal waste in degraded ecosystems with an impoverished scavenger guild. The need for research on animal waste consumption by scavengers in human-dominated landscapes has been recently recognized (Mateo-Tomás et al. 2015), and the ecosystem services provided by these species could be important for future waste management, as well as for mesocarnivore conservation through improving their often negative image among general public.

Here we explore this so far neglected potential of mesocarnivores as providers of ecosystem services. As a case study, we use the golden jackal (*Canis aureus*) in European human-dominated landscapes. The golden jackal is a typical mesocarnivore with high degree of adaptability and plasticity in its behaviour, which has facilitated its recent expansion throughout South-eastern and part of Central Europe (Šálek et al. 2013; Trouwborst et al. 2015). Opportunistic dietary habits have also enabled jackals to profit from anthropogenic food sources in the area (Lanszki et al. 2015). Studies comparing jackal feeding habits with other mesocarnivores, such as the red fox (*Vulpes vulpes*), suggest that diet and foraging behaviour of the golden jackal is typical for a mesocarnivore in human-dominated landscape (Lanszki et al. 2006).

We first analysed jackal diet in rural areas of Serbia, where waste management faces numerous challenges, including the incapacity to process large quantities of domestic animal carcasses and widespread unregulated disposal of slaughter remains (Gvozdenac 2015; Slamnig 2015). Despite being under strong hunting pressure, the jackal population is increasing in the country (Appendix A, Figure A1). We evaluated the amount of animal waste (remains from slaughtering and hunting) and rodents removed by jackals at the individual and population levels. For animal waste removal we also estimated annual monetary value of this service. We also reviewed the literature to gain a general understanding of ecosystem services provided by this mesocarnivore throughout Europe. To put these services in perspective, we also provide data to evaluate potential costs that are associated with presence of jackals. We then call attention to the importance of recognizing ecosystem services provided by species with predominantly negative public images for their conservation, as well as the importance of facultative scavengers for waste management in developing countries (Appendix A, Figure A2).

MATERIAL AND METHODS

Sample collection and diet analysis

Stomachs of shot animals and road kill were collected during 2004-2014 in all seasons, throughout the jackal distribution in Serbia (Appendix A, Figure A3). All jackals were sexed, weighed and measured before the stomachs were removed. Stomach content (Appendix A, Figure A4) was processed and analysed according to standard procedures (Ćirović et al., 2014a). Only samples from adult animals with food remains in the stomach were used for further analysis (N=606). Bones, teeth, hairs, and feathers were identified using identification keys (e.g. Teerink, 1991) and our own reference collections of wild and domestic animals. Food items were classified into 12 categories (Table 1) and for each category percentage of biomass consumed (%B) and relative frequency of occurrence (% O) was calculated. For animal remains found in stomachs it is generally difficult to differentiate between predation in scavenging. In our case, absence of muscles from livestock in the jackal stomachs and no reported livestock losses attributed to jackals according to the questionnaires made among livestock owners in the study area suggest that at least vast majority of livestock remains found in stomachs come from scavenging and not predation. Similarly, most of wild ungulate remains found in jackals stomachs were limited to hide, bones and intestines (i.e. parts that hunters discard in the field after dressing shot game), although we acknowledge that some of the wild ungulates consumed might have originate from predation.

Diet composition at the continental level

In order to evaluate consumption of the three food categories concerned (domestic animals, rodents and wild ungulates) at the European level, we reviewed all available literature on jackal diet in Europe. The primary search for references was carried out on Web on Science and Google Scholar using various combinations of keywords: golden jackal, *Canis aureus*, feeding, diet, and Europe. We also searched in the literature-cited sections of all retrieved articles. We retained those studies where food items were categorized in a way that enabled evaluation of the consumed biomass of categories concerned. Data from 13 references were considered (Appendix A, Table A3). For studies where consumed biomass was not reported we calculated conversion factors from our data from Serbia and estimated these values based on reported frequencies of occurrence (Appendix, Table A1). We estimated average diet composition of jackals in Europe by first calculating mean values from all studies for each country. Then we used country averages to calculate overall average diet at the continental level. In this way we reduced bias due to variable number of diet studies in individual countries. Because not all studies reported species composition among rodent species consumed by jackals, we first estimated overall proportion of rodents in jackal diet across Europe and then applied average proportion of crop pest taxa among the rodents (85.7 %B) from studies (N= 6) that reported rodent species composition.

Evaluation of ecosystem services

We estimated consumed biomass of domestic animals (presumably from illegal dumps or road kills), wild ungulates (presumably from hunting remains) and rodents, which are often regarded as major crop pests (Brown et al. 2003). Most of the damage in agriculture caused by rodents in the study area in Serbia is caused by the species from genera *Microtus*, *Apodemus* and *Cricetus* (Jokić 2012). We evaluated ecosystem services based on jackal consumption of rodents from these taxa (termed “crop pest rodents”).

Estimation of biomass removed from environment was based on dietary data (see above), daily food intake rate, and estimated number of jackals. According to previous dietary studies on jackals (Klare et al. 2010; Mukherjee et al. 2004) we used 850 g for mean daily food intake, which corresponds also to information obtained from feeding of captive jackals at five zoos (800-1000 g; M. Heltai, M.T. Cortez García and K. Ovari, pers. comm.) and general estimate of 7-10% of body weight for carnivores (Mukherjee et al. 2004) and a mean body weight of 11.3 ± 1.5 kg for adult jackals in Serbia (N=769; own unpublished data), which corresponds to 777-1111 g.

For evaluation of ecosystem services on the continental scale we reviewed available literature or contacted local jackal experts to obtain current estimates of jackal numbers in European countries and thus roughly estimate number of jackals on the continent (Appendix, Table A2).

To estimate the monetary value of the animal waste removal services that jackals provide, we contacted a Serbian carcass processing plant and inquired about the price for destroying animal waste (18 Serbian dinars = 0.15 €/kg; Proteinka Sombor, pers. comm.). Transport costs were not included. For rodents we also estimated number of animals consumed, based on mean weight of the most frequently recorded rodent, *Microtus arvalis* (22.7 ± 3.4 g, N=83; own unpublished data).

RESULTS

Diet composition of golden jackals

Serbia

Mean biomass of individual stomach contents was 182 g (N=606). At 71.8%, the remains of domestic animals (mostly pigs) was the most frequent food type, followed by rodents at 10.1% and wild ungulates (wild boar [*Sus scrofa*] and roe deer [*Capreolus capreolus*]) at 8.0% of consumed biomass (Table 1). Jackals were also eating small amounts of birds, hares, and plants (grass, grapes, plums etc.). Remains of domestic animals and wild ungulates found in jackal stomachs mostly consisted of skin and digestive system organs, indicating that jackals were mainly scavenging on animal waste discarded by humans after slaughtering or hunting.

Europe

Among diet studies across Europe, jackal diets include 0-71% consumed biomass of domestic animals, 0-80% wild ungulates and 1-80% rodents. Among these three categories, European jackals on average consume 40.5% domestic animals, 19.7% wild ungulates and 19.4% rodents (details are provided in Appendix, Table A3).

Table 1. Stomach content of jackals in Serbia (N=606). %B - proportion of consumed biomass; %O - relative frequency of occurrence.

Food categories	%B	%O
Domestic animals	71.82	49.69
Crop pest rodents	6.45	17.06
Other rodents	3.61	5.4
Wild ungulates	7.99	5.84
European brown hare	2.65	2.74
Birds	2.63	4.16
Plants	2.38	7.96
Medium size carnivores	1.86	1.06
Invertebrates	0.32	1.50
Indigestible	0.24	3.63
Amphibians and reptiles	0.03	0.53
Insectivores	0.03	0.27
Fish	0.01	0.27

Evaluation of ecosystem services provided by jackals

Serbia

On average each golden jackal in Serbia annually consumes 222.8 kg remains of domestic animals, 24.8 kg remains of wild ungulates and 31.2 kg rodents, among which are 20.0 kg of crop pest rodents. Biomass of crop pest rodents corresponds to approximately 881 individuals. Given its estimated population size in Serbia (15,000 jackals; Appendix, Table A2), the jackal population annually removes 3,341 tonnes of domestic animal remains, 372 tonnes of wild ungulate remains, and 13.2 million crop pest rodents. Annual monetary value of animal waste removal provided by jackals (excluding transport costs) sums to 60 million Serbian dinars (0.5 million €) for domestic animal waste and 6.7 million Serbian dinars (55 800 €) for wild ungulates.

Europe

At the European scale of an estimated population of approximately 70,000 jackals (Appendix, Table A2), jackals annually remove 8,842 tonnes of domestic animal remains, 4,301 tonnes of wild ungulate remains, and 3.590 tonnes of crop pest rodents or 158.2 million individuals, with an estimated monetary value of animal carcass removal (without transport costs and assuming the prices given for Serbia) of 2 million €.

DISCUSSION

Our evaluation of ecosystem services provided by golden jackals in human-dominated Euopean landscapes highlights the neglected aspect of mesocarnivore ecology in the modern world. Results indicate that every year jackals remove substantial amounts of discarded animal waste and potential crop pests. Ecosystem services involving waste removal are especially important in developing countries, where, in contrast to more developed countries, organized animal waste disposal is often challenging due to limited funds and infrastructure available (transport vhicles and processing plants). For example, in Serbia only one carcass-processing plant is currently functional and reportedly 14,600 tonnes of animal waste remain unprocessed annually; the remainder is likely discarded in the environment, either on illegal garbage dumps or scattered in rural landscape (Gvozdenac 2015). Our estimates indicate that jackals are an important agent in animal waste removal in this country, and the estimated monetary value of this service suggests considerable economic savings for local communities.

At the continental level, we noticed some regional variation in the regulating services provided by jackals. This is likely connected with differences in human activities, especially availability of animal waste, which appears to be the preferred food of jackals whenever available. Thus in most countries the main role of jackals is in the removal of slaughter remains. The exception is a large portion of Hungary, where jackals appear to have adapted their diet to widespread agriculture and abundant rodents. Accordingly, pest control is their more pronounced role. Further research is needed, however, to evaluate whether rodent removal by jackals actually translates into reduced crop damage.

Benefits associated with consumption of animal waste by carnivores also needs to be put into perspective and contrasted with possible negative consequences of using anthropogenic food sources, such as increased transmission of parasites and other pathogens, conflicts with humans, or excessive predation on other wildlife (Moleón et al. 2014a; Newsome et al. 2015; Oro et al. 2013). At least in the case of jackals in Serbia, it is interesting to note that despite the high level of anthropogenic animal waste in jackal diet, the average parasite load was lower than in other canids in the region that use less anthropogenic food (Ćirović et al. 2014b). This may be due to non-concentrated disposal of animal waste and regular boiling of pig carcasses in Serbia. Although part of the consumed game and domestic animals could have come from predation, data from body parts found in the stomachs, seasonal dynamics of diet patterns, and records of reported livestock depredations suggests that the vast majority of ungulate biomass is consumed through scavenging. Also, in general, jackals in Europe cause substantially fewer livestock losses in comparison to large carnivores (Bošković et al. 2013; Lanszki et al. 2015; Mihelič and Krofel 2012; Spassov 1989). We also reviewed the hunting statistics from Serbia for the period of most rapid jackal population increase (8-fold increase in 2000-2008). There is no indication that this substantial increase in jackal abundance has affected other game animals, as the number of European brown hares shot remained relatively stable, and the numbers for roe deer and wild boar have even increased (Appendix, Figure A1). This is in accordance with previous studies from other countries indicating that jackals do not have important impacts on other game species (Bošković et al. 2013; Lanszki et al. 2015). There are no known attacks on people by jackals.

The potential for food subsidies from anthropogenic animal waste to cause a substantial increase in conflicts with humans or threats to other wildlife seems low in case of golden jackal. This pattern contrasts with examples from large carnivores in which anthropogenic food often brings them into proximity and serious conflict with humans (Dickman et al. 2011; Nelson 2009), although recent study on spotted hyenas (*Crocuta crocuta*) suggest that co-existence is sometimes possible even in such cases (Yirga et al. 2016). Therefore we caution against generalizing about the consequences of human-food subsidies provided to carnivores. In conclusion, it appears that the benefits to local communities from jackal-provided services are higher than the costs associated with this mesocarnivore.

We suggest that, despite being neglected in previous studies, mesocarnivores might be important providers of ecosystem services in general, and especially in human-dominated landscapes. This is supported by frequent observations of mesocarnivores dominating the consumption of animal carcasses (e.g. DeVault et al. 2011; Vicente et al. 2011), as well as by a global review on consumption of animal waste discarded from hunting, which identified mesocarnivores and corvids as the most frequent scavengers worldwide (Mateo-Tomás et al. 2015). Given the enormous amount of food discarded each year in the environment by humans (estimates suggest that 30–40% of all food produced on Earth is wasted; Oro et al. 2013), there is a clear dependence on ecosystem services in removing this huge amount of waste. However, consumption of human-generated food by predators is often perceived negatively and several authors have suggested it should be prevented (Newsome et al. 2015; Oro et al. 2013). This is arguably an important consideration in large carnivore management, as access to anthropogenic food is one of the key factors promoting conflicts with humans, particularly when residential areas and garbage dumps are close together. However, this situation can be very different with mesocarnivores, as exemplified in the case of golden jackals in Europe, wherein conflicts with humans are rare. Further, reduced food availability around settlements because of consumption by mesocarnivores could prevent conflicts with large carnivores.

Mesocarnivore scavengers' frequent consumption of carcasses likely also supports other key ecosystem functions and services, similar to those already noted for vultures. These include acceleration of nutrient recycling, a key global supporting service (Moleón et al. 2014b), as well as limiting disease transmission, which has important implications for human health and associated medicine costs (Markandya et al. 2008). Results presented here suggest that the amount of animal waste removed by mesocarnivores is in a similar quantity as ecosystem services provided by vultures (e.g. entire Spanish vulture population annually removes 5,551–8,326 tonnes of meat; Margalida and Colomer 2012).

Based on the ecosystem service they provide, we call for a re-evaluation of how the use of anthropogenic animal waste by mesocarnivores is perceived. When no serious negative consequences are observed, like in the case of golden jackals in Europe, we suggest that their use of animal waste should not be prevented. Especially in poorer and rural areas with challenges in waste management, there might be reason to promote the services provided by mesocarnivores, or at least to manage mesocarnivore populations in a way that maintains effective densities. We also suggest that there is a need for managers and the general public to recognize this neglected aspect of mesocarnivore ecology. Appreciation of ecosystem services provided by mesocarnivores could improve their often negative public image and thus aid their conservation. Similarly, the role of mesocarnivores in controlling rodent populations and reducing damage to agricultural crops needs further evaluation. If pest-control role is significant, the public, especially farmers, might be even more inclined to appreciate the importance of mesocarnivores. As a comparable example, bats have come to be appreciated for their role in the control of agricultural pests (Kunz et al. 2011).

Since mesocarnivores are regularly subjected to intensive lethal control campaigns, we also call for studies focusing on effects of such management measures on ecosystem services provided by mesocarnivores. These studies would provide valuable input for improving the management of natural resources and using the full potential of services provided by ecosystems, especially in human-dominated landscapes.

Acknowlegments:

DĆ was founded by the Ministry of Science and Technological Development of the Republic of Serbia (TR 31009) and MK was funded by the Slovenian Research Agency (grant no. P4-0059). We wish to express our gratitude to all collaborators in the field who helped in collecting the material for this study. We are also grateful to Lucy Zipf, Amanda Gallinat, and two anonymous reviewers for their useful advices and editing of the English.

References

Berger, K.M., 2006. Carnivore-Livestock Conflicts: Effects of Subsidized Predator Control and Economic Correlates on the Sheep Industry. Conservation Biology 20, 751-761.

Bošković, I., Šperanda, M., Florijančić, T., Šprem, N., Ozimec, S., Degmečić, D., Jelkić, D., 2013. Dietary habits of the golden jackal (*Canis aureus* L.) in the Eastern Croatia. Agriculturae Conspectus Scientificus 78, 245–248.

Brashares, J.S., Prugh, L.R., Stoner, C.J., Epps, C.W., 2010. Ecological and conservation implications of mesopredator release, In Trophic Cascades. eds Terborgh J., J.A. Estes, pp. 221-240. Island Press, Washington DC.

Brown, P.R., Singelton, G.R., Colin, R.T., Mock, I., 2003. Increasing sowing depth to reduce mouse damage to winter crops. Crops Protection 22, 653-660.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Naeem, S., Limburg, K., Paruelo, J., O'Neill, R.V., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Ćirović, D., Penezić, A., Milenković, M., Paunović, M., 2014a. Winter diet composition of the golden jackal (*Canis aureus* L., 1758) in Serbia. Mammalian Biology - Zeitschrift für Säugetierkunde 79, 132-137.

Ćirović, D., Penezić, A., Pavlović, I., Kulišić, Z., Ćosić, N., Burazerović, J., Maletić, V., 2014b. First records of Dirofilaria repens in wild canids from the region of Central Balkan. Acta Veterinaria Hungarica 62, 481-488.

DeVault, T.L., Olson, Z.H., Beasley, J.C., Rhodes, O.E., 2011. Mesopredators dominate competition for carrion in an agricultural landscape. Basic and Applied Ecology 12, 268-274.

Dickman, A.J., Macdonald, E.A., Macdonald, D.W., 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. Proceedings of the National Academy of Sciences 108, 13937-13944.

Duffield, J.W., Neher, C.J., Patterson, D.A., 2008. Wolf recovery in Yellowstone: Park visitor attitudes, expenditures, and economic impacts. Yellowstone Science 16, 20-25.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333, 301-306.

Gvozdenac, S., 2015. Animalni otpad iz cele Srbije obrađuje samo Proteinka. Radio-televizija Vojvodine 4th February 2015. http://www.rtv.rs/sr_lat/vojvodina/sombor/animalniotpadizcelesrbijeobradjujesamoproteinka_564816.html. Accessed 17 July 2015.

Jokić, G., 2012. Distribution, harmfulness and the possibility of rodents control in the field using different formulations of natural and synthetical rodenticides (PhD thesis. Belgrade, Serbia: University of Belgrade, Faculty of Agriculture)

Kellert, S.R., 1985. Public perceptions of predators, particularly the wolf and coyote. Biological Conservation 31, 167-189.

Klare, U., Kamler, J.F., Stenkewitz, U., Macdonald, D.W., 2010. Diet, Prey Selection, and Predation Impact of Black-Backed Jackals in South Africa. Journal of Wildlife Management 74, 1030-1042.

Krofel, M., Jerina, K., Kljun, F., Kos, I., Potočnik, H., Ražen, N., Zor, P., Žagar, A., 2014. Comparing patterns of human harvest and predation by Eurasian lynx *Lynx lynx* on European roe deer *Capreolus capreolus* in a temperate forest. European Journal of Wildlife Research 60, 11-21.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223, 1-38.

Lanszki, J., Heltai, M., Szabo, L., 2006. Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannonian ecoregion (Hungary). Canadian Journal of Zoology-Revue Canadienne De Zoologie 84, 1647-1656.

Lanszki, J., Kurys, A., Helatai, M., Csanyi, S., Ács, K., 2015. Diet composition of the golden jackal in an area of intensive big game management. Annales Zoologici Fennici 52.

Margalida, A., Colomer, M.À., 2012. Modelling the effects of sanitary policies on European vulture conservation. Sci. Rep. 2.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. Ecological Economics 67, 194-204.

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions, OnlineEarly.

Mihelič, M., Krofel, M., 2012. New records of the golden jackal (*Canis aureus* L.) in the upper Soča valley, Slovenia. Natura Sloveniae 14, 51-63.

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: Synthesis. Island Press, Washington, DC.

Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., Donázar, J.A., 2014b. Humans and Scavengers: The Evolution of Interactions and Ecosystem Services. Bioscience.

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A., Owen-Smith, N., 2014a. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89, 1042-1054.

Mukherjee, S., Goyal, S.P., Johnsingh, A.J.T., Pitman, M.R.P.L., 2004. The importance of rodents in the diet of jungle cat (*Felis chaus*), caracal (*Caracal caracal*) and golden jackal (*Canis aureus*) in Sariska Tiger Reserve, Rajasthan, India. Journal of Zoology 262, 405-411.

Nelson, F., 2009. Developing Payments for Ecosystem Services Approaches to Carnivore Conservation. Human Dimensions of Wildlife 14, 381-392.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., Dickman, C.R., 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24, 1-11.

Ogada, D.L., Keesing, F., Virani, M.Z., 2012. Dropping dead: causes and consequences of vulture population declines worldwide. Annals of the New York Academy of Sciences 1249, 57-71.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16, 1501-1514.

Popović, Z., 1998. Hunting and production characteristics of Roe deer (*Capreolus capreolus*). (MSc thesis. Belgrade, Serbia: University of Belgrade, Faculty of Agriculture)

Posner, S.M., McKenzie, E., Ricketts, T.H., 2016. Policy impacts of ecosystem services knowledge. Proceedings of the National Academy of Sciences 113, 1760-1765.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The Rise of the Mesopredator. Bioscience 59, 779-791.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343.

Roemer, G.W., Gompper, M.E., Van Valkenburgh, B., 2009. The Ecological Role of the Mammalian Mesocarnivore. Bioscience 59, 165-173.

Slamnig, S., 2015. Lešinama hrane pse. Kurir 26. February 2012. http://www.kurir.rs/lesinama-hrane-pse-clanak-142304. Accessed 17 July 2015.

Spassov, N., 1989. The position of Jackals in the Canis genus and life-history of the Golden Jackal (*Canis aureus* L.) in Bulgaria and on the Balkans. Historia Naturalis Bulgarica 1, 44–56.

Šálek, M., Červinka, J., Banea, O., Krofel, M., Ćirović, D., Selanec, I., Penezić, A., Grill, S., Riegert, J., 2013. Population densities and habitat use of the golden jackal (*Canis aureus*) in farmlands across the Balkan Peninsula. European Journal of Wildlife Research, 1-8.

Trouwborst, A., Krofel, M., Linnell, J.C., 2015. Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (*Canis aureus*) in Europe. Biodiversity and Conservation, 1-18.

Vicente, J., Carrasco, R., Acevedo, P., Montoro, V., Gortazar, C., 2011. Big Game Waste Production: Sanitary and Ecological Implications. Integrated Waste Management – Volume II (ed. by S. Kumar), pp. 97–128. InTech, Rijeka, Croatia.

Yirga, G., Leirs, H., De Iongh, H.H., Asmelash, T., Gebrehiwot, K., Deckers, J., Bauer, H., 2016. Spotted hyena (*Crocuta crocuta*) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildlife Research 42, 563-569.