



Short communication

Golden jackal as a new kleptoparasite for Eurasian lynx in Europe

Miha Krofel^{a,*}, Lan Hočevar^{a,1}, Urša Fležar^a, Ira Topličanec^b, Teresa Oliveira^a^a Department of Forestry, Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia^b Veterinary Faculty, University of Zagreb, Heinzelova ulica 55, 10000 Zagreb, Croatia

ARTICLE INFO

Keywords:

*Canis aureus**Lynx lynx*

Kleptoparasitism

Interspecific interactions

Scavenging

ABSTRACT

The arrival of a new carnivore can have important effects on local communities. While several effects of introduced alien species have been well documented, few studies have reported the ecological consequences of an expanding native species. Golden jackals (*Canis aureus*) are rapidly expanding their distribution in Europe, far beyond their historic range. While this raises many concerns about their potential impact on native wildlife, actual consequences are rarely recorded. Besides being a predator, the jackal is also an efficient scavenger and could function as a kleptoparasite for other predators living in areas colonized by jackals. Large felids are among the predators most vulnerable to kleptoparasitism and Eurasian lynx (*Lynx lynx*) are already known to be negatively affected by several scavengers. Here we report on the first confirmed cases of jackals scavenging on lynx kills in the Dinaric Mountains, Slovenia. We used camera traps to monitor scavengers at 65 lynx kills and recorded two cases of groups of jackals feeding on roe deer killed by lynx. To determine the potential for jackal kleptoparasitism on lynx at the continental level, we also calculated trends in the overlap in distribution ranges of both species in Europe. To date, jackals have colonized 13% of lynx range, including parts of two highly threatened populations. Finally, we highlight the potential impact of sympatric grey wolves (*Canis lupus*) to modulate this newly described jackal-lynx kleptoparasitic interaction.

1. Introduction

The return or arrival of a new carnivore can have important effects on local communities and, in some cases, trigger trophic cascades with substantial changes in the ecosystems (Ripple et al., 2014; Newsome et al., 2017). While impacts of introduced alien species have already been well documented (e.g. see Davis, 2009 for a review), few studies have reported the ecological consequences of naturally-expanding native species beyond their historic ranges (Mumma et al., 2017). Golden jackals (*Canis aureus*; hereafter jackals) are rapidly expanding across Europe (Trouwborst et al., 2015; Krofel et al., 2017). They are highly adaptable species with an opportunistic feeding behavior and diverse diet (Lanszki et al., 2015; Ćirović et al., 2016). Although many aspects of jackal ecology remain poorly studied (Krofel et al., 2022), their expansion is raising many concerns among researchers and managers about the possible negative impacts towards local wildlife, including the reduction of ungulate populations and threatened birds, transmission of diseases and parasites, as well as hybridization with other canids (Szabó et al., 2009; Rutkowski et al., 2015; Trouwborst et al., 2015; Ćirović et al., 2016). However, despite documented predation of several taxa and certain overlap in ecological niches with other mesocarnivores (e.g. Lanszki et al., 2015; Tsunoda et al., 2017, 2020), most studies reported so far did not detect negative effects on the

* Corresponding author.

E-mail addresses: miha.krofel@bf.uni-lj.si, miha.krofel@gmail.com (M. Krofel).¹ Both authors contributed equally to this work.<https://doi.org/10.1016/j.gecco.2022.e02116>

Received 25 January 2022; Received in revised form 18 March 2022; Accepted 4 April 2022

Available online 6 April 2022

2351-9894/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

local wildlife populations (e.g. [Lanszki et al., 2015](#); [Ćirović et al., 2016](#)), with exception of a study on red fox (*Vulpes vulpes*) in Romania, where presence of jackals was correlated with lower body weights of juvenile foxes ([Farkas et al., 2017](#)).

One of the potential interactions between jackals and local wildlife that remains unstudied is kleptoparasitism, also known as food stealing ([Iyengar, 2008](#)). This includes scavenging on prey killed by apex predators, which can cause considerable food loss for the predators ([Allen et al., 2015](#); [Krofel and Jerina, 2016](#)), indirectly increase kill rates ([Krofel et al., 2012](#)), reduce reproductive success ([Balme et al., 2017](#)), or even pose a threat for the predator population ([Gorman et al., 1998](#)). It has been also suggested that, in the long term, kleptoparasitism may trigger changes in prey choice, social system, and evolution of predators ([Iyengar, 2008](#); [Krofel et al., 2012](#)).

Due to their long feeding times and lower resource holding potential compared to gregarious competitors, large solitary felids are among the predators most vulnerable to kleptoparasitism and frequently reported to lose considerable amount of food to scavengers (see [Krofel et al., 2012](#) for review). The Eurasian lynx (*Lynx lynx*; hereafter lynx) is the largest felid in Europe with several populations being critically endangered ([Kaczensky et al., 2013](#)). Wild ungulates are the most frequent prey of lynx, which typically need several days to consume their kills ([Breitenmoser, Breitenmoser, Würsten, 2008](#)). This often results in various kleptoparasites scavenging on their kills, ranging from small carnivores and birds to large dominant scavengers, with highest losses so far attributed to brown bear (*Ursus arctos*) ([Krofel and Jerina, 2016](#)) and wild boar (*Sus scrofa*) ([Jędrzejewska and Jędrzejewski, 1998](#); [D'ula & Krofel, 2020](#)). Lynx can respond to these losses by increasing their kill rates, but their capacity for such compensation can be limited ([Krofel et al., 2012](#)). Therefore, additional kleptoparasitism from novel scavengers could have a negative impact on this apex predator and potentially influence its role in the ecosystem.

Jackals are known to be very efficient scavengers ([Lanszki et al., 2015](#)) and can attain high local densities (up to 5 territorial groups/10 km²; [Giannatos et al., 2005](#)). For example, in Serbia, they have been estimated to annually consume > 3700 tons of domestic and wild ungulate carcasses ([Ćirović et al., 2016](#)). Despite this potential of jackal as a kleptoparasite, to our knowledge so far no study has documented jackal scavenging on a predator kill in Europe, although they co-occur with several species of large predators (e. g. [Guimaraes et al., 2021](#)). Thus, it remains unclear whether jackals avoid such food sources due to the potential danger of being killed by a larger predator or the lack of such cases is due to limited research attention given to this interaction. So far there has also been no attempt to evaluate the potential for kleptoparasitic interactions between jackals and apex predators. To fill this knowledge gap, we report on the first cases of jackals scavenging on prey remains of lynx recorded during the long-term video surveillance of lynx kill sites in Slovenia. Additionally, we evaluated the potential for kleptoparasitic interactions between these two species by estimating how overlap between the species range changed through time. We also discuss the implications of jackal expansion for the threatened lynx populations in Europe and how the presence of grey wolves (*Canis lupus*) could modulate this interaction.

2. Methods

The surveillance of lynx kill sites was conducted in the Northern Dinaric Mountain Range in Slovenia (4525'–4547'N, 1415'–1450'E) dominated by mixed temperate forests. The two observations further detailed here were recorded in the north-western part of the Dinaric Mountains at the foothills of Javorniki Mountains and on the edge of Menišija plateau. Lynx in this region belong to the Dinaric population, which is currently regarded as one of the most endangered lynx populations in Europe ([Krofel and Jerina, 2016](#)). Dinaric lynx mainly hunt wild ungulates, which represent 88% of biomass consumed by lynx, with roe deer (*Capreolus capreolus*) being the main prey species ([Krofel et al., 2011](#)). Besides lynx, brown bears and grey wolves are present in the area, as well as several species of smaller carnivores ([Fležar et al., 2019](#)).

To locate lynx kill sites and monitor prey consumption, we used a combination of GPS telemetry, field-checking GPS location clusters and remote video surveillance of the kill sites (for details on these methodologies see [Krofel et al., 2013, 2019](#)). Lynx equipped with GPS telemetry collars (Vectronic Aerospace GmbH, Germany) included animals from the remnant Dinaric population, as well as several lynx translocated from the Carpathian Mountains for genetic rescue of the Dinaric population ([Fležar et al., 2022](#)). The kill sites were monitored with camera traps (Reconyx XR6 Ultrafire and Moultrie M40-i) with black-IR reflector, programmed to trigger when movement was detected and to record 30-seconds videos in continuous mode. In most cases two camera traps were set per kill site.

To assess the potential for jackal-lynx interactions in Europe and how this changed in time, we collected distribution data for jackal and lynx from the literature and separated the data into three periods: (1) 1950–1970, representing the period when lynx populations were around the historic minimum and when jackal expansion was in the early phase, (2) 2000–2011, when several lynx populations recovered or were reintroduced and when jackal populations were rapidly expanding in south-eastern Europe, and (3) current distribution (2012–2018), representing the period when several of the lynx populations continued to recover, while others declined or

Table 1

Eurasian lynx (*Lynx lynx*) and golden jackal (*Canis aureus*) distribution range and their overlap in proportion to lynx distribution range in Central and Southern Europe during three time periods. The range reported for the second and third period refers to different estimates of lynx distribution (lower number for permanent occurrence only and higher number for permanent and sporadic occurrences). See [Fig. 2](#) for data sources and countries included.

Period	Eurasian lynx (km ²)	Golden jackal (km ²)	Overlap (km ²)	Overlap (%)
1950–1970	100,633	117,636	18	0.02
2000–2011	175,244–276,608	326,427	3548–9995	1.28–3.61
2012–2018	280,559–291,658	499,458	37,631–37,831	12.90–12.97

stabilized, and jackal populations approached saturation in some parts of south-eastern Europe and continued to expand elsewhere in Europe. For the jackal distribution in the first and second period we used data compiled by Krofel et al. (2017) and, for the third period, by Ranc et al. (2018). For the lynx distribution during the first two periods we used data compiled by Chapron et al. (2014) and, for the third period, data from Kaczensky et al. (2021). According to available data, we separated between the permanent and sporadic occurrence of lynx for the second and the third period. We used QGIS v3.4.3 (QGIS Development Team, 2018) to estimate the total distribution range of both species in continental Europe (i.e. without British islands, Fennoscandia and the Baltics) for each of the three periods mentioned above, as well as % of lynx range that overlap with the jackal range (Table 1).

3. Results

3.1. Video surveillance of jackals scavenging on lynx kills

We deployed camera traps on 65 lynx kill sites in 2006–2021 (on average 4 kill sites per year; range: 0–26), and detected presence of jackal groups at two of them (3% of all kills surveilled). Both cases of prey remains scavenged by jackals were located at the periphery of the lynx home ranges and occurred during the last two years of the study (i.e. 2020 and 2021).

On 24.1.2020 we found a male adult roe deer carcass killed by lynx in a hornbeam-ash tree forest stand at the foothills of Javorniki Mountains. At the time of the discovery (3 days after the predation event), 70% of the roe deer was already consumed. Fifty meters away we found another completely consumed roe deer carcass. We set camera trap on the fresh carcass and surveilled it for 3.5 days, until camera failure. While lynx was not detected to return to feed on the prey, four scavenger species were recorded: two common buzzards (*Buteo buteo*), two ravens (*Corvus corax*), a red fox (*Vulpes vulpes*), and a pair of jackals. Avian scavengers were feeding on the carcass during the daytime, while both canid species visited the carcass during the night. The two jackals were recorded at the carcass for 5 min, during which they were alternatively consuming prey remains and looking around (Fig. 1). Unfortunately, the camera trap failed while jackals were still feeding on the carcass, therefore the full length of the jackal use of the carcass, as well as potential return of the lynx or other scavengers, remains unknown.

On 28.10.2021, we found a 3-day old adult female roe deer carcass killed by lynx, near the edge of a high karstic plateau Menišija at the spruce-forest edge. At the time of the field visit, around third of the carcass was already consumed. The camera traps surveilled the kill for 9 days and recorded four scavenger species: red fox, badger (*Meles meles*), stone marten (*Martes foina*), and two jackals. Jackals visited the carcass on two consecutive nights. First, only one animal was recorded while two individuals were recorded on the second



Fig. 1. Still photographs from videos showing golden jackals scavenging on prey remains of Eurasian lynx at the foothills of Javorniki Mountains (above) and on the edge of Menišija plateau (below) in Dinaric Mountains, Slovenia.

visit (Fig. 1).

3.2. Overlap in lynx and jackal distribution range in Europe

Historically, jackal distribution was mainly limited to islands and coastal regions of southeastern Europe (Krofel et al., 2017) and therefore contact with lynx was likely minimal or non-existent. The situation remained similar until the mid-20th century, when jackal expansion mostly took place in areas without lynx (species overlap <0.1%; Fig. 2a, Table 1). In the next decades and especially after 2011, the overlap increased, as jackal distribution rapidly expanded and several lynx populations were reintroduced or recovered (Fig. 2b, Table 1). The current distribution data suggests that approximately 13% of lynx distribution range in Central and Southern Europe is already colonized by jackals, with vast majority linked to the Dinaric, Balkan and Carpathian lynx populations (Fig. 2c, Table 1).

4. Discussion

We explored the so-far unstudied role of jackal as a kleptoparasite in Europe and recorded the first cases of scavenging on prey remains of lynx. Although it could not be established whether the lynx abandoned these kills before the arrival of jackals or if abandonment could be connected with jackal presence, our observations confirm the potential impact that expansion of this meso-carnivore could have on apex carnivores through kleptoparasitic interactions. Such changes in carnivore assemblages are mostly associated with invasive alien species (e.g. domestic cats; Davis, 2009), since ranges of native carnivores rarely expand at the scale observed in the case of jackal in Europe. This represents a rare opportunity to study the impacts that changes in the distribution of native carnivores can have on local fauna.

Although we recorded jackals scavenging in relatively small proportion of lynx kills, it is noteworthy that both cases occurred in the last two years of the 16-year surveillance of lynx kill sites, while no such records were noted in the past. This concurs with the data obtained during the lynx camera-trapping surveys in Slovenia (Fležar et al., 2022), which showed increasing number of jackal records inside the lynx range in the last years (i.e. since 2019; Fležar et al., unpublished data).

Review of historic distribution ranges of jackal and lynx suggests that in Europe these two species were most likely not interacting in the past. However, in the last two decades and especially since 2011, trends in distribution patterns showed that the overlap between them is increasing rapidly, mainly due to extensive expansion of jackal populations, but also due to recovery of lynx in some parts of Europe (Fig. 2). Currently, most of the overlap is observed in three lynx populations, among which two (Balkan and Dinaric) are considered as highly threatened (Melovski et al., 2015; Krofel and Jerina, 2016).

Although little is known about the potential consequences of jackal kleptoparasitism on lynx and how successfully lynx could defend prey remains from jackals, previous research has shown vulnerability of this felid to several scavengers (e.g. lynx lost 15% and 25% of all edible biomass to brown bears and wild boar, respectively; Krofel et al., 2012; Duřa and Krofel, 2020). Besides, jackals are known to be able to attain high densities (up to 5 territorial groups/10 km²) and form large groups (up to 20 individuals/group) in suitable conditions (Macdonald, 1979; Giannatos et al., 2005). Even if lynx can successfully defend their kills in direct confrontations with jackals, this is unlikely to completely prevent kleptoparasitism, as indicated by interactions with other smaller scavengers. For example, competitively-inferior red foxes regularly scavenge on lynx prey remains, despite the risk of being killed by the lynx (Krofel et al., 2019). What remains unknown in this context is the extent to which jackals could suppress foxes and therefore their impact on lynx, which might to some degree offset the losses from kleptoparasitism by jackals. Important to consider is also the time needed for

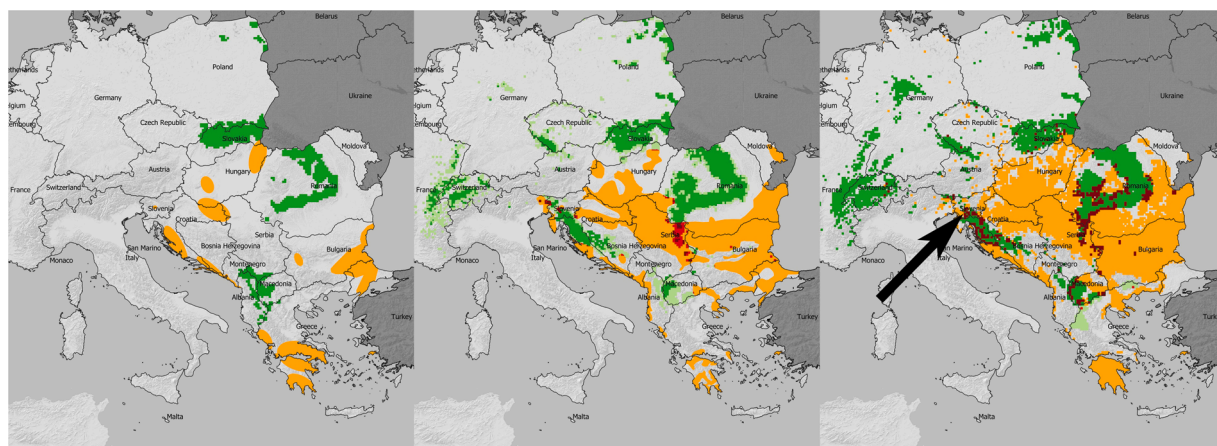


Fig. 2. : Distribution of Eurasian lynx (sporadic: light green; permanent: dark green) and golden jackal (yellow) and their overlap (jackal-sporadic lynx: light red; jackal-permanent lynx: dark red) in Central and Southern Europe (countries not included are marked with grey) during the three time periods: (a) 1950–1970, (b) 2000–2011, and (c) 2012–2018. Arrow on (c) indicates study area in Slovenia.

Distribution data sources: Chapron et al. (2014), Krofel et al. (2017), Ranc et al. (2018) and Kaczensky et al. (2021).

jackals to find lynx kills, as the losses are generally much higher when a kleptoparasite finds prey remains in the early phases of consumption (Krofel and Kos, 2010). On the other hand, if the prey remains are found after most of the meat has already been eaten, impact of scavenging might be limited, because jackals will be mostly eating parts rarely used by lynx (e.g. head, skin and digestive tract).

These uncertainties call for further research on this novel interaction among lynx and jackals, especially since projections indicate that vast areas of Europe could become colonized by jackals in the near future (Ranc et al., 2018) and bring this opportunistic scavenger into contact with other lynx populations across Europe. The risk of jackal kleptoparasitism could, however, be reduced through interaction with another European apex carnivore, i.e. the grey wolf. Persistence and abundance of jackals can be substantially suppressed by top-down control from grey wolf (Krofel et al., 2017; Newsome et al., 2017; Ranc et al., 2018) and the current distribution of this apex predator overlaps with most of lynx populations in Europe (Kaczensky et al., 2021). Although sympatric wolves and lynx often compete for the same prey, previous studies did not show negative effects of wolves on lynx or interspecific avoidance (Schmidt et al., 2009; Wikenros et al., 2010) and wolves rarely scavenge on lynx kills (wolves were recorded at only 1% of lynx kills in our study area; Krofel et al., 2012). Therefore, it could be possible that the protection from jackal kleptoparasitism provided by wolves to lynx might eventually outweigh the costs of wolf-lynx competition.

However, with jackal numbers increasing across Europe, including their colonization of parts of wolf distribution range, especially at its periphery, we can expect increasing contact with lynx populations. This appears to concur with data presented here, as both detected cases of jackal scavenging on lynx kills occurred on the periphery of lynx home ranges, which coincides with the periphery of wolf territories in this region (Krofel et al., 2017; Ražen et al., 2020). On the other hand, we did not detect jackals on any of the lynx kills located within the core areas of wolf territories.

The new addition to the carnivore guild of Dinaric forests and other ecosystems across Europe caused by jackal expansion opens numerous questions and conservation concerns that are typically limited to invasive alien species. Our study provides one of the first empirical evidence of the impact that jackal colonization can cause, although its importance in the future is difficult to predict. Therefore, we recommend further research on the impact of jackals on lynx and other large predators, as well as on several scavengers that compete with jackals for animal carcasses. Data presented here indicate several potential direct and indirect interactions connected with arrival of jackals. These offer opportunities to study complex interspecific relationships within carnivore guilds and provide researches, as well as conservationists, with crucial insights into dynamic systems perturbed by human-caused or natural changes in animal assemblages.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank Peter Krma for help with the fieldwork and two anonymous reviewers for useful suggestions. This study was financed by the European Commission (LIFE16 NAT/SL/000634). M.K. was supported by the Slovenian Research Agency (ARRS, grants no. N1–0163 and P4–0059) and T.O. was supported by Portuguese Foundation for Science and Technology (FCT, grant no. SFRH/BD/144110/2019).

References

- Allen, M.L., Elbroch, L.M., Wilmers, C.C., Wittmer, H.U., 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *Am. Nat.* 185, 822–833. <https://doi.org/10.1086/681004>.
- Balme, G.A., Miller, J.R.B., Pitman, R.T., Hunter, L.T.B., 2017. Caching reduces kleptoparasitism in a solitary, large felid. *J. Anim. Ecol.* 86, 634–644. <https://doi.org/10.1111/1365-2656.12654>.
- Breitenmoser, U. & Breitenmoser-Würsten, C., 2008. *Der Luchs – ein Grossraubtier in der Kulturlandschaft*. SalmVerlag, Bern, Switzerland.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., et al., 2014. Recovery of large carnivores in Europe's modern humandominated landscapes. *Science* 346, 1517. <https://doi.org/10.1126/science.1257553>.
- Čirović, D., Penezić, A., Krofel, M., 2016. Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biol. Conserv.* 199, 51–55. <https://doi.org/10.1016/j.biocon.2016.04.027>.
- Davis, M.A., 2009. *Invasion Biology*. Oxford University Press, Oxford.
- Duřa, M., Krofel, M., 2020. A cat in paradise: hunting and feeding behaviour of Eurasian lynx among abundant naive prey. *Mamm. Biol.* 100, 685–690. <https://doi.org/10.1007/s42991-020-00070-6>.
- Farkas, A., Bidló, A., Bolodár-Varga, B., Jánoska, F., 2017. Accumulation of Metals in Liver Tissues of Sympatric Golden Jackal (*Canis aureus*) and Red Fox (*Vulpes vulpes*) in the Southern Part of Romania. *Bull. Environ. Contam. Toxicol.* 98, 513–520. <https://doi.org/10.1007/s00128-017-2035-4>.
- Fležar, U., Pičulin, A., Bartol, M., Černe, R., Stergar, M., Krofel, M., 2019. Eurasian lynx (*Lynx lynx*) monitoring with camera traps in Slovenia in 2018–2019. *Ljubljana*.
- Fležar, U., Hočevar, L., Sindičič, M., Gomerčić, T., Konec, M., Slijepčević, V., Bartol, M., Hočevar, Š., Črtalič, J., Jelenčić, M., Kljun, F., Molinari-Jobin, A., Pičulin, A., Gotar, T., Javornik, J., Portas Perez, R., Potočnik, H., Rot, A., Skrbineš, T., Topličanec, I., Blasković, S., Molinari, P., Černe, R., Krofel, M., 2022. Surveillance of the reinforcement process of the Dinaric - SE Alpine lynx population in the lynx-monitoring year 2020–2021. Technical report. University of Ljubljana, Ljubljana, 59 p.
- Giannatos, G., Marinos, Y., Maragou, P., Catsorakis, G., 2005. The golden jackal (*Canis aureus* L.) in Greece. *Belg. J. Zool.* 135, 145–149.
- Gorman, M.L., Mills, M.G., Raath, J.P., Speakman, J.R., 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* 391, 479–481. <https://doi.org/10.1038/35131>.
- Guimaraes, N., Bučko, J., Slamka, M., 2021. At the table with the big three carnivores - a sympatric occurrence of the golden jackal with bear, wolf and lynx captured on a camera trap in Slovakia. *Eur. J. Ecol.* 7, 1.

- Iyengar, E.V., 2008. Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biol. J. Linn. Soc.* 93, 745–762. <https://doi.org/10.1111/j.1095-8312.2008.00954.x>.
- Jędrzejewska, B., Jędrzejewski, W., 1998. Predation in Vertebrate Communities. The Białowieża Primeval Forest as a Case Study. Springer Verlag, Berlin, Germany.
- Kaczensky, P., Chapron, G., von Arx, M., Huber, D., Andrén, H., Linnell, J., 2013. Status, Management and Distribution of Large Carnivores – Bear, Lynx, Wolf and Wolverine in Europe. Part 1. IUCN/SSC Large Carniv. Initiat. Eur.
- Kaczensky, P., Linnell, J.D.C., Huber, D., Von Arx, M., Andren, H., Breitenmoser, U., Boitani, L., 2021. Distribution of large carnivores in Europe 2012 - 2016: Distribution maps for Brown bear, Eurasian lynx, Grey wolf, and Wolverine, Dryad, Dataset, <https://doi.org/10.5061/dryad.pc866t1p3>.
- Krofel, M., Kos, I., 2010. Modeling potential effects of brown bear kleptoparasitism on the predation rate of Eurasian lynx. *Acta Biol. Slov.* 53, 47–54.
- Krofel, M., Huber, D., Kos, I., 2011. Diet of Eurasian lynx *Lynx lynx* in the northern Dinaric Mountains (Slovenia and Croatia): importance of edible dormouse *Glis glis* as alternative prey. *Acta Theriol.* 56, 315–322.
- Krofel, M., Giannatos, G., Čirović, D., Stoyanov, S., Newsome, T.M., 2017. Golden jackal expansion in Europe: A case of mesopredator release triggered by continent-wide wolf persecution? *Hystrix* 28, 9–15. <https://doi.org/10.4404/hystrix-28.1-11819>.
- Krofel, M., Jerina, K., 2016. Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. *Biol. Conserv.* 197, 40–46. <https://doi.org/10.1016/j.biocon.2016.02.019>.
- Krofel, M., Kos, I., Jerina, K., 2012. The noble cats and the big bad scavengers: Effects of dominant scavengers on solitary predators. *Behav. Ecol. Sociobiol.* 66, 1297–1304. <https://doi.org/10.1007/s00265-012-1384-6>.
- Krofel, M., Skrbinišek, T., Kos, I., 2013. Use of GPS location clusters analysis to study predation, feeding, and maternal behavior of the Eurasian lynx. *Ecol. Res.* 28, 103–116.
- Krofel, M., Skrbinišek, T., Mohorović, M., 2019. Using video surveillance to monitor feeding behaviour and kleptoparasitism at Eurasian lynx kill sites. *Folia Zool.* 68, 274.
- Krofel, M., Hatlauf, J., Bogdanowicz, W., Campbell, L.A.D., Godinho, R., Jhala, Y.V., et al., 2022. Towards resolving taxonomic uncertainties in wolf, dog and jackal lineages of Africa, Eurasia and Australasia. *J. Zool.* 316, 155–168. <https://doi.org/10.1111/jzo.12946>.
- Lanszki, J., Kurys, A., Heltai, M., Csányi, S., Ács, K., 2015. Diet Composition of the Golden Jackal in an Area of Intensive Big Game Management. *Ann. Zool. Fenn.* 52, 243–255. <https://doi.org/10.5735/086.052.0403>.
- Macdonald, D.W., 1979. The flexible social system of the golden jackal, *Canis aureus*. *Behav. Ecol. Sociobiol.* 5, 17–38.
- Melovski D., Breitenmoser U., Von Arx M., Breitenmoser-Würsten C., Lanz, T., 2015, *Lynx lynx* ssp. *balkanicus*. The IUCN Red List of Threatened Species.
- Mumma, M.A., Holbrook, J.D., Rayl, N.D., Zieminski, C.J., Fuller, T.K., Organ, J.F., Mahoney, S.P., Waits, L.P., 2017. Examining spatial patterns of selection and use for an altered predator guild. *Oecologia* 185, 725–735.
- Newsome, T.M., Greenville, A.C., Čirović, D., Dickman, C.R., Johnson, C.N., Krofel, M., Letnic, M., Ripple, W.J., Ritchie, E.G., Stoyanov, S., Wirsing, A.J., 2017. Top predators constrain mesopredator distributions. *Nat. Commun.* 8, 1–7. <https://doi.org/10.1038/ncomms15469>.
- QGIS Development Team, 2018, QGIS Geographic Information System. Open Source Geospatial Foundation. (<http://qgis.org>).
- Ranc, N., Álvares, F., Banea, O., Berce, T., Cagnacci, F., Cervinka, J., et al., 2018, The golden jackal in Europe: where to go next? In: Proceedings of the 2nd international jackal symposium, Marathon Bay, Attiki, Greece, *Hell Zool Arch*, p 9.
- Ražen, N., Kuralt, Ž., Fležar, U., Bartol, M., Černe, R., Kos, I., Krofel, M., Luštrik, R., Majić Skrbinišek, A., Potočnik, H., 2020. Citizen science contribution to national wolf population monitoring: what have we learned? *Eur. J. Wildl. Res.* 66, 46.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343 (6167), 1241484.
- Rutkowski, R., Krofel, M., Giannatos, G., Čirović, D., Mannil, P., Volokh, A.M., et al., 2015. A European concern? Genetic structure and expansion of golden jackals (*Canis aureus*) in Europe and the caucasus. *PLoS One* 10, e0141236. <https://doi.org/10.1371/journal.pone.0141236>.
- Schmidt, K., Jędrzejewski, W., Okarma, H., Kowalczyk, R., 2009. Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. *Ecol. Res.* 24, 207–214.
- Szabó, L., Heltai, M., Szucs, E., Lanszki, J., Lehoczki, R., 2009. Expansion range of the golden jackal in Hungary between 1997 and 2006. *Mammalia* 73, 307–311. <https://doi.org/10.1515/MAMM.2009.048>.
- Trouwborst, A., Krofel, 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. <https://doi.org/10.1007/s10531-015-0948-y>.
- Tsunoda, H., Raichev, E.G., Newman, C., Masuda, R., Georgiev, D.M., Kaneko, Y., 2017. Food niche segregation between sympatric golden jackals and red foxes in central Bulgaria. *J. Zool.* 303, 64–71.
- Tsunoda, H., Newman, C., Peeva, S., Raichev, E., Buesching, C.D., Kaneko, Y., 2020. Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina Mountains, Bulgaria. *Zoology* 141, 125801.
- Wikenros, C., Liberg, O., Sand, H., Andren, H., 2010. Competition between recolonizing wolves and resident lynx in Sweden. *Can. J. Zool.* 88, 271–279.