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Research Article

Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution?

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Abstract

Top-down suppression by apex predators can limit the abundance and spatial distribution of mesopredators. However, this phenomenon has not been studied over long time periods in human-dominated landscapes, where the strength of this process might be limited. Here, we used a multiscale approach to analyse interactions between two canids in the human-dominated landscapes of Europe. We tested the hypothesis that the range expansion of golden jackals (*Canis aureus*) was triggered by intensive persecution and resulting decline of the apex predator, the grey wolf (*Canis lupus*). To do so, we (1) reviewed literature to reconstruct the historic changes in the distribution and abundance of the two canid species on the continental scale, (2) analysed hunting data patterns for both species in Bulgaria and Serbia, and (3) surveyed jackal persistence in eight study areas that became re-colonized by territorial wolves. The observed trends were generally consistent with the predictions of the mesopredator release hypothesis and supported the existence of top-down suppression by wolves on jackals. We observed inverse patterns of relative abundance and distribution for both canid species at various spatial scales. In most (seven out of eight) cases of wolf re-colonization of jackal territories, jackals disappeared or were displaced out or to the periphery of the newly established wolf home-ranges. We suggest that wolf extermination could be the key driver that enabled the expansion of jackals throughout Europe. Our results also indicate that top-down suppression may be weakened where wolves are intensively persecuted by humans or occur at reduced densities in human-dominated landscapes, which has important management implications and warrants further research.

Introduction

Humans exert strong pressures on apex predators by direct persecution, modifying habitats and depleting prey, often leading to changes in interspecific interactions among predators (Ripple et al., 2014). An example is mesopredator release, which occurs when a mid-sized predator expands its distribution or abundance due to the decline of a larger apex predator (Prugh et al., 2009). Numerous studies support top-down suppression of mesopredators by apex predators (for review see Prugh et al., 2009; Ritchie and Johnson, 2009). However, those studies mostly come from areas with low human densities, such as Africa (Brashares et al., 2010), Australia (Letnic et al., 2011) and North America (Newsome and Ripple, 2015). Examples from human-dominated landscapes are lacking or focused on smaller members of the carnivore guild, such as the Iberian lynx (*Lynx pardinus*) and Egyptian mongoose (*Herpestes ichneumon*) (Palomares et al., 1998) or the Eurasian otter (*Lutra lutra*) and American mink (*Mustela vison*) (McDonald et al., 2007).

To help fill this knowledge gap, we studied interactions between a mesopredator, the golden jackal (*Canis aureus*), and a larger apex predator, the grey wolf (*Canis lupus*), in the human-dominated landscapes of Europe. The jackal is an omnivorous and opportunistic mid-sized canid and is considered ecologically equivalent to the coyote (*Canis latrans*) (Jhala and Moehlman, 2004). Today the jackal is widespread throughout southern Asia, the Middle East and southeastern and central Europe, where it inhabits a wide variety of habitats, from semi-deserts and grasslands to forested, agricultural, and semi-urban habitats (Jhala and Moehlman, 2004; Šálek et al., 2014; Koepfli et al., 2015; Trouwborst et al., 2015). Jackals most likely colonised Europe in the early Holocene (Spassov, 1989; Sommer and Benecke, 2005; Zachos et al., 2009), but until the 20th century their numbers remained low and were limited to the Mediterranean and Black sea coastal regions. During the 20^{th} century jackals increased in their distribution and abundance in what is arguably the most dramatic recent expansion among the native predators on the continent (Trouwborst et al., 2015). For example, in Bulgaria jackals expanded their distribution by 33-fold in the period between 1962 and 1985 (Kryštufek et al., 1997) and the number of jackals hunted by humans increased from around 40 per year in the 1940s (Spassov, 1989) to almost 30000 nowadays (Stoyanov, 2012). Similar trends have been observed throughout southeastern Europe and in the last two decades the jackal expansion front reached Switzerland, Germany, Poland, and the Baltics (Trouwborst et al., 2015).

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The reasons behind the expansion of golden jackals remain an unresolved question (Lapini et al., 2011; Markov, 2012; Šálek et al., 2014; Trouwborst et al., 2015). Potential answers include the socio-ecological modifications induced by climate change (Fabbri et al., 2014), the Balkan wars (Toth et al., 2009), as well as changes in hunting management (Markov, 2012) or land-use (Šálek et al., 2014). But while some of those factors likely eased the expansion process, they are unlikely to have initiated such a dramatic change in jackal distribution. There is also an alternative explanation that has received little attention to date: changes in interactions with other predators. The main candidate that could have affected jackals is the grey wolf, whose population has undergone dramatic changes in the 20th century. For example, in the same period when the jackal population substantially increased in Bulgaria, the wolf population experienced a major decline due to intense human persecution and until the 1970s only a small number of wolves remained in the most remote mountains of Bulgaria (Markov, 2014; Moura et al., 2014). Some authors have already speculated that wolves could affect jackal distribution and abundance (Brelih, 1955; Spassov, 1989; Kryštufek and Tvrtković, 1990; Giannatos et al., 2005; but see Milenković, 1987 for opposite view), but there have been no attempts to compare their distributions, population trends or interactions.

Here we explore the hypothesis that grey wolves exert strong top-down effects on golden jackals and that the observed expansion of jackals across Europe was connected to human-caused decreases of wolf populations. If true, inverse patterns of relative abundance and distribution for both species should be observed. Since jackals readily use carrion, including prey remains left by large carnivores (Jhala and Moehlman, 2004; Aiyadurai and Jhala, 2006), the alternative hypothesis is that wolves have positive effects on jackals by providing additional scavenging opportunities and thus offsetting the effects of interference competition and intraguild predation. In this case, there should be a positive correlation in the relative abundance and distribution for both species in time and space.

To test our hypotheses we assessed data collected at three different spatial scales. At the continental scale, we reviewed available information from published literature to reconstruct changes in the distribution and relative abundance of grey wolf and golden jackal populations in Europe. At the regional scale, we analysed patterns in the relative abundance of wolves and jackals using hunting data from Bulgaria and Serbia, the two European countries where these species have the largest overlap in distribution. Finally, at the local scale, we surveyed jackal persistence in eight study areas that became re-colonized by wolves. We end by discussing the implications of the results for conservation and management and by providing recommendations for further research.

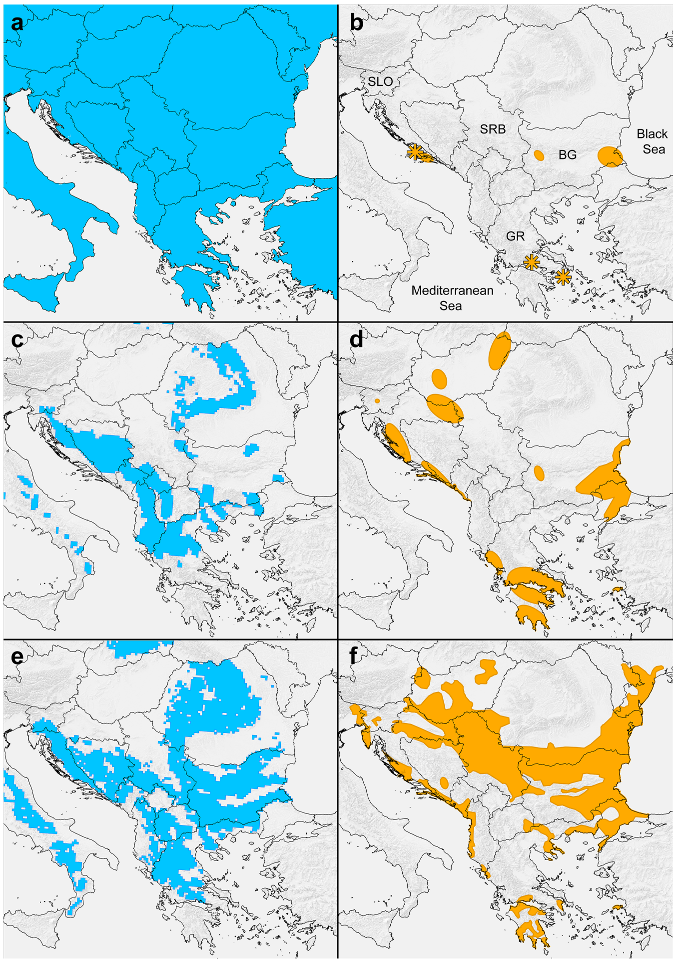

Figure 1 – Distribution of grey wolves (left) and golden jackals (right) in Europe in three time periods: pre-1500 (above), 1950-1970 (middle), and post-2000 (below). Asterisks represent localities with subfossil jackal finds from early Holocene and shaded areas represent areas of permanent presence of both canids. Letters corresponds to each inset map as referenced in the text. Countries where additional analyses were conducted at regional and local scales are marked with: SLO (Slovenia), SRB (Serbia), BG (Bulgaria), and GR (Greece). Data sources: wolves pre-1500: Boitani (2000); Masseti (2010); wolves 1950-1970 and post-2000: Pimlott (1975); Chapron et al. (2014); jackals pre-1500: Vuletić-Vukasović (1908); Malez (1984); Sommer and Benecke (2005); Spassov (1989); jackals 1950-1970: Atanasov (1953); Milenković (1987); Kryštufek and Tvrtković (1990); Toth et al. (2009); jackals post-2000: Trouwborst et al. (2015).

Material and methods

Continental scale population trends

We conducted a literature review to obtain information on golden jackal and grey wolf distribution and abundance, focusing primarily on south-eastern and central Europe. The literature search was carried out on Google Scholar using combinations of the following keywords: golden jackal, *Canis aureus*, wolf, *Canis lupus*, canid, Canidae, range expansion, expansion, distribution, recovery, population trend, population size, population dynamics, historic range, historic, prehistoric, Holocene, occurrence, abundance, Europe, Balkan, Greece, Bulgaria, Serbia, Croatia, Slovenia, Hungary, and Romania. We also retrieved literature from the reference lists of all relevant studies found during the initial search. We combined data from studies with distribution maps or those that reported absolute or relative trends in abundance or distribution of either species, as well as with individual historic and (sub)fossil records of jackal presence.

To map the spatial distribution of (sub)fossil records, historic and current distributions, we separated the data into three periods: (1) pre-1500, representing the historic distribution of both species, and when wolves were widespread throughout the continent; (2) 1950-1970, representing the period when grey wolf populations were lowest; and (3) current, representing the period after 2000. For the current distribution of golden jackals we used data already compiled by Trouwborst et al. (2015), and for the 1950-1970 and current wolf distribution data compiled by Chapron et al. (2014). Although the resolution proved too coarse to enable precise evaluation of whether the two species segregated or overlapped in some areas for all time periods, the data derived were useful to depict broad distribution patterns at the continental scale and to calculate approximate range and overlap during the last two periods.

For changes in relative abundance of grey wolves and golden jackals through time we reviewed studies that compared distribution ranges, hunting bags or other records of species presence in different time periods, usually limited to single countries. Although available data do not enable the exact quantification of changes in population dynamics, general trends among countries were similar, thus enabling us to re-

Table 1 – Golden jackal and grey wolf distribution range and their overlap in 1950–1970 and post–2000 period. See Fig. 1 for data sources.

Period	Jackal	Wolf[a]	Overlap	% overlap[b]
1950–1970	129505 km^2	186700 km^2	9131 km^2	7.1%
Post–2000	384367 km^2	358800 km^2	87318 km^2	22.7%

[a] Wolf distribution range refers to the two populations in the region: the Dinaric-Balkan and Carpathian (south of Ukraine) wolf populations.
[b] In proportion to jackal distribution range.

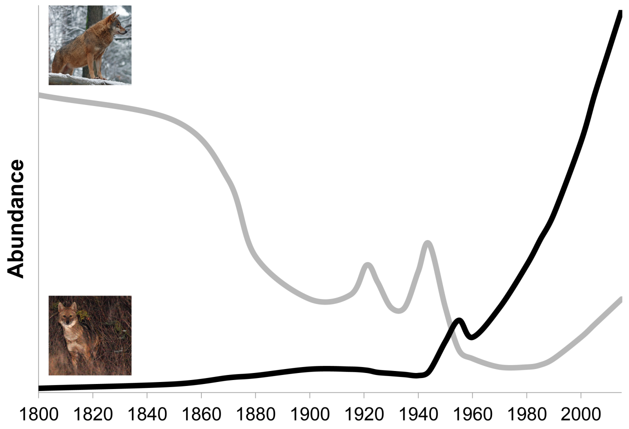

Figure 2 – Schematic reconstruction of the relative population dynamics for grey wolves (grey line) and golden jackals (black line) in central and southeastern Europe since 1800. Not drawn to scale. For details see Appendix S1. Data sources, wolves: Pimlott (1975); Jędrzejewska et al. (1996); Adamič et al. (1998); Štrbenac (2005); Mihaylov and Stoyanov (2012); Markov (2014); jackals: Spassov (1989); Kryštufek and Tvrtković (1990); Kryštufek et al. (1997); Spitzenberger (2001); Giannatos et al. (2005); Szabó et al. (2007); Krofel (2008); Toth et al. (2009); Szabó et al. (2010); Lapini et al. (2011); Banea et al. (2012); Markov (2012); Heltai et al. (2012); Trouwborst et al. (2015). (Photo credit: M. Krofel).

construct relative changes in the species' abundance. We assumed a decrease in abundance when majority of reports indicated decrease in observations or detected mortalities, or when local extinctions were reported; and an increase in abundance when the literature provided evidence of increasing numbers of observations, mortalities or expansion of distribution (details on literature data we used for reconstruction of relative temporal trends and schematic representation are provided in Appendix S1). We took into consideration that some reported changes in hunting pressure might not be connected with changes in species abundance (e.g. absence of harvest records during the world wars or in periods when either species was fully protected as this may not indicate a decrease in abundance).

Regional scale population trends

We obtained hunting records of golden jackals and grey wolves killed in 255 hunting zones in Bulgaria between 2004 and 2009, and in 148 hunting zones in Serbia between 2000 and 2008. Bulgaria and Serbia were selected because these two countries have the greatest overlap in distribution of the two species (Fig. 1). We used the hunting records to derive an index of abundance for each species by calculating the total number killed in each hunting zone. We then used quantile regressions as recommended by Johnson and VanDerWal (2009) and adopted by Letnic et al. (2011) to test if there is a negative relationship between the relative abundance of wolves and jackals in each country. To do so, we first removed hunting zones with no harvest records of wolves or jackals. We then used a Lilliefors' test to determine if the frequency distributions of wolf and jackal index of abundances differed from normal. For the quantile regression, we modelled the slope of the relationship at the 0.5, 0.7, and 0.9^{th} quantile. We chose the 0.5^{th} quantile to assess the relationship between median jackal and wolf values, and the higher quantiles were chosen to determine if the size of the effect of wolves on jackals increases progressively. To estimate standard errors and p-values, we used a bootstrap method with 10000 replacements. As a secondary test, we computed nonparametric Spearman's rank correlation coefficients. All analyses were conducted in R, v 3.1.2 (R Development Core Team, Vienna, Austria) using the `Quantreg`, version 5.11 package (Koenker, 2012).

To graphically display the hunting trends using an alternative approach, we plotted the average number of golden jackals killed in Bulgaria and Serbia under three scenarios, (1) in hunting units where grey wolves were absent versus present, (2) in hunting units where the number of wolves hunted was low versus high, with the cut-off between low and high being the average number of wolves killed across all hunting units, and (3) in hunting units where the number of wolves hunted was low versus high, with the cut-off between low and high being the median number of wolves killed across all hunting units. We included the median values as cut-off points in case the average values were skewed by outliers.

Local scale population trends

To test if grey wolves affect golden jackals at a local scale we compiled jackal and wolf presence data from systematic jackal howling surveys (for details on methodology used see Giannatos et al., 2005; Krofel, 2009), wolf telemetry (Ražen et al., 2016), literature data, as well as opportunistic sightings and interviews with local inhabitants and game wardens. We chose eight study areas in three countries, where we had information that jackals colonised an area after wolf extirpation, and then wolves later re-colonized the areas. The size of study areas ranged between 110–450 km^2 (mean: 218 km^2).

The first two study areas were in Slovenia (Central 45°56′N, 14°20′E and Southwestern Slovenia 45°32′N, 13°57′E). Golden jackals colonised these two areas following grey wolf extirpation in the 1950s and early 1900s, respectively. Wolf packs re-colonized the two areas in the early 1990s. Systematic jackal howling surveys commenced in 2008 in Central Slovenia and were repeated every year until 2015, and in Southwestern Slovenia systematic howling surveys were conducted in 2009, 2013 and 2015.

Five study areas were in Greece, two in the Fokida province (38°23′N, 22°14′E and 38°23′N, 22°4′E), two in the Thessaloniki province (40°32′N, 22°38′E and 40°42′N, 23°8′E), and one in Chalkidiki peninsula (40°29′N, 23°48′E). In all areas golden jackals were known to be present at least until 1990 and later grey wolves recolonized all of these areas. We conducted systematic jackal howling surveys in the Fokida province in 2000 and in 2015, in the Thessaloniki province in 2001, 2002 and 2015, and in the Chalkidiki peninsula in 2014.

The eighth study area was in Serbia in Veliko Gradište (44°45′N, 21°30′E). Golden jackals appeared in this area in the 1980's. Grey wolves re-colonized the area in 1991, but they were regularly persecuted and probably no stable packs were ever formed. We conducted a systematic jackal howling survey in 2010.

Further information about presence of both canid species in each of the study areas is provided in Appendix S2.

Results

Continental scale population trends

Fossil records suggest that grey wolves have been present in Europe at least since the Late Middle Pleistocene around 200 kyBP (Brugal and Boudadi-Maligne, 2011). During most of the Holocene (i.e. before 20^{th} century) wolves occurred throughout continental Europe (Boitani, 2000). They were also present on the British Isles, but absent from most of Mediterranean islands (Malez, 1984; Boitani, 2000; Masseti, 2010, 2012) (Fig. 1a).

In contrast to the Middle East (Kurtén, 1965), golden jackals were evidently absent in Europe during the Pleistocene. Bulgarian and Italian records of Pleistocene jackals were later shown to be erroneous determinations (Spassov, 1989; Lapini et al., 2011). The species was first confirmed in Europe in the Neolithic era between 7000–6500 yBP (Sommer and Benecke, 2005). Through most of the Holocene jackals were limited to the Mediterranean and Black sea islands and coastal regions (Fig. 1b), as records dating before 1500 AD are known only from Kitsos and Delphi in Greece (Sommer and Benecke, 2005), Adriatic islands Hvar and Korčula in Croatia (Vuletić-Vukasović, 1908; Malez, 1984) and from the Strandža region in Bulgaria (Spassov, 1989). These historic records were confirmed by the patterns of population genetic structure revealed by recent molecular data (Rutkowski et al., 2015). Jackals were reported during the 18^{th} and 19^{th} centuries also from several Greek islands, such as Samos and Corfu, where they were likely present already earlier (Masseti, 2012). The only pre-1500 record from the mainland comes from the 14^{th} century from the Sofia plains in Bulgaria (Spassov, 1989).

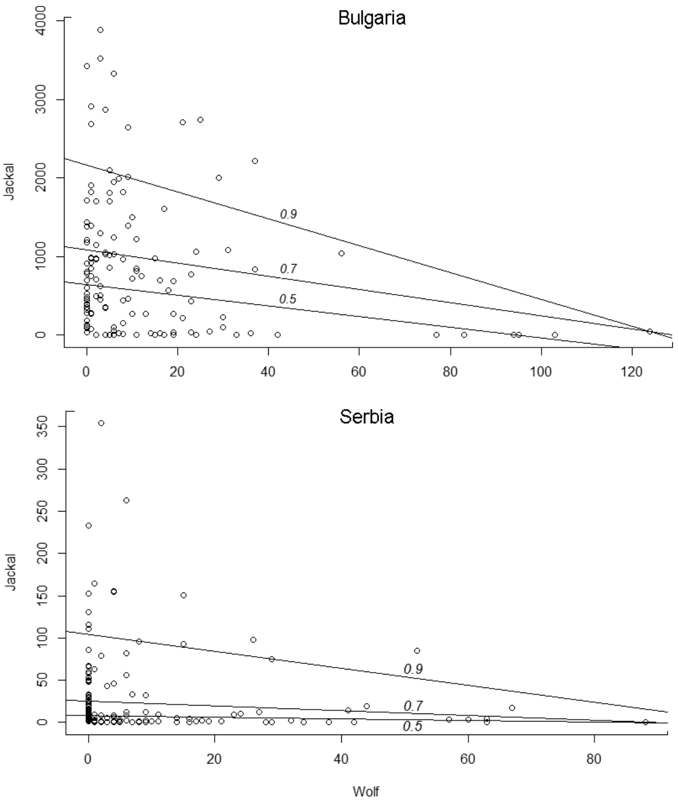

Figure 3 – Relationship between grey wolves and golden jackals based on abundance indices derived from hunting statistics in Bulgaria from 2004–2009 (above) and Serbia from 2000–2008 (below). Regression lines are shown for the 0.5th, 0.7th and 0.9th quantile of jackal abundance versus wolf abundance.

Table 2 – Quantile regression results at three levels comparing abundance indices for jackals as a function of abundance indices for wolves. Abundance indices are based on hunting statistics in Bulgaria from 2004–2009.

	Intercept			Slope		
Regression quantile	**Value**	**Stand. Error**	**t**	**Value**	**Stand. Error**	**t**
0.5	643.31	119.02	5.40**	-6.77	1.89	-3.57**
0.7	1085.55	124.37	8.72**	-8.39	3.18	-2.63*
0.9	2162.71	371.40	5.82**	-17.07	11.72	-1.45a

** p<0.001 * p<0.05 a p=0.147

Table 3 – Quantile regression results at three levels comparing abundance indices for jackals as a function of abundance indices for wolves. Abundance indices are based on hunting statistics in Serbia from 2000–2008.

	Intercept			Slope		
Regression quantile	**Value**	**Stand. Error**	**t**	**Value**	**Stand. Error**	**t**
0.5	8.00	2.29	3.51**	-0.09	0.06	-1.49a
0.7	25.00	6.86	3.64**	-0.29	0.16	-1.78b
0.9	104.00	23.33	4.45**	-1.00	0.68	-1.45c

** p<0.001 a p=0.14 b p=0.07 c p=0.15

In the 19th century grey wolf persecution in Europe intensified and their range and numbers decreased substantially, especially after 1850 (Pimlott, 1975; Zimen, 1978; Jędrzejewska et al., 1996; see also Appendix S1). At the same time, golden jackal expansion started and the first records appeared in the Pannonian basin from what is nowadays Hungary, Serbia, continental Croatia, Romania, and Ukraine (Toth et al., 2009). In the first half of the 20th century, new hunting technologies made wolf persecution even more effective, which in combination with habitat loss and a decrease in wild ungulates caused further declines in wolf population, although they rebounded somewhat during both world wars (Pimlott, 1975; Jędrzejewska et al., 1996; Adamič et al., 1998). For jackals, increasing population trends stabilized during this period with a slight decline noted between 1920 and 1945 (Spassov, 1989; Toth et al., 2009).

After the World War II (post-1945), grey wolf persecution intensified again and poison use became widespread, resulting in all-time lows in wolf populations (Pimlott, 1975; Chapron et al., 2014) (Fig. 1c). In contrary, golden jackal numbers started to rise after the World War II and in the 1950s the first jackals reached the Alps (Brelih, 1955). In the mid-20th century the distribution of wolves and jackals almost completely excluded each other (7.1% of jackal range overlapped with wolves'; Tab. 1), with wolves being mainly confined to remote mountain areas, while jackals expanded mostly through lowlands along the Adriatic and Black Sea coastal regions and the Pannonian basin (Figs. 1c and 1d).

In the 1960s and 1970s golden jackal expansion appears to have somewhat halted, most likely due to widespread poisoning campaigns (Giannatos et al., 2005; Szabó et al., 2007; Lapini et al., 2011). In the 1980s, when grey wolves continued to be intensively suppressed by humans, the next wave of jackal expansion occurred (Spitzenberger, 2001; Lapini et al., 2011). In the 1990s wolves gained protection in several countries and they re-colonized some parts of their former range (Chapron et al., 2014) (Fig. 1e). At the same time, jackals continued to expand through central Europe, especially where wolves were absent (Trouwborst et al., 2015) (Fig. 1f). Population estimates suggest that around 70000 jackals (Ćirović et al., 2016) and 12000 wolves (Chapron et al., 2014) currently live in Europe.

Relative trends reconstructed upon literature data generally indicate opposite trends in the abundance of golden jackals and grey wolves during last two centuries, with the exception being the decreasing trends in the 1960s and increasing trends of both species after 1990 (Fig. 2; Appendix S1). Their current distribution remains largely segregated, with wolves mainly (but not exclusively) occurring in mountainous regions, while jackals are most widespread in the lowlands, although they occur also in the mountains of Peloponnesus peninsula and eastern part of the Alps, where wolves are absent (Figs. 1e and 1f). However, both species do appear to come into contact in some regions, especially in eastern lowland Serbia and parts of Bulgaria. Overall, jackals nowadays overlap with wolves on 22.7% of their distributional range (Tab. 1, Fig. 1).

Regional scale population trends

The scatter plot of golden jackal versus grey wolf abundance in Bulgaria generally revealed a negative relationship, with the highest values for jackal abundance occurring at the lowest values for wolf abundance. This was supported by the regression at the 0.5th and 0.7th quantile (Tab. 2, Fig. 3), and by the Spearman's rank correlation (r=-0.22, n=138, p<0.01). However, the frequency distributions of wolf (Lilliefors' test n=138, D=0.27, p<0.001) and jackal (Lilliefors' test n=138, D=0.17, p<0.01) were non-normal and skewed. There was also no significant relationship at the 0.9th regression quantile (Tab. 2, Fig. 3), suggesting there are areas in Bulgaria where relatively high numbers of wolves and jackals co-occur, at least at the hunting zone level.

In Serbia, the scatter plot of golden jackal versus grey wolf abundance also revealed a negative relationship (Fig. 3) and this was supported by the Spearman's rank correlation (r=-0.31, n=148, p<0.001). However, the frequency distributions of wolf (Lilliefors' test n=148, D=0.28, p<0.001) and jackal (Lilliefors' test n=148, D=0.29, p<0.01) were non-normal and skewed and there was no significant relationship at the 0.5th, 0.7th, or 0.9th regression quantile (Tab. 3).

Comparison of the average number of golden jackals under three different scenarios of grey wolf abundance, generally demonstrate that more jackals were present in areas with fewer wolves, except in the case of Bulgaria where more jackals were shot at hunting zones where wolves were present (Fig. 4).

Local scale population trends

In seven out of the eight study areas (88%) we found evidence that re-colonizing grey wolves displaced golden jackals. In the two study areas in Slovenia and in Chalkidiki, Greece we recorded jackals after

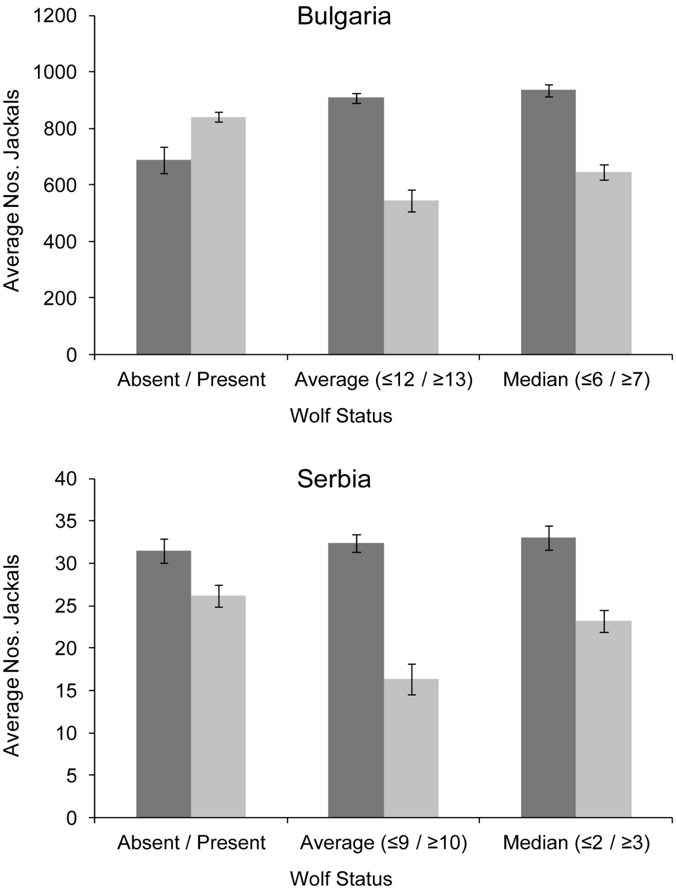

Figure 4 – Comparison of the number of golden jackals killed (mean ± 95% confidence intervals) in Bulgaria and Serbia in relation to the status of grey wolves. Status refers to whether or not wolves were present (light) or absent (dark) in a given hunting unit, or whether they were in high (light) or low (dark) numbers as indicated by hunting statistics. For the high/low values we chose the cut-off point as the average number of wolves killed across all hunting units, as well as the median number of wolves killed across all hunting units.

wolf re-colonization only outside the home range areas of the territorial wolf packs (>1 km from the borders of the known wolf home-ranges) during jackal howling surveys following wolf re-colonization. In the year when one of the wolf packs disappeared (2015 in study area 2), one jackal group was recorded 1 km inside of the previous wolf home-range. No jackals were detected during jackal howling surveys in the four study areas in Fokida and Thessaloniki province in Greece, but wolves responded with howling to the jackal recordings or wolves were spotted approaching the calling stations where jackal howling was broadcasted. In Veliko Gradište in Serbia, jackals were detected after wolf re-colonization and the howling survey estimated a jackal density of 1.9 groups/10 km^2.

For further information on local scale population trends see Appendix S2.

Discussion

The observed trends of grey wolf and golden jackal distribution and abundance in Europe were generally consistent with the predictions of the mesopredator release hypothesis. Although variable, inverse patterns of relative abundance and distribution for both species were found at multiple spatial scales. This supports the existence of top-down effects exerted by wolves on jackals in human-dominated landscapes in Europe. We suggest that intensive persecution and resulting decline of the dominant canid is a credible explanation to explore further as a key driver that enabled the dramatic expansion of the jackal throughout Europe, millennia after being limited to the fringes of the continent.

Although part of our analysis is correlative, and while the results could be affected by confounding effects such as differences in habitat use between the two species, the general distributional patterns at the continental and regional scales are supported with the outcomes of the quasi-experimental (before-after) case studies at the local scale. In seven out of the eight cases, golden jackals were either not detected or were displaced out or to the periphery of the newly established grey wolf home-ranges. This negative trend is in contrast to neighbouring regions without wolves and the general jackal population dynamics in Europe, which show increasingly positive trends (Szabó et al., 2007; Trouwborst et al., 2015). The example from the regional study area in Serbia also indicates that when wolves are regularly persecuted by humans, jackals can maintain their presence in high densities. Separate data from Bulgaria even suggest that intensive wolf persecution and resulting low social stability of wolf packs facilitates hybridization between wolves and jackals (Moura et al., 2014). Based on these results we suggest that further research is needed, to assess the importance of wolf presence in respect to stability of their packs, as well as various habitat parameters.

We also suggest that future hunting bag data from countries with overlapping ranges of the two species should be collected at a finer spatial scales, since spatial segregation between golden jackals and grey wolves can be very narrow (e.g. see Fig. S1 in Appendix S2). Therefore, our regional scale data probably limits the insights that could be gained from them and may underestimate the effects of the top-down suppression. Data from hunting statistics are also under the influence of various administrative, social and habitat-related factors. For example, the number of hunters, hunting methods, hunting effort and hunting success could simultaneously affect the number of animals of both species killed (Merli and Meriggi, 2006; Newsome and Ripple, 2015) and create a false positive correlation. Other survey methods that have a lower tendency to introduce bias may provide more accurate results. These include camera-trapping, GPS telemetry and howling surveys. Application of a combination of these methods would enable understanding of exact mechanisms behind the patterns we detail. Since both species differ considerably in their diets (wolves mainly hunt large ungulates, whereas jackals predominantly eat anthropogenic foods and hunt rodents; Lanszki et al., 2006; Zlatanova et al., 2014; Ćirović et al., 2016), we suggest that competition for resources may be limited, but temporal and spatial avoidance could occur if intraguild predation is common (Donadio and Buskirk, 2006; Wilson et al., 2010).

The overall distribution of grey wolves and golden jackals, suggest a general parapatric pattern with limited overlap, although in some areas the two species can occur in sympatry, such as in parts of Bulgaria and Serbia. Until recently, wolf hunting was considerably more intense in those two countries compared to most other parts of Europe, which resulted in low social stability of the wolf packs (Moura et al., 2014). At the same time, Bulgaria and surrounding areas contained the highest jackal numbers, and the strength of top-down effects from wolves could be limited, or reduced, if persecution continues and wolves occur at reduced densities (Newsome and Ripple, 2015). This could, in combination with abundant anthropogenic food sources for jackals, potentially explain why the quantile regression at the 0.9^{th} level was only weakly significant in Bulgaria and non-significant in Serbia (Fig. 3), and why more jackals were killed at sites where wolves were present in Bulgaria (Fig. 4).

Patterns observed for grey wolves and golden jackals in Europe are similar to canid interactions observed in North America, where wolves appear to exert strong effects on coyote numbers at large spatial scales, although in certain situations the two species can coexist (Berger and Gese, 2007; Newsome and Ripple, 2015). Detailed studies from North America have also demonstrated that wolves can kill coyotes (Stenlund, 1955; Carbyn, 1982; Merkle et al., 2009) and that spatial and temporal separation can occur (Sargeant et al., 1987; Arjo and Pletscher, 1999; Gosselink et al., 2003), but also that coyotes can benefit from scavenging on wolf kills (Paquet, 1992). Determining what factors allow coexistence between wolves and jackals will therefore be integral to understanding their trophic dynamics.

Given the detrimental implications of mesopredator release on co-occurring species in other systems (Ripple et al., 2013), there is a need for further research on the cascading effects that could have emerged following the expansion of golden jackals in Europe. For example, large dietary overlap observed between jackals and red foxes (*Vulpes vulpes*) in Hungary (Lanszki et al., 2006) suggests potential resource competition between these two species. Therefore the grey wolf-triggered cascading effects through increased jackal abundance could have had negative effects on red foxes. There is also limited knowledge about the effects of jackals on prey species, although the data available so far does not provide any detectable detrimental effects, at least on populations of important game species (Stoyanov, 2012; Bošković et al., 2013; Heltai et al., 2012; Lanszki et al., 2015; Ćirović et al., 2016). Also, it remains to be seen, whether other European predators affect jackal populations. For example, although the range of Eurasian lynx lies mainly outside jackal distribution (Chapron et al., 2014; Trouwborst et al., 2015) future expected expansion of jackals, as well as the lynx, could bring the two species in contact. Indeed, studies from Scandinavia suggest that in some environments lynx can have important top-down effect on other predators (Elmhagen and Rushton, 2007; Elmhagen et al., 2010).

Mesopredator release scenarios have already been proposed for several other carnivore guilds, especially in environments with lower impacts of humans (Prugh et al., 2009; Brashares et al., 2010; Newsome and Ripple, 2015). Our study suggests that similar trends can be expected in human-dominated landscapes, such as central and south-eastern Europe. Although apex predators are often severely reduced or even completely exterminated in such environments, many parts of Europe are recently experiencing recoveries of apex predators, despite high human densities (Chapron et al., 2014). We hypothesise that in human-dominated landscapes, spatial segregation between apex and mesopredators could be pronounced due to two factors. Firstly, human-provided food, which is often abundant in the vicinity of human settlements, is regularly used by mesopredators (Prugh et al., 2009; Roemer et al., 2009; Newsome et al., 2015). Indeed, several dietary studies have noted that anthropogenic resources are the main source of food for golden jackals in Europe (see Ćirović et al., 2016 for review). Secondly, human-altered habitats are often the preferred habitats for generalists like mesopredators (Prugh et al., 2009), including the jackal (Šálek et al., 2014). In contrast, apex predators like wolves usually select more remote and less human-degraded habitats (Schadt et al., 2002; Jędrzejewski et al., 2004; Llaneza et al., 2012) and are less likely to feed on anthropogenic resources without being persecuted by humans. Frequent conflicts and fear for human safety, could result in decreased tolerance of large carnivores in the vicinity of their settlements (Treves et al., 2006). This could increase segregation between apex and mesopredators in human-modified landscapes. It could also partly explain the observed top-down effects even in areas with intense grey wolf persecution, such as in Bulgaria and Serbia (Figs. 3 and 4).

Further studies will be needed to test the possible explanations suggested above, as well as to better understand the importance of maintaining ecologically effective densities of apex predators in human-dominated landscapes. This will have important conservation and management implications, especially for regions where overabundant mesopredators are causing significant problems (e.g. excessive predation on endangered wildlife; Prugh et al., 2009; Brashares et al., 2010) and where management goals are oriented toward mesopredator reduction. Experiences from past and existing lethal programs indicate limited effectiveness of lethal methods for reducing mesopredator abundance, as well as being costly (Berger, 2006; Stoyanov, 2013; Kapota, 2014; McManus et al., 2015; Minnie et al., 2016; Treves et al., 2016). On the other hand, apex predators generally appear to be effective in reducing mesopredator abundance (Ritchie and Johnson, 2009). Therefore, restoration or maintenance of ecologically effective densities of apex predators could serve as a cost-effective management tool to effectively control mesopredators. Application of this approach in human-dominated landscapes will, however, need to be applied in parallel with measures that ensure coexistence of humans and apex predators, which is often challenging, although not unattainable, as demonstrated in several areas in Europe (Chapron et al., 2014). Thus, the full range of trade-offs must be evaluated when designing protection or reintroduction of apex predators to harness their ecosystem services (Prugh et al., 2009).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Appendix S1 Literature data used for schematic reconstruction of the relative population trends at continental scale for grey wolves and golden jackals since 1800.

Appendix S2 Detailed information on presence of golden jackals and grey wolves in the eight study areas used for assessing local scale population trends.