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Ph.D. dissertation

Monitoring the Occurrence and Distribution of Large and Medium-Sized Carnivores in Georgia

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DECLARATION

I, Alexandra Kalandarishvili hereby declare that the work presented in this thesis is my own and

has been conducted in accordance with the academic and ethical standards expected of doctoral

research. All sources of information and ideas from other authors have been appropriately

acknowledged and referenced.

I affirm that this thesis has not been submitted, in whole or in part, for any other academic degree

or qualification at this or any other institution.

I am fully responsible for the content, analysis, and conclusions contained herein and I present this

work in fulfilment of the requirements for the degree of Doctor of Philosophy.

Alexandra Kalandarishvili

Budapest, June 2025

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1. BACKGROUND OF THE WORK AND ITS AIMS

1.1. Study Background.

Large and medium-sized carnivore species are integral to healthy, functioning ecosystems (Beschta & Ripple, 2009; Costanza et al., 1997). Grey wolf (*Canis lupus* Linnaeus, 1758), Brown bear (*Ursus arctos* Linnaeus, 1758), Eurasian lynx (*Lynx lynx* Linnaeus, 1758), and Golden jackal (*Canis aureus* Linnaeus, 1758) have become important species in Europe that came to define the region's environmental identity and have culturally been taken to high values. During the majority of the 20th century, European countries recognized the worrying declining trends of the carnivore species and enforced legal protection under The Berne Convention for the Protection and its European Union directives, encouraged the the restoration of habitats, and promoted the natural recolonization of former habitats (Council Directive 92/43/EEC of 21 May 1992). Additionally, changing societal attitudes towards wildlife conservation and increased awareness of their ecological importance have supported these efforts. As a result, carnivore populations have experienced a significant increase in population numbers.

The ecological values of carnivore species derive from their direct and indirect impacts on the prey populations. Predators tend to directly influence the prey population by controlling their numbers and are able to regulate the impacts on the surrounding ecosystems (Winnie & Creel, 2017). In terrestrial ecosystems, top-down and bottom-up effects among the trophic levels occur simultaneously, however, there is a high variation in their effect making the interactions among trophic levels can be complex (Ripple & Beschta, 2004). This becomes an overly critical ecological service in forestry practices where overbrowsing is the main problem limiting forests and grasslands' economic value. Such a top-down regulation further encourages the preservation of other smaller species, including smaller mammals, birds, and insects (Ripple & Beschta, 2012; Van Beeck Calkoen et al., 2023).

In addition to the direct effect, predators can influence the surrounding ecosystem indirectly through a phenomenon known as the "landscape of fear," where prey animals adjust their feeding and movement patterns to avoid predation (Ganz et al., 2024; Laundre et al., 2014). This behavioral shift can also lead to positive cascading effects throughout the ecosystem, such as the recovery of vegetation in areas that were previously overgrazed (Kie, 1999). The extent of such top-down effects by any predator will be determined by factors like abundance, diet, and per capita consumption rate which is dictated by the predator's metabolic rate and the quality of its prey. When ecological models were based on a bottom-up approach for describing the relationship of the trophic level, carnivore species were thought to have little impact on the whole ecosystems (Ripple & Beschta, 2004). The realisation that the bottom-up and top-down regulation could work simultaneously (e.g. Gandiwa, 2013; Garvey et al., 2016) brought a new understanding in ecology and recognized carnivores as an important part of ecosystem construction.

While native species play a significant role in maintaining ecosystem balance by regulating prey populations and promoting biodiversity, alien—and especially invasive—species (IAS) pose serious threats to local ecosystems, often leading to the decline or extinction of native species (Scalera et al., 2012). Alien species being typically generalists tend to outcompete indigenous species for essential resources such as food, water and habitat, therefore disrupting the balance of the ecosystem. It is important to note that general lack of natural predators of the IAS, has further intensified their effect on altering the physical characteristics of the environment, such as changing soil composition or water availability, which in turn affects other species reliant on these conditions (Hayama et al., 2006). The loss of biodiversity and the disruption of ecosystem functionality caused by invasive species can have long-lasting ecological, economic and social consequences (Scare et al., 2012).

However, the growing presence of these predators in areas where human activities such as agriculture and livestock farming are prevalent has led to more frequent encounters with local communities, often resulting in human-predator conflicts (in the form of safety concerns or property damage), leading to economic losses (Blanco & Sundseth, 2023). This conflict further intensifies as human populations and infrastructure encroach into natural habitats. These conflicts often stem from fear, cultural attitudes, and the challenge of coexisting with species that, while ecologically beneficial, can pose risks to human livelihoods and safety (Sillero-Zubiri & Laurenson, 2001; Findo et al., 2013; van Eeden et al., 2017). Addressing these conflicts requires a sensible approach that includes effective livestock protection measures, community engagement, and continued efforts to educate the public on the carnivores' critical ecological roles.

1.2. Research Problem

Predator species that have been persecuted throughout have been documented to be increasing in numbers and range, occurring in previously unsuitable areas in Europe (Linnell et al., 2005, Ripple et al., 2014). Legal protection of wolves, bears, and lynx, successful conservation initiatives such as the EU's Habitats Directive, as well as the efforts for restoring the landscapes and creating favourable habitats for these species have all played a significant role in safeguarding these predator populations (Fitness check of the EU Nature Legislation (Birds and Habitats Directives) Directive 2009/147/EC on the conservation of wild birds and Council Directive 92/43/EEC). It is important to note that there is very few specific legal document solely focused on "rewilding" in the EU; the EU Nature Restoration Law is a significant legal framework that aligns with rewilding principles (Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869). This law, which entered into force in 2024, aims to restore at least 20% of the EU's land and sea areas by 2030 and all degraded ecosystems by 2050. It sets legally binding targets for ecosystem restoration across land and sea, which can indirectly support restoration efforts by enhancing biodiversity and ecosystem resilience.

Species adaptability and climate change have also been recognized as critical contributing factors to the expansion in range, as they alter ecosystems and allow predators to extend their ranges into previously uninhabitable areas. This trend is also visible in the Caucasus region (Zazanashvili & Mallon, 2009). In addition to the expanding populations of native predators, both Europe and the Caucasus regions face ecological challenges from alien species. Raccoons (*Procyon lotor* Linnaeus, 1758) were introduced worldwide to enrich biodiversity or for the fur trade at the beginning of the 20th century (Aliev & Sanderson, 1966). At the time, understanding the impacts the alien species may have had on the local ecosystems was largely absent. The raccoons are highly adaptable generalist species that often outcompete native species for vital resources (Kays, 2009).

The expansion of native and alien predator species both have distinct impacts on local ecosystems and local and rural human communities. On the one hand, the return of native predators like wolves has been shown to play a significant part in promoting ecosystem functionality by controlling populations of herbivores, thereby preventing overgrazing and promoting forest regeneration and economic value (Balnco & Sundseth, 2023). However, the lack of effective management of these species often conflicts with the activities of local human communities, particularly in rural areas where livestock depredation can lead to economic losses for farmers (Sillero-Zubiri & Laurenson, 2001; Findo et al., 2013; van Eeden et al., 2017). On the other hand, alien species often disrupt local ecosystems in more harmful ways. The raccoon for instance, preys on native species, especially the small game species that are most vulnerable to predation; at the same time it can outcompete for resources, leading to declines in native populations (Hayama et al., 2006).

1.3. Rational

Overall, the increase and expansion of various predator species in Europe and Georgia highlight the complex interplay between successful conservation, ecological dynamics, and human-wildlife conflict. Effective management strategies are essential to balance the benefits and harms of predator resurgence and the need to protect local communities and ecosystems from the adverse effects of invasive species.

Georgia once held large populations of red deer (Cervus elaphus Linnaeus, 1758), wild boar (Sus scrofa Linnaeus, 1758), chamois (Rupicapra rupicapra Linnaeus, 1758), mouflon (Ovis gmelini Blyth, 1841), ibex (Capra ibex Linnaeus, 1758) and countless other ungulate or carnivore species whereas today, many of the most common species are experiencing a strict decline (Zazanashvili & Mallon, 2009). While similar in its environment and climate to European ecosystems, Georgia has many unique elements in its habitats. Studying the same species in different habitats gives a deeper understanding of the ecology of that species. In this regard, we want to investigate how the differences between Georgian and European habitats affect carnivore activity and space distribution.

The planned species for investigation include medium and large-sized carnivores: grey wolf, golden jackal, and raccoon. It is important to note that among the medium-sized carnivores, the

raccoon is an alien species (Aliev & Sanderson, 1966; Lavrov, 1971), while the golden jackal and grey wolf are native to both European and Georgian ecosystems (Boitani et al., 2018; Hoffmann et al., 2018). Local hunters and farmers have become increasingly concerned about the rapidly increasing populations of golden jackals and wolves, as well as the potential impact these species may have on small game and domestic animals (Kopaliani et al., 2009). Although raccoons have not generated significant complaints due to their currently low population numbers, there is strong evidence suggesting that these species could soon become invasive (Kalandarishvili & Heltai, 2019; Louppe et al., 2019). By studying their current distribution, we can gain a clearer understanding of the situation and make more accurate future predictions. This, in turn, will provide a basis for drafting a management strategy for alien invasive species, which currently does not exist in Georgia.

One of the most significant issues in Georgia is a severe lack of scientific research. This not only discourages adaptation and implementation of an effective policy, but it also results in the rural public being unaware of how to use the riches of nature sustainably. The presented research aims to enrich scientific knowledge and educate rural residents on sustainable management of natural resources to benefit their livelihood. The results of this thesis will lay the foundation of a viable management plan for predator species in Georgia. As of the time of writing, all essential data for adequate and sustainable management is missing, and a considerable lack of research concerning the ecology of large carnivores in Georgia can be seen. Therefore, the outcomes of this study will directly inform the drafting process of the National Biodiversity Strategy by the Ministry of Environmental Protection and Agriculture of Georgia.

1.4. Aims and Objectives of the Study

The main aim of the research is to understand the presence and, where possible, estimate the minimum population of native as well as introduced species of large and medium-sized predators, namely the wolf, golden jackal, and raccoon in Georgia, as these species have experienced an exceptionally rapid population increase in the later decades. The thesis further aims to investigate the public perception of the predator species and the extent of the human-predator conflict that is taking place in rural environments. The research will be divided into two types of analyses: Analytical work (literature review and citizen science) and fieldwork (bioacoustics survey for estimating jackal density and camera trapping). The samples were collected in Georgia throughout 2021 - 2024 using traditional and more modern methods of analyses to get as detailed an understanding of the matter as possible.

The research will be focused on four major topics listed below. For a more comprehensive structure, the topics were broken down into specific research objectives. As the research question is rather extensive, objectives listed below contain sub-questions to ensure complete topic coverage.

1. **General Systematic Literature Review:** The aim of conducting a general and global literature review is to reveal 1) how frequently were the livestock remains found in the diet of the wolf, golden jackal, and stray dog; 2) which livestock species were consumed most frequently by each of the three carnivores? While stray dogs were not directly the subject of this thesis, it is essential to recognize the large number of stray dogs that live near the rural areas of Georgia. Therefore, based on the international literature, we aimed to understand the likelihood of these species causing damage to domestic livestock.

Objective 1: Investigate the general impact of canids on livestock damages.

- 1.1 Which canid species is causing the most damage to livestock based on the current scientific literature?
- 1.2 Which livestock species are most affected by the canids?

Objective 2: Investigate the impacts that increasing carnivore population has on domestic prey.

- 2.1 Which European countries report the highest number of cases of the damages inflicted by canids?
- 2.2 Which canid species is causing the most damage to domestic animals in Europe?
- 2.3 What are the most frequently used conflict mitigation methods in Europe against carnivore damage?
- 2. Understand the public attitude towards neighboring wildlife: The goal of asking this question is to gain direct insight into rural residents' attitudes toward the neighboring wildlife, and the most effective method is to apply the citizen science methodology. First and foremost, the reason for choosing citizen science is the significant lack of otherwise scientific information. Only a minimal amount of field studies has been done in Georgia, the results of which are rarely available to the public. The goal is to consider the attitude of the local public and potentially integrate them into future management activities. We will evaluate the human-predator conflict in the country and study site level based on a similar data collection method that we will use for determining the presence or absence of the species, meaning we will use detailed questionnaires and surveys that will be distributed to professionals and non-professionals throughout the country.

Objective 3: Understand the extent of the Human-Carnivore conflict in Georgia.

- 3.1 Are the studied species a nuisance to the local communities? If so, what type of problems are they causing?
- 3.2 What is the most common method used by the local communities to mitigate and prevent the damages?
- 3.3 What are the significant factors that need to be considered in management effort concerning these carnivore species?

3. Monitoring predator species on the local and country level: The research aims to understand whether the studied species are responsible for the reported damages. Based on citizen science data collection with a 10 to 10 km resolution, we aim to map the presence/absence of the target species on a country level. In addition, we aim to conduct a detailed monitoring of the target species using different monitoring methods (acoustic surveys, camera traps, and direct observations).

Objective 4: Understand the coexistence between wild canids, domestic species and humans in a semi-urbanized environment.

- 4.1 What are the possible factors that encourage their occurrence in the semi-urban area?
- 4.2 How do large and medium-sized carnivores interact and coexist with domestic animals and humans in semi-urbanized areas in Georgia?
- 4.3 Are there seasonal differences in the occurrence of large and medium-sized canids in semi-urban areas?
- 4. Estimating minimum population size and growth of the golden jackal: We aim to understand what population size is causing the existing predation pressure. Based on the results of the acoustic survey, we aim to deduce the minimal population size of the golden jackal and its potential growth rate.

Objective 5: Investigate the population size of golden jackals in Georgian regions.
5.1 What is the minimum population size of the golden jackal on country and country level?
Furthermore, which factors influence its occurrence in different regions of Georgia?
5.2 What regions do these species occupy and what type of habitats are they mostly found in?

1.4.1. Hypotheses

With regards to the general impacts of carnivores on wild and domestic prey species in Europe and consequently in Georgia, following hypotheses have been developed.

- H₁ Wolves consume the highest proportion of livestock due to their larger body size and pack-hunting behavior and show preference for larger domestic animals. In contrast, golden jackals, having more omnivorous feeding habits, primarily target medium- or small-sized domestic species such as goats, sheep, and poultry. Stray dogs consume the least livestock, as their diet mainly consists of anthropogenic food sources due to their close association with human settlements.
- H₂ The human-carnivore conflict in Georgia is most severe in rural areas, where livestock depredation is prevalent, leading to increased reliance on lethal control methods such as trapping and shooting.
- H₃ Wolf and golden jackal are present throughout all the regions of the country including in the semi-urban areas in significant numbers which presumes their coexistence through space and time.

- H4 Alien species like raccoon are present in semi-urban areas in Georgia and are having potential conflicts with same-sized mammals.
- H₅ The distribution and occurrence of the golden jackal are significantly influenced by environmental variables and interspecific competition. Specifically, golden jackals preferentially inhabit agricultural landscapes due to high resource availability while actively avoiding areas with high competition from wolves.

1.5. Expected Research Contribution

As wildlife management is a new field in Georgia, there is a significant shortage of scientific research related to carnivore management. Human-carnivore conflict is a frequent complaint from local communities, which often lack appropriate preventive measures. While authorities have made many attempts to mitigate the conflict, the current reality shows that these efforts have been unsuccessful. For Georgia, a country that is just beginning to take its first steps toward sustainable wildlife management, understanding carnivore distribution and population sizes is essential. The results of this study will provide valuable insights for carnivore management practices. Effective carnivore management will, in turn, greatly benefit both large and small herbivore species. A well-managed ecosystem is a successful approach to promoting and implementing the sustainable use of natural resources.

The research will benefit the discipline in two significant ways. On the one hand, new scientific knowledge will emerge, which will help local managers to sustain a balance between wild ecosystems and human settlements. This knowledge will also benefit policymakers who are better equipped to create policies that work towards effective management and sustainable use of wildlife. On the other hand, by using traditional and modern methods of studying and analysing samples, this research will introduce these new methods to Georgian wildlife managers and stakeholders, which will benefit future research efforts.

Studying the current distribution of wolves, golden jackals, and raccoons will enable us to predict their future distribution. This is vital information, primarily in the case of the raccoon, as alien species are known for causing substantial damage to their surroundings. Studying well-known species in slightly different environments will also give European experts new knowledge and a better understanding of their adaptations.

2. REVIEW OF THE SCIENTIFIC LITERATURE

This chapter explores medium and large predators' direct and indirect effects on wild prey, emphasizing their key role in maintaining ecosystem processes. It reviews recent recovery trends of these predators in Europe and the Caucasus and examines their impact on livestock due to declining natural prey. The chapter also addresses the challenges of coexistence with predators in human-dominated areas, offering a detailed look at European and Georgian contexts. It discusses the extent of rural damages caused by predators and potential solutions to mitigate these impacts.

2.1. Role Of Large and Medium-Sized Carnivores in Ecosystems' Functioning

Large and medium-sized carnivores play a crucial role in maintaining ecosystem processes by significantly contributing to biological control through top-down regulation of pest animal populations (Beschta & Ripple, 2009; Costanza et al., 1997). The ecosystem function of the predators can be measured by their economic and ecological role (Glen et al., 2007; Lanszki et al., 2018b). Predators are known for their critical role in sanitation around settlements by removing waste and carcasses (Cirovic et al., 2016; Treves & Karanth, 2003). Furthermore, mesopredators limit the abundance of smaller predators, which indirectly positively affects biodiversity by controlling mammalian pests (Lanszki et al., 2006). Such functional roles of mesopredators in regulating the trophic cascades play a significant role in ecosystem structures (Lanszki et al., 2018b). However, over the past decade, some of the large carnivore's keystone species experienced significant global decline, leading to the disruption of these essential ecological functions. The recent recovery of wolves and other large carnivores in Europe (Chapron et al., 2014) has a clear potential to restore the above noted regulatory ecological functions (Estes et al., 2011; Ripple et al., 2014).

The ecological impact of large predators, such as reducing herbivore and mesocarnivore populations, has been well-documented following their removal or reintroduction into ecosystems (Ripple & Beschta, 2012). In Romania, wolves and bears were shown to have a negative effect on the density of red deer and roe deer. Dorresteijn (2015) found that carnivores' top-down effect on herbivores was stronger than the bottom-up effects of the habitat. For example the effect of wolves on red deer was larger than the positive effect of pasture cover. Interestingly, human top-down effects on red deer were larger than the top-down predator effects of wolves, while human topdown effects on roe deer were similarly strong as top-down effects of bears (Dorresteijn et al., 2015). Van Beeck Calkoen et al. (2023) show that a reduction in deer density only occurred in areas where wolves, Eurasian lynx, and brown bears coexisted, particularly in regions with minimal human land use. This suggests that multiple large carnivores and low human interference are key to restoring natural population controls, although this scenario is close to impossible to achieve considering that most of Western and Central Europe is dominated by human presence. However, the situation in Georgia is different as the intense poaching pressure and the absence of a national management strategy for wildlife have led to critically low populations of wild prey such as roe deer and red deer, with red deer now classified as a protected species (Kopaliani et al.,

2009). Furthermore, inadequate waste management in remote areas has increased predator populations, further straining the already vulnerable wild prey populations. To address these issues, developing a comprehensive plan to manage carnivore populations is essential, which would also help reduce human-wildlife conflict.

The ecological role of wolves becomes particularly complex in Mediterranean ecosystems, where free-ranging livestock competes with wild prey and simultaneously offers wolves an easy food source. This inevitably alters wolf population dynamics and their pressure on natural prey populations (Figueiredo et al., 2020; Lagos & Barcena, 2018; Pimenta et al., 2018). This shows that the ecological effects of wolves in anthropogenic landscapes and the potential for trophic cascades are limited (or context-dependent). Studies show that the growth rates of red deer are being kept in check by wolves in Poland (Jędrzejewski et al., 2012), and of wild boars in Spain (Tanner et al., 2019). In the Polish Białowieza Primeval Forest, female red deer densities were shown to be lowest in areas heavily occupied by wolves (Bubnicki et al., 2019). Wolves were also shown to provide carrion for scavengers (Selva et al., 2005) and may potentially decrease golden jackal densities in certain areas (Krofel et al., 2017).

Another characteristic ecological function of large carnivores is the reduction of incidences of disease transmission between wild ungulates and domestic livestock. Tuberculosis is among the diseases most transmitted by wild ungulates to cattle (Blanco & Sundseth, 2023). In the south of Spain, for example, where wolves have not yet spread, studies have documented the difficulty of resolving the problem of tuberculosis in cattle because of the high infection rate in wild ungulates (Blanco, 2019; Tanner et al., 2019). Wild boars in southern Spain were shown to have exceptionally high rates of tuberculosis infection (52% in Doñana National Park and 58% in Sierra Morena, reaching 94% in some fenced hunting estates). Compared to Southern Spain, in northern areas such as in Galicia and Asturias, the prevalence of tuberculosis in wild boars was only 2.6% (Blanco, 2019).

Another example is African swine fever (ASF), which has widely spread among wild boar and domestic pig populations in Eastern and Central Europe, causing severe economic losses. Field and laboratory research that followed the outbreak of ASF has shown that wolves consumed ASFV-positive wild boars. As the virus does not survive the passage through their digestive system, wolves can effectively limit the transmission of ASFV by scavenging on infected carcasses. While wolves are unlikely to be biological vectors, there is a slight possibility they could act as mechanical vectors by transporting parts of infectious carcasses or having contaminated fur. However, this risk is considered minimal due to their grooming habits and the short-range nature of their food-caching behavior (Szewczyk et al., 2021).

Compared to the wolf, the golden jackal is a mesocarnivore with a wide distribution across Eurasia whose habitat ranges from tropical to cooler temperate zones (Lanszki et al., 2015; Tsunoda &

Saito, 2020). This species, unlike the wolf, is unique in its high tolerance towards anthropogenic disturbance, which has allowed populations to become established in human-modified landscapes (Šálek et al., 2014; Tsunoda & Saito, 2020), where they show high utilization of anthropogenic foods (Ćirović et al., 2014; Lanszki et al., 2015). The study by Giannatos et al. (2010) highlighted the jackal's ecological role in its ability to exploit readily available food sources, particularly in wildlife-poor, human-modified environments like the Mediterranean lowlands of Southern Greece, where the availability of natural prey like wild ungulates and small mammals may be limited. Scavenging is one of the most critical roles that jackals fulfil in the ecosystem - they tend to turn to easily accessible food sources provided by human activities (Lanszki et al., 2015).

Most of the jackal's diet consists of domestic mammals, particularly livestock, which Giannatos et al. (2010) show are scavenged as carcasses rather than actively hunted. The authors observed the presence of larvae, and carrion beetles in a notable percentage of scats containing dog remains, suggesting that these animals were consumed as carrion rather than live prey. Cirovic et al. (2016) used the golden jackal as a model species to evaluate the scale of their ecosystem service provision in the Balkans, where improper waste management creates numerous challenges. Based on the analysis of 606 jackal stomachs and data on food intake and population size, the study estimated that in Serbia, the jackal population annually removes over 3,700 tons of animal waste and 13.2 million crop pest rodents. In monetary terms, animal waste removal alone is valued at more than 0.5 million euros per year. The authors extrapolated these findings to assess the ecosystem services provided by jackals on a continental scale to suggest that jackals play a significant role in removing over 13,000 tons of discarded animal waste and controlling over 158 million crop pest rodents across Europe's human-dominated landscapes. This behavior also has ecological implications, as it can lead to increased human-wildlife conflicts, particularly when jackals scavenge on livestock carcasses or encroach on human settlements in search of food. Their presence near human activity can also influence the dynamics of other scavenger species, potentially leading to resource competition.

2.2. Recent Population Trends of Large and Medium-Sized Carnivores

In much of Europe, humans have assumed the role of the top predators, exerting significant influence on wildlife populations and their behaviors. This human influence often has a more profound effect on prey's antipredator behavior than that of the natural predators (Kuijper et al., 2016; Mols et al., 2022). Specifically, hunting and human-induced disturbances significantly affect the vigilance, movement, grouping patterns, circadian rhythms, and stress levels of cervids compared to large carnivores (Mols et al., 2022). Nevertheless, one factor that repeatedly prevents the local communities from effectively coexisting with carnivore species, particularly the wolf, is the species' predatory behavior. Wolves are seen as one of the species that generates the most conflict with humans due to their repeated attacks on livestock and the managed ungulate species (Linnell et al., 2005; Ripple et al., 2014). This conflict has led to the continuous extirpation and persecution of wolves, leading to their declining populations in many parts of the world. This effect

was further intensified due to impacts of habitat loss and fragmentation (Ripple et al., 2014). As a result of these strong actions against large carnivores, populations in past decades have been small and restricted to isolated fragments of their former range (Wolf & Ripple, 2017). This came as a large concern to the scientific community given the important ecological role that large carnivores play in food webs and ecosystems (Ripple et al., 2014).

Restoring large carnivore populations has become a global conservation goal in recent years. However, achieving these ambitious goals in highly human-dominated areas was a significant challenge (Di Minin et al., 2016). On the one hand, past continuous practices of land conversion have led to transformations and fragmentations of natural habitats that no longer allowed the majority of those landscapes to sustain large and viable populations of carnivore species. On the other hand, protected areas designated for wildlife protection are generally not large enough to accommodate and host viable populations (Akçakaya et al., 2007; Linnell et al., 2005). One of the strategies to ensure increasing and sustainable populations of large carnivores is to support the establishment of metapopulations, which consist of several connected subpopulations. Ensuring the genetic exchange in these fragmented habitats is key to recolonizing suitable but abandoned patches (Akçakaya et al., 2007). The difficulty with this strategy comes with understanding the potential of specific landscapes in maintaining such metapopulations and connectivity between the patches (Akçakaya et al., 2007).

Regardless of the legal protection status, the persecution of large carnivores is still taking place, especially in populated rural areas, due to continuous emerging conflicts over livestock (Ripple et al., 2014). In Scandinavian countries, despite the government-driven legal population control measures (Trouwborst et al., 2017a,b), the illegal killing and other human-induced mortality of large carnivores remains prominent. The Scandinavian wolf population is estimated to be just a quarter of what it would be in the absence of poaching. illegal killing also appears to be the main reason for the near-complete disappearance of wolves in southern Sweden (Liberg et al., 2012). In Italy 15-20% of wolves are illegally killed every year (Ciucci, 2015) while in Germany (DBBW, 2018) and western Poland (Nowak and Mysłajek, 2017) the majority of registered wolf mortality was recorded to be due to motor-vehicle collisions, and poaching.

It is often argued that controlling wolf populations and/or fencing are problematic because of their ecological impacts and often conflict with European legislation. On the other hand, a no-intervention approach is likely to heighten human-wolf conflicts. In Europe's highly human-dominated landscapes, Kuijper et al. (2019) argue that effective wolf management should focus on reinforcing the separation between humans and wolves by shaping their behaviours at a fine spatio-temporal scale to minimize conflict. The authors also emphasize that this separation requires a robust wild prey base and advocate for the restoration of natural ungulate populations to help reduce tensions between humans and wolves.

Public attitudes toward wolves also shape conservation outcomes and potential conflict mitigation strategies. A study by Ericsson et al. (2004) examined perceptions across the general public, hunters, residents in wolf-populated areas, and hunters within wolf-populated areas. Majorities across all four groups (53–91%) supported hunting wolves to prevent livestock depredation or when wolves entered populated areas (54–86%). However, support dropped significantly when the justification was fear alone (22–46%) or competition with humans for game (11–45%). While most hunters endorsed wolf hunting if dogs were threatened, the general public—including those living in wolf territories—largely rejected this as a valid reason. Interestingly, around 20% of the Swedish public remained neutral toward any justification, suggesting that a particularly severe or high-profile event could rapidly shift public opinion.

In several areas where the persecution has been reduced, carnivore populations have successfully recovered (Balme et al., 2009b; Persson et al., 2015). However, the effects of unsustainable take of the predators are further intensified by the depletion of natural prey which also indirectly threatens large carnivores (Wolf & Ripple, 2017). Natural prey disappearance is reflected in the quality of habitats, where in areas with declining prey biomass, large carnivores tend to have larger home range sizes and lower net reproduction, ultimately leading to declining populations (Fuller & Sievert, 2001; Hayward et al., 2007). Additionally, without sufficient prey, large carnivores tend to move closer to the human settlements in search of food, often causing damage to livestock (and pets), eventually leading to retaliatory killings (Khorozyan et al., 2015). It has also been the case that these types of retaliatory killings emerge due to wrong assumptions and blaming the wild predators rather than directly investigating the damage by taking decisive clues into consideration, e.g., genetic identification (Khorozyan et al., 2015).

Starting from the last 30 years of the 20th century, across Europe and the Caucasus, the populations of large carnivore species showed a significant increase in their distribution range, among many others; these species typically include grey wolves and golden jackals (Krofel et al., 2023; Ripple et al., 2014; Rutkowski et al., 2015; Spassov & Acosta-Pankov, 2019). The wolf population in 2023 was estimated at 23,000 individuals, which is a 35% increase in population size since 2016 in Europe (Kaczensky et al., 2024). Moreover, they are currently recolonizing human-dominated areas in the continent while also inducing changes in mesocarnivore communities (Kuijper et al., 2024).

In recent years the occurrence of the golden jackal has been reported in Baltics (Trouwborst et al., 2015), Belarus (Grichik et al., 2018), Czech Republic (Jirků et al., 2018), Germany (Trouwborst et al., 2015), Poland (Kowalczyk et al., 2015), Greece (Karamanlidis et al., 2023), Italy (Lapini et al., 2011), as well as in the far north in Finland (Kojola et al., 2024), and most recently in Spain (Miranda, 2024).

It is interesting to note that Hungary was one of the first countries where the golden jackals reappeared in Europe in the 1980s. Hungary is considered as one of the countries with the fastest

jackal expansion, seeing an exponential increase in the golden jackal population since the mid-1990s, with an average annual growth rate of 40% in the hunting bag and an occupancy of 86% of the country (Bijl et al., 2024).

Such growth and expansion in the golden jackal population could have also been facilitated by several other factors, including flexible social behavior (Lanszki et al., 2018b; Macdonald, 1979), varied dispersal patterns (Lanszki et al., 2018a), legal protection that took place in Bulgaria in the 1960 (Lanszki et al., 2018b) the scarcity of larger competitors (Trouwborst et al., 2015), poor population management (Krofel et al., 2017), abundant food resources (Lanszki et al., 2015), poor sanitation conditions around settlements (Lanszki et al., 2018b), transformation of habitats: e.g. land use changes, intensification of agricultural production (Kleijn et al., 2008), global climate change induced range shifts and many more, however, there is no clear consensus on what drives this rapid range expansion (Trouwborst et al., 2015).

It was observed in many areas that jackals generally tend to avoid wolves. For example, its range in Europe has significantly and quickly expanded from the Balkan Peninsula to central and western countries (Arnold et al., 2012; Rutkowski et al., 2015) in which the wolf, acting as a dominant competitor, is absent (Newsome et al., 2017; Tsunoda & Saito, 2020). Interestingly, the jackal range expansion is often mirrored by the decline in wolf distribution (Krofel et al., 2017). However, the opposite is true in other regions, where jackals benefit from scavenging on wolf kills (Boitani et al., 2018) and successfully coexist with wolves. A similar relationship is seen with red foxes (*Vulpes vulpes* Linnaeus, 1758) and coyotes (*Canis latrans* Say, 1823) in North America (Levi & Wilmers, 2012; Wikenros et al., 2017). The distribution area overlap of wolves and jackals has increased from about 7.1% during 1950–1970 to 22.7% after 2000, with wolves reclaiming historical ranges and jackals colonizing new areas (Krofel et al., 2017).

Similarly, in Georgia, wolves started recolonizing their historical range, such as the Kolkheti plains (western Georgia), where the species was eradicated in the middle of the 20th century. Kopaliani et al. (2009) observed golden jackals at an altitude of 1,500 - 1,700m in the region of Racha, even though the jackal is primarily a lowland species. The authors argue that in the available literature, there is no mention of the existence of jackals at such an altitude in Georgia. The local inhabitants often do not realize that the animals they kill are often golden jackals, commonly called "red wolves." It is said that the species started to occur in Racha in the early 2000s.

Consequently, this type of range expansion has heightened the concerns about zoonotic disease transmissions (Tsunoda & Saito, 2020) and depredations of domestic animals in the newly colonized areas. Still, as a primary scavenger, this species is also recognized to play an important ecological role by removing discarded animal remains and facilitating detritus food chains, In the sense that scavengers contribute to the detritus food chain by initiating the breakdown of larger dead organic matter, which then facilitates the work of detritivores and decomposers (Cirovic et al., 2016). Due to such variability and their sudden expansion, there is a growing interest in jackal

ecology and the species influence on its prey species as well as on the competing carnivores (Arnold et al., 2012; Cirovic et al., 2016). The factors associated with their range expansion, ecological plasticity and environmental tolerance have emerged as a significant area of study in wildlife biology (Arnold et al., 2012; Krofel et al., 2017).

Interestingly, the number of stray domestic dogs has also shown an increase in the southern and eastern EU Member States (Voslárová & Passantino, 2012) 'which intensifies the effects of the carnivore population increase. In 1993, the global population of stray dogs was estimated at 500 million individuals (Wandeler et al., 1993), while the most recent review by Smith et al. (2019) estimated the global population of dogs at 700 million individuals with around 75% classified as "free-roaming". Stray dog attacks result in significant financial losses; however, the damages caused by dogs are often wrongly attributed to wolves (Kossak, 1998).

2.3. The Impacts and Challenges of Coexistence and Conservation of Large and mediumsized Carnivores in Human-Dominated Landscapes.

Such significant population increases can potentially result in severe consequences, especially when these fastly increasing predator populations are expanding near many rural human settlements and in areas with ineffective management strategies, which lead to the emergence of human-predator conflicts in the form of damage to livestock, private property as well as in the form of attacks on humans (Sillero-Zubiri & Laurenson, 2001; Chapron et al., 2014). One of the main reasons that led to large carnivore persecution over the last centuries is the predation on livestock species and disturbances brought to the local communities living in the remote areas. Livestock damage is not only an economic issue but an ecological one in areas where it plays a significant role in maintaining healthy grassland biodiversity through grazing patterns. Livestock is most vulnerable when unprotected, making it easy prey for the predators, therefore, the potential of these types of damages remains the main concern among local communities regarding the human-wildlife conflict today (Mech & MacNaulty 2015).

Large carnivores' food habits vary across their distribution area (Newsome et al., 2016; Peterson & Ciucci, 2003). Wolves mostly prey on large wild ungulates, e.g., moose (*Alces alces* Linnaeus, 1758), caribou (*Rangifer tarandus* Linnaeus, 1758), elk (*Cervus canadensis* Erxleben, 1777), white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) and other medium-sized mammals in North America, whereas in Europe, they mainly focus their consumption on wild ungulates such as the red deer, roe deer, and wild boar that are supplemented by livestock or other anthropogenic food sources, where wild ungulates are in low numbers (Meriggi & Lovari, 1996; Newsome et al., 2016). Moreover, wolves have shown a dietary shift in Europe in the past few decades by consuming more wild ungulates compared to previous records (Newsome et al., 2016; Boitani et al., 2022; Blanco & Sundseth, 2023), which could be attributed to the recent large increase of wild prey species during this time (Apollonio et al., 2010; Burbaitè & Csányi, 2009; Valente et al., 2020). However, it is still reported that wolves consume livestock where they are available, easily

accessible, and vulnerable (e.g., Migli et al., 2005; Gazzola et al., 2008; Torres et al., 2015), although this highly depends on livestock species and husbandry practices (Newsome et al., 2016).

The extent to which wolves depend on domestic livestock as their food source varies according to the geographical region and seasons (Migli et al., 2005). For example, wolves may be preying intensively on wild ungulates during spring and summer when the fawns are most vulnerable but will switch to preying on domestic species during winter when fawns have had time to learn how to avoid predators. The prey diversity depends on the prey community's availability and vulnerability for each region (Marquard-Petersen, 1998) for example in countries like Portugal and Greece, where wild ungulate numbers are low, wolves feed mostly on livestock (Papageorgiou et al., 1994; Vos, 2000). It is interesting to note that in countries like Germany sheep losses are determined by state, year, and number of living sheep, instead of wolf numbers. Study by Khorozyan and Heurich (2022) showed that in the northern areas where most wolf territories are concentrated, the number of sheep killed by wolves increased consistently by 41% per year and by 30% for every additional 10,000 sheep. The authors conclude that the determinant of the extent of wolf predation is the quality of livestock protection. The study demonstrated that sheep losses in Germany have been driven by the expansion of the wolf population, not by increasing wolf numbers, and by the number of sheep available.

Another study by Mayer et al, (2022) found that occupancy by resident wolves were positively correlated with forested and semi-natural habitats that support wild ungulate prey, while the occupancy by non-resident wolves were correlated with increasing forest cover and higher sheep densities. The authors concluded that livestock predation by wolves is a context-dependent response which primarily occures when dispersing wolves enter agricultural landscapes with limited wild prey availability and abundant livestock rather than reflecting a specific preference for sheep. The study further concludes that the predation levels were lower in areas where livestock protection measures were in place, particularly in territories with established wolf pairs or packs, therefore while improved fencing can effectively reduce livestock attacks in established wolf territories, managing depredation by non-resident wolves in agricultural areas poses a serious challenge. Although technically feasible, implementing predator-proof fencing and other preventive measures in these infrequently visited areas would entail high economic costs.

The situation of the wolf in the European Union (Blanco & Sundseth, 2023) showed that in the EU wolves are responsible for killing at least 65,500 heads of livestock annually. Sheep and goats account for 73% of the prey, while 19% are cattle and 6% are horses and donkeys bred for meat products. These results are higher than the analyses conducted by Boitani et al. (2022), who concluded that 53,530 heads of livestock were killed annually. While these different estimates may be attributed to bias, the impact of wolves on livestock is well evident to be a worrying issue. Blanco and Sundseth (2023) state that Western European countries bear the most significant livestock damage. However, it is important to note that there is a substantial lack of reporting data

in many Eastern European Countries that currently harbor large wolf populations, such as Bulgaria and Romania. Therefore, the conclusions about the degree of damage may be incomplete.

Spain, in 2022, where there are more than 300 wolf packs (Blanco & Cortes, 2023), suffered around 14,000 livestock animals (Blanco & Sundseth, 2023). Compared to France, which accounted for 1,100 wolves in 2023 reported the damage of 12,000 livestock heads. Based on the review, France has the EU's highest rate of livestock killed per wolf. As wolves were eradicated in France over a century ago, livestock breeders and herders were unprepared when wolves reappeared from Italy in 1993 (Blanco & Cortes, 2023). By 2019, France had 580 wolves, whose numbers were rapidly growing and spread across one-third of the country. According to (Meuret et al., 2021), livestock deaths due to wolves increased from 3,215 in 2009 to 12,451 in 2019 despite extensive damage protection measures.

In addition to livestock, wolves target pet animals. While the number of dogs killed by wolves is significantly small compared to livestock predation, such incidents can greatly influence people's perceptions and attitudes toward wolves (Blanco & Sundseth, 2023). Northern European countries frequently suffer from wolf-dog conflict, especially where dogs are valuable in moose hunting. Between 2010 and 2017, wolves were reported to have killed, on average, 38 dogs per year in Finland (Tikkunen & Kojola, 2020). In the following years, from 2018 to 2022, this figure increased to 45.4 dogs per year (Tikkunen, 2023). The situation is less critical but significant in Sweden, where during 2003-2018, an annual average of 29.2 dogs were killed/injured by wolves (Dalerum et al., 2020). Wolves were shown to be killing, on average, 60 domestic dogs every year between 2006-2011 on hunting grounds in Poland. This is particularly the case in regions where wolves reside in areas with stable populations of wolves and well-established wolf packs (Wierboska et al., 2016). The issue is less intense in Greece, where losses amount to approximately one dog per decade (Iliopoulos et al., 2021). In Croatia, wolves killed 34 dogs and wounded 14 in 2022, which is still a relatively insignificant part of the total of 3,516 domestic animals that were killed and injured by wolves that year (Blanco & Sundseth, 2023). Golden jackals are more omnivorous feeders compared to the wolf.

While the golden jackal's primary diet component is animal matter, it is complemented significantly with plant matter (Lange et al., 2021; Markov & Lanszki, 2012; Penezić & Ćirović, 2015). Several studies about its diet showed that the species mainly feeds on small mammals, e.g., in Greece, the jackal was shown to mostly forage on livestock carcasses and waterfowl (Giannatos et al., 2010; Lanszki et al., 2009, 2010) while in Hungary, the jackals have been found to prey on small mammals as well as on young wild ungulates (Lanszki & Heltai, 2002, 2010). Although the conflicts (including disturbances) or damages inflicted on humans are minimal with the golden jackal, the public attitude toward the animal is still shown to be hostile or indifferent. In Greece, Giannatos et al. (2005) argue that this perception is due to the official recognition of the species as harmful in the country until 1990. The jackals in Greece were found only in Mediterranean-type

habitats and lowland wetlands, close to human settlements, implying a likely dependence on human-produced food that would fuel the conflict.

Another interaction that is harmful to both dogs and wolves is hybridization. Dog-wolf hybridization is problematic as it leads to gene flow between domestic dogs and wild wolf populations, which can significantly impact the genetic makeup of both species. Kopaliani et al., 2009 found significant hybridization between wolves and dogs in Georgia, where about 13% of wolves showed detectable dog ancestry, 10% of dogs showed detectable wolf ancestry, and 2-3% of the wolves and dogs were identified as first-generation hybrids. The study found that hybridization is widespread in areas where large livestock guarding dogs are prevalent and not strictly controlled. This ongoing gene flow can alter the gene pools of both wolves and dogs, ultimately leading to the dilution of unique wolf characteristics and the introduction of domestic traits into wild populations. This genetic mixing poses a threat to the conservation of pure wolf populations, as it can reduce the genetic integrity of wolves and potentially affect their survival and adaptability in the wild.

In Europe, the highest wolf-dog hybridization has been reported in Italy in the Province of Grosseto. In this study carried out between 2012–2014, Salvatori et al. (2019) found a minimum proportion of admixed individuals of 30.6%, comprising 8 out of the 13 surveyed wolf packs; however, they suspected that the rate of recent admixture could be closer to 50%. Their results showed a widespread occurrence of admixed individuals of older generations of a backcross, and they concluded that this high level of admixture raises serious wolf conservation concerns and exemplifies the expected dynamics of wolf-dog hybridization if left unmanaged in human-dominated landscapes. Hybridization with dogs was also found in the case of the golden jackal. Hybridization between golden jackals and stray dogs has already been reported in Bulgaria (Moura et al., 2014), Croatia (Galov et al., 2015), and the Carpathian basin (Ninausz et al., 2023). It has been shown that in areas where intensive agriculture is actively practiced and where free-ranging dogs are present in areas with low population densities, jackals will have more opportunities for mixing with the local dogs (Ninausz et al., 2023).

2.4. Challenges with Wildlife Management and Human-Wildlife Conflict in Georgia

Human-wolf conflicts frequently occur in countries with significant and well-established wolf populations. Finland and Lithuania are only a few examples where studies have actively highlighted these issues (Balčiauskas, 2008; Bisi et al., 2007). Georgia is a country among those examples grappling with human-wolf conflicts, as it is hosting viable wolf populations genetically connected to those in neighboring countries like Armenia, Turkey, and Russia (Kopaliani et al., 2014; Pilot et al., 2014). Over the last few decades, villages and rural areas of Georgia have experienced a significant increase in reports of wolf attacks, which naturally have become a major concern and worry for local farmers. In some extreme cases, there have even been reports of

wolves attacking humans, leading to heightened fear and tension within these communities (Kopaliani et al., 2009).

The challenges of coexisting with large carnivores are not at all unique to Georgia. In Scandinavia, for example, continuous efforts to restore the large predator populations have been challenged and complicated by negative attitudes towards these species by the local rural communities, particularly wolves (Bisi et al., 2007; Røskaft et al., 2007; Bennett et al., 2022). These negative perceptions are exceptionally severe among the villagers living close to wolf populations and directly experiencing the consequences of predator damage (Balčiauskas, 2008). There are a number of factors that contribute to the negative attitudes towards predators. Mainly due to lack of knowledge about the habits and behaviors of large carnivores, as well as due to misinformation and myths about wolves, have intensified the fear and hostility towards the animals. Additionally, the high probability of conflicts between humans and wolves, particularly where there is an increased number of livestock, further fuels these negative attitudes (Røskaft et al., 2007; Zscheischler et al., 2022).

The study conducted by Kikvidze and Tevzadze (2014) in Georgia argues that the problem with wolves is less due to fear but is more rooted in the poor practices of livestock management. The study effectively discusses the contrast between villagers who unbrokenly kept the tradition of livestock husbandry and those who recently switched to livestock husbandry after the economic crisis around 2000. The study concludes that the respondents who adhered to traditional livestock husbandry practices (using shepherd dogs to protect their cattle and including bulls in their herds) reported no increase in wolf-related damage. In contrast, respondents who had only recently transitioned to livestock husbandry and did not use shepherd dogs reported more damage from wolves. This explains the negative relationship between dog presence and perceived wolf damage, and they also did not keep bulls.

Kikvidze and Tevzadze (2014) explain this poor knowledge and practices of livestock husbandry by the region's recent economic history. In the past years, the role of livestock husbandry was minor in the local economies. Instead, the priorities lay in primary agricultural activities and focused on producing export crops such as tea in the Lanchkhuti area and greenhouse vegetables in the Kazbegi District. During this period, cattle - typically housed at or near the home- did not require pasture protection. Traditionally, herds were kept on pastures for months, led by bulls and protected by the shepherd dogs. The milking cows were the only ones brought home in the evenings accompanied by shepherd dogs. This routine movement from pasture to village took place without any wolf attacks. In contrast, the newer farmers who transitioned to livestock husbandry organized 'herding' differently. They either hired other villagers as herders or shared their herding duties. Consequently, the use of shepherd dogs declined, and these families deemed bulls unnecessary.

In the early 1970s, the local economies were mainly specialized and oriented towards export production. In the Lanchkhuti region, mandarin oranges and tea cultivation for export purposes to Russia became the primary source of income for many local communities. Meanwhile, the geographic location of the Kazbegi District resulted in the region turning into a gas pipeline corridor connecting Russia to Armenia. Villages along the pipeline were granted access to free gas, ultimately encouraging the locals to build gas-heated greenhouses to grow fruits and vegetables for export to Russia. Due to this economic specialization, villagers often abandoned livestock husbandry.

However, this only lasted until the early 2000s, when Russia closed the market to Georgian agricultural goods and cut the supply of free gas for greenhouses. This resulted in a collapse of export-oriented economies and forced villagers to revert to livestock husbandry. Consequently, cattle numbers increased about tenfold (Kikvidze & Tevzadze, 2009). The economic crisis in the early 2000s resulted in a drastic shift in local economies towards livestock husbandry, ultimately resulting in a dramatic increase in cattle numbers. However, the increase in livestock numbers did not come with appropriate measures for protecting the free-grazing cattle. The traditional practice of training and keeping shepherd dogs or incorporating bulls into the cow herds gradually disappeared despite the growing importance of livestock husbandry in the economy. As a result, inappropriate livestock management led to increased damage from predators such as wolves. Similar patterns were observed in other regions, such as southern Italy (Ciucci & Boitani, 1998; Meriggi & Lovari, 1996).

The year 2003 was an important milestone for the economic transition toward animal husbandry in Georgia, and this is the year when the wolf attack reports started to emerge. This timing coincides with the rise in livestock numbers, which shows a clear correlation between the increase in herd sizes and the frequency of wolf attacks. It is common to see a typical farmer in the Lanchkhuti area owning 10–15 heads of livestock, almost entirely cows. In Kazbegi District, a typical farmer would now have about 50–100 heads of livestock, predominantly cows (approximately 80%), sheep (up to 15%), horses (up to 4%), and very few donkeys (less than 1%). Before this economic shift, tea farmers in the Lanchkhuti area typically owned only one or two cows. Similarly, before the change in Kazbegi District, greenhouse farmers owned no more than one or two cows and no sheep. Traditionally, farmers would keep the herds on the pasture led by bulls, and the converted farmers tend to either hire other villagers as herders or share the duty among themselves. However, this measure has primarily been insufficient, and these herds tend to suffer from wolf attacks during the evenings when returning from pastures in poor visibility conditions (Kikvidze & Tevzadze, 2009).

2.5. Available Measures to Improve Coexistence

While in some instances, preventing wolf depredation only requires minimal changes in husbandry practices and inexpensive resources, livestock protection usually implies elaborate methods and

creative modifications of husbandry practices and a corresponding increase in labor intensity (Boitani et al., 2022). However, in regions where livestock is free-ranging and is spread all over the area, implementing such practices becomes somewhat different. Such is the case in Norway, where sheep graze freely in the forested and the alpine-tundra regions and are minimally supervised, as during traditional times. The recent recovery and the expansion of the large carnivores did not result in any changes to this conventional husbandry system. The result is that depredation rates per capita (number of livestock killed per carnivore individual) are comparatively higher in Norway than in Sweden (Boitani et al., 2022). The key difference is that Swedish sheep are kept behind fences, often electrified, while Norwegian sheep graze freely and unprotected. Consequently, Norway not only has the highest depredation rates in Europe but also much smaller populations of large carnivores compared to Sweden (Boitani et al., 2022). One of the most efficient ways to reduce livestock losses after wolf recolonization is to apply measures to prevent wolf depredation.

Oliveira et al. (2021) reviewed 135 LIFE projects that focused on livestock depredation prevention between 1992 - 2019 and found that the majority of projects concentrated on wolves and brown bears were located in Mediterranean countries and in Romania, where the human-carnivore problem is quite severe. In addition to information dissemination, the most commonly employed methods are carnivore-proof fencing and livestock-guarding dogs. Other strategies for a similar purpose require more significant changes in husbandry practices, such as replacing highly vulnerable small stock (sheep and goats) with large stock (cattle, horses for meat). This shift, observed in many regions of the northwestern Iberian Peninsula and other parts of Europe, can also alter the landscape, as small and large stocks have different grazing patterns.

Employing shepherds is another highly effective strategy, as wolves generally avoid areas with human presence. However, the expense of hiring shepherds can be a significant challenge for many producers. Expert guidance during the early stages of implementing these measures is essential to ensure their success. According to Oliveira et al. (2021), electric fences were identified as the most successful method for reducing damage caused by large carnivores, though most non-lethal methods demonstrated at least moderate effectiveness. Preventing attacks is especially challenging for free-ranging livestock, such as sheep in alpine meadows, free-ranging horses raised for meat in the northwestern Iberian Peninsula or Italy, or free-ranging beef cattle in certain regions of Spain. These animals often spend most or all of the year dispersed in the field, making it difficult to protect them with fences and not always feasible to use guarding dogs effectively

Some countries in the EU spend significant amounts of money on deploying livestock damage prevention methods. In this endeavor, in 2022, France attributed 32.7 million euros to damage prevention efforts and 4.1 million euros for damage compensations (Prefete de la region Auvergnerhone-alpes, 2022). In Germany, costs for livestock protection measures in 2021 amounted to €16,639,800, more than 30 times higher than expenditure on compensation payments for damage

which amounted to €498,433 (DBBW 2022). Despite substantial investment in protection measures, some French researchers remain skeptical about their effectiveness. Meuret et al. (2021) showed that between 2009 and 2019, the number of livestock lost to predation increased linearly with the growing wolf population, rising from 3,215 in 2009 to 12,451 in 2019, despite France implementing a wide range of protective measures since 2004, including enhanced human presence, livestock guarding dogs, secure pasture fencing, and electrified night pens.

Between 2009 and 2017, most of the increase in damages occurred in the French regions, which were historically predated by wolves, this contradicts the belief that the main damages were in areas that are new to colonization and where farmers were unprepared to protect their livestock. Moreover, over 92% of wolf attacks targeted producers, who effectively implemented protection contracts in the most affected areas. These findings led Meuret et al. (2021) to conclude that damage prevention methods have failed in France. In contrast, the evaluation of damage prevention efforts in Germany is more positive. Although livestock damage has increased with the growing wolf population, the number of attacks in 2021 rose by 3.5% compared to the previous year, while the number of livestock killed or injured decreased by 15%, suggesting that preventive measures may have effectively reduced wolf damage. Sheep losses appear to be related to the expansion of the wolf population rather than an increase in wolf numbers. This downward trend implies that mitigation is possible even with a high number of attacks, which primarily occur where sheep and goat farmers have not yet adapted to the presence of wolves by implementing protective measures (Khorozyan et al., 2022).

A study conducted in the Iberian Peninsula highlights the potential of preventive measures to mitigate long-term wolf-human conflicts. The LIFE Coex project, implemented between 2004 and 2008 across five European countries, focused on reducing livestock losses to wolves at 144 holdings in Spain and Portugal., A decade after the project's conclusion, a survey revealed that 83% of these holdings were still using prevention measures or had done so until they ceased farming. Conventional fences (93% still in use) and large guarding dogs (87%) proved more durable than electric fences (61%). Most measures remained in place ten years later, with damages remaining low and farmers reporting continued satisfaction (Cortés et al., 2020). An important factor to consider is the cost of these prevention methods. The high cost of prevention methods would reduce the incentive by the farmers to utilize them and lower the level of protection from the large carnivores.

To compensate for the damage caused by large carnivores, especially by wolves, the EU has allocated 18.7 million euros annually. The countries that were recorded to pay the most amount of compensation are France (4.1M euros in 2022), Spain (3.2M euros in 2022), Finland (almost 3M euros in 2021, more than 90% for semi-domestic reindeer), Greece (2.3M euros) and Italy (about 2M euros in 2019) (Boitani et al., 2022). Husbandry practices largely influence variations in compensation costs between countries. For example, in regions where livestock roams freely,

wolf-related damage and compensation expenses tend to rise significantly (Linnell et al., 2020; Singer et al., 2022). Studies have shown that the annual compensation costs per carnivore positively correlate with a country's economic wealth, measured by gross domestic product per capita. Still, this relationship is not driven by differences in the prices of livestock or agricultural products across nations. The connection between national wealth and conservation expenditures has been observed at the European level and globally. In wealthier countries, damage management policies typically receive more institutional support, helping cover damage compensation costs (Blanco & Sundseth, 2023).

2.6. Invasive Alien Species in Europe and Georgia

Over 10,000 species have been introduced to Europe, and while most of them remain relatively harmless, at least 15 % are known to have a negative ecological and/or economic impact (Scalera et al., 2012). Among the introduced species, Invasive Alien Species (IAS) group is considered one of the biggest threats to native ecosystems around the globe (Louppe et al., 2019). By modifying habitats around them either by feeding behavior or habitat use, IAS vividly and significantly disrupt the local ecosystems. These problems are also rooted in the lack of natural predators of the IAS in their new environments (Hayama et al., 2006). IAS are the leading direct drivers when it comes to biodiversity loss and degradation of ecosystem functioning.

Raccoons have been introduced in Europe and Asia for the fur trade and enriching biodiversity. Now, raccoons are considered an invasive alien species. Interestingly, while raccoon was introduced to different locations in Europe, it only became invasive in Germany (Bartoszewicz 2011) and shows potential signs of invasion in the Caucasus (Kalandarishvili & Heltai, 2019). In the second half of the 20th century, to enrich biodiversity, the Caucasus region introduced a number of mammal species. Raccoon was exceptionally successful in adapting to Zaqatala - a region East of Azerbaijan, from where the species has made its way to the Easternmost region of Georgia (Aliev & Sanderson, 1966). The climate in eastern Georgia –where the raccoon was first seen – is quite different from the climatic regions in central Georgia, where the raccoon is currently spreading. A study by Louppe et al. (2019) predicted that by the year 2050, favorable areas are more likely to expand in the northern regions while also maintaining current favorable spaces. Such expansion is attributed to climate change's effects, namely the rise in temperature.

This mesocarnivore species is highly abundant and native to North and Central America. However, because of their high adaptability, they are now found in most parts of Europe and almost all kinds of environments, including wooded areas, open and marshy areas, near lakes, along streams, and urbanized areas (Sanderson, 1987). Currently, in most parts of Europe, the raccoon populations are expanding and are causing concern among the rural residents (Salgado, 2018); this is true for Georgia as well (Kalandarishvili & Heltai, 2019). Raccoons can exploit almost all available resources as a food source, including garbage and leftovers. Consequently, they are frequently found close to urban and suburban areas, causing an intense conflict between rural residents (Kays et al., 2009). Raccoons are also highly effective predators and pose an especially significant threat

to insular ecosystems, where they prey on native fauna species. In addition, they are known to be vectors of diseases like nematode-mediated pathogens and rabies (Arjo et al., 2008). These diseases are potentially transmitted to humans, domestic animals, and/or other wildlife species, causing serious, if not lethal, consequences.

It is challenging, almost impossible, to eradicate IAS once they have been introduced to the new area and established a breeding population. The effects of climate change intensify this biological invasion. Besides endangering local fauna, IAS cause major economic damage to agriculture, forestry, and fisheries (Scalera et al., 2012). This realization caused the global attitude to change and recognize the IAS as an issue that needs to be addressed.

In the second half of the 19th century, several mammal species were brought into Georgia to enrich native fauna. At the same time, similar activities were taking place in the neighboring countries. Therefore, several species not initially introduced in Georgia found their way into the country, either from Azerbaijan, Turkey, or Russia (Aliev & Sanderson, 1966). Since 1958, it has become extremely popular in Georgia to introduce different alien subspecies of wild boar. Since the 1960s, more than 1000 individuals belonging to alien subspecies of wild boar were brought into the country. It was only natural for the newly introduced individuals to start interbreeding with members of native subspecies (NACRES). At the end of the first half of the 20th century, a fox farm was established in Bakuriani. Silver fox individuals were introduced to the area for fur farming, some of which managed to escape into the wild. Consequently, the escaped silver foxes were interbreeding with red foxes. The same phenomena were noted in 1939-1940 in Telavi, Akhaltsikhe, Tskhinvali, Bagdadi, and Abkhazia region fox farms. Currently, camera traps have observed hybrid individuals in the same region (NACRES). Today, there is a growing understanding that a solution to the Alien species needs to be formulated and implemented in the country to avoid the devastation of the small game and native fauna.

2.7. Methods for Estimating Carnivore Populations

Multiple tools and methods have been developed over the last decades to monitor different aspects of carnivores' populations (O'Connell et al., 2010; Boitani & Powell, 2012), nevertheless, estimating wildlife population densities still pose specific operational challenges (Podgórski et al., 2020). This is particularly true for carnivore species as they are often cryptic, nocturnal, and typically have large home ranges.

Carnivore population estimation has often relied on track counts to measure relative abundance (Hayward et al. 2002). Although such indices can be informative for specific management purposes, it is generally more desirable to determine absolute abundance to inform conservation and management decisions more reliably (Bart et al. 2004). Moreover, indices are not consistent when applied in different habitats or over broad geographic areas, making them less reliable for comparative studies or broad-scale monitoring (Stephens et al. 2006). Balme et al. (2009a) argue that the relationship between track-based indices and true abundance is not always linear or stable,

particularly at population extremes, which can result in significant deviations from actual population sizes. An alternative method involves using track frequency sampling in conjunction with closed capture–recapture models, which assume that individual animals can be uniquely identified by their tracks and that every individual has an equal probability of detection (Sharma et al. 2005; Choate et al. 2006). By compiling capture histories from repeated track encounters during a defined sampling period, researchers can estimate detection probabilities and population sizes.

In their study, Croose et al. (2019) evaluated the efficacy and cost-effectiveness of live trapping, hair tubes, and scat sampling to estimate the abundance and density of a small-sized carnivore - European pine marten. Live trapping was the single most effective method for detecting individuals, identifying 77% of known martens and achieving a 100% genotyping success rate. However, there were drawbacks to this method - it was invasive, required licensing, and introduced a bias toward male detections. Hair tubes, while providing the highest number of detections per individual, were the most costly and least effective alone, detecting only 48% of individuals with a lower genotyping success rate (44%). Scat sampling was the most cost-effective and balanced method, detecting 52% of individuals with a slight female bias, though its genotyping success was even lower (32%). Notably, the combination of hair tubes and scats outperformed any single method by detecting 81% of known individuals, offering a non-invasive, cost-conscious, and more representative alternative to live trapping.

Camera trapping has emerged as a powerful tool allowing non-invasive data collection to study behavioral and ecological aspects of target species (Delisle et al., 2021). Information from camera traps allows unambiguous individual identification, making its data helpful in generating accurate population estimates from capture-recapture analysis (Macdonald et al., 2020; Joubert, C.J, 2020). While camera traps have long been used to study population densities, they have grown into being utilized for more complex elements of carnivore populations, such as age structures, predatory behavior, and daily activities (Joubert, C.J, 2020). However, several factors may impact the camera traps' overall performance, such as users' expertise, the condition of the study area, the quality of the equipment, and bias due to systematic error. Limitations - technical, user, or otherwise are further limited by significant differences among the cameras, namely in their sensitivity, detection zones, and performance under variable environmental conditions.

Camera traps offer a better alternative to traditional methods like line transects, animal track monitoring, or scat surveys (Gompper et al., 2006; Balme et al., 2009a; Jiménez et al., 2017). When comparing different methods, Silveira et al. (2003) similarly concluded that for the population diversity and abundance evaluation, camera traps are the better choice for the carnivore population survey. This reasoning is further supported by the practicality of camera traps in remote areas that are difficult to access and where conducting traditional methods are rather hard to implement. Jiménez et al (2017) extended the usability of camera traps to estimating carnivore community structures and concluded that an integrated, multi-method approach combining camera traps, live-

trapping, telemetry data, and spatially explicit Bayesian models enables reliable and comparable estimates of carnivore community structures, including for species where individuals cannot be uniquely identified.

There are two parameters to assess the effectiveness of a technique: latency to initial detection (LTD) and probability of detection (POD). LTD measures the time it takes for the first detection of a species at a survey site to be documented. POD looks at the probability of detecting a species with a specific technique. In an ideal scenario, more efficient survey methodologies should result in a low LTD and high POD. Gompper et al (2006) found that the value for each of those parameters varies depending on the target species and concluded that for mid-sized carnivores, for example, raccoon, fisher, opossum, and domestic cat, camera traps and plate tracks had a very similar detection efficiency. This is also confirmed by the study by Shamoon et al. (2017) that investigated medium-sized carnivores in Mediterranean agricultural areas and concluded that camera traps are specifically effective methods for mid-sized and large carnivore species. Similarly, Balme et al. (2009a) noted that Camera-trap surveys, when applied correctly, provide the most accurate and cost-effective method for estimating the abundance and density of individually identifiable cryptic carnivore species (like leopards), compared to track counts or other traditional methods.

Bioacoustics surveys have also emerged as an essential tool for estimating populations of golden jackals (Szabó et al., 2007) and wolves (Passilongo et al., 2015). Similar to camera trapping, it offers a highly effective yet non-invasive and scalable monitoring method that builds on the unique vocal characteristics of the species and relies on their territorial behavior. Bioacoustic monitoring has proved especially useful for elusive and nocturnal species where, unlike the traditional methods, there is no requirement for physical capture or tagging (Comazzi et al., 2016; Suter et al., 2017). Since sound travels long distances, it enables detection from kilometres away and determines the responding group size (Navine et al., 2024). This is especially useful for species that move around large distances (Suter et al., 2017).

While the method has largely been successful in international research (Giannatos et al., 2005; Krofel, 2009; Lapini et al., 2009; Szabó et al., 2009; Banea et al., 2012; Comazzi et al., 2016), they carry certain limitations that need to be accounted for. The primary limitation of the method comes from the fact that unlike camera traps or genetic sampling, bioacoustic survey struggles to distinguish between individual animals, which can affect the overall population estimation (Comazzi et al., 2016). Given that not all animals howl at the same rate, can lead to population density being either underestimated or overestimated (Comazzi et al., 2016). Additionally, environmental factors, such as wind, terrain, and background noise, can interfere with sound detection, making it difficult to gather reliable data in certain conditions (Suter et al., 2017). Another important consideration is the potential disturbance from elicited calls: using recorded howls to provoke vocal responses can alter natural behavior and cause unnecessary stress to the

studied animals (Suter et al., 2017). Nevertheless, this method is actively being used to produce some effective, comparable results internationally.

Historically, carnivore species conservation programs have been primarily based on knowledge derived from scientific research. However, wildlife conservation science has undergone several shifts in recent decades, including the growing recognition of integrating diverse knowledge systems to strengthen the evidence base. Both in the fields of academics and in the policy-making circles, combining citizens' perceptions with field-based results is becoming more common (Kutz & Tomaselli, 2019). Such growing inclusion of citizen science in academic research is largely associated with technological advancement (Frigerio et al., 2018), which has enabled effective communication with all volunteers and reduced the costs of equipment needed for data collection. This broadened the variety of tasks that can be performed in a shorter time frame (Blaney et al., 2016). Citizen engagement now includes activities that range from generating research questions to the data collection and scientific analysis of data and communicating the research results back to the public (Bela et al., 2016; Shirk et al., 2012).

Incorporating the perception of the local communities into scientific research offers information that is otherwise hard to obtain by costly and time-consuming scientific methods. Most of the studies in the field of ecology that used knowledge of the local communities focused on collecting information on the ecosystem level (Kutz & Tomaselli 2019). Knowledge of the local communities offers a deeper understanding of the impacts of climate change on land use and agriculture, habitat degradation and its effect on human livelihoods, as well as nature's contribution to people (Fernández-Llamazares et al., 2017).

It is also worth noting that most of the studies that have been using citizen science as the main method of investigation for population trend and abundance estimation mainly focus on species that are easy to detect, highly abundant, and less wary of humans (Fernández-Llamazares et al., 2017). Fewer studies have been conducted on nocturnal, cautious, and rare species. Using public perception is a handy tool for investigating species that are potentially a cause for the conflict or are a threat to human livelihoods. Information from the local communities is often overlooked and criticized for bias and reliability. However, it is important to remember that any conservation program's success highly depends on such communities' support (Dolrenry et al., 2016). Therefore, it is crucial and necessary for the scientific community to engage and closely collaborate with rural residents in implementing conservation actions.

There are many advantages to incorporating the knowledge of the local communities into scientific knowledge. Depending on the research goal, camera traps, track counts, or other surveys were frequently used; however, given the natural world's complexity, the estimated results often vary between the methods (Wilson & Delahay 2001). Carnivore species that are rare in the area call for more frequent and continuous sampling. Local communities can help in this regard to a great extent by providing information about sightings and occurrence frequencies in the areas where the target

species are scarce. In addition, close partnerships between local communities and researchers can further understand the target species' spatial distribution and trends (Skroblin et al., 2019). Moreover, citizen science provides insight into local perceptions, attitudes, and values toward wildlife species under study.

However, while citizen science offers rich insights to the everyday interactions between wildlife and people, it also comes with a certain level of bias, and mitigating this bias in citizen questionnaire surveys is absolutely critical to ensure the reliability and validity of collected data. To mitigate potential bias in the citizen science data collected through questionnaires, it is essentia; to incorporate structured sampling methods to ensure that all demographic and geographic segments of the target population are proportionally represented. Additionally, pre-testing of questions and the use of cognitive interviews are an efficient way to help identify and correct potentially confusing or culturally sensitive wording that may have influenced non-response. Providing training or orientation materials—such as videos or examples of how to complete the survey—can help reduce misunderstanding of questions and improve the quality of responses. Digital tools that collect metadata could also be used to validate and cross-reference responses. To improve participation in sensitive or low-response areas of the questionnaire, anonymized formats and stronger engagement with community representatives may help increase the level of trust towards the surveyors. Feedback mechanisms and community-based validation (e.g., workshops to discuss results) could also enhance local buy-in and data reliability

3. MATERIALS AND METHODS

This chapter aims to demonstrate the methodological approach that was used to achieve the objectives of the thesis. To address the research questions outlined in section 1.4 and test the hypotheses, this chapter, *Materials and Methods*, is divided into two parts, where 3.1 Off-Site Studies describes the systematic literature review conducted online. This chapter notes used methods of variable selection and methods of statistical analyses 3.2 Studies Conducted in Georgia describes the onsite investigations undertaken in different regions of Georgia, including the questionnaire, camera trapping, and bioacoustic survey. Similarly, this chapter first briefly overviews the methods used and outlines the statistical analysis conducted.

3.1. Off-Site Studies

3.1.1. Literature Survey

3.1.1.1. Data Collection

We performed the general literature review on diet analyses of the grey wolf, golden jackal, and stray dog using two major platforms to retrieve publications: **Web of Science** and **Scopus** using the combination of the following keywords: Total Search = (("Grey wolf" OR "Canis lupus") AND ("diet" OR "food" OR "feeding") AND ("livestock" OR "domestic")). All the articles that used the keywords in the article title, abstract, and keywords sections were included in the analyses, as well as all the publication dates and geographical regions. Non-English papers were also included given that at least the abstract was available in English. Publications whose titles and abstracts lacked any indication of livestock predation were excluded, as it was assumed that their research focus was not on livestock. Consequently, it was not sure that the potentially mentioned results on livestock consumption could be considered reliable enough for the analysis. However, if the search terms were present in the title or abstract but no livestock species were reported in the diet, the value for livestock consumption was recorded as zero (0). The variables we selected for the analyses are frequency of occurrence (%O) and percentage of biomass (%B).

Sources derived from the Web of Science and Scopus repositories were compared against each other to filter out duplicates and only focus on the above-mentioned selection criteria. As a result, I found 71 papers for grey wolves, 22 for golden jackals, and only 4 for stray dogs since many articles dealt with dingoes, and some of them introduced them as "wild dogs" in their studies, which were also excluded. Nine were overlapped, involving data about more than one canid species.

3.1.1.2. Data Analyses

To ensure the thorough reporting and examination of the retrieved literature, this study follows the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses Statement (PRISMA**

Statement) that lists a minimum set of items for reporting in systematic reviews and meta-analyses (Page et al., 2020).

The information and metadata derived from the papers were the year of publication, the country where the study was conducted, the studied canid predator(s), and the livestock species consumed (categorized into cattle, pig, sheep, goat, horse, and donkey, poultry if specified). Those cases when distinct livestock species cannot be identified or reported only in groups (e.g., "cattle, sheep, and horse" together) or referred only as "livestock" in the articles were categorized as "not specified".

The most commonly used indices expressing the diet composition of the canid species of interest in the related studies were the frequency of occurrence (%O) and percentage of biomass (%B). The frequency of occurrence of livestock was expressed as the percentage of scats or stomachs containing the livestock item considered (Vos, 2000). The percentage of biomass is estimated by weighing the dry food remains within a sample (dry matter remains from scat or stomach) and then multiplying this mass data by an appropriate conversion factor (Lanszki et al., 2006).

When observing the consumption of the livestock species, it is critical to look at both the %O and the %B data. The %O indicates the individual variability of feeding habits of the predator, while the %B shows the actual food intake from different diet components. In other words, the first variable shows us whether livestock consumption is a common phenomenon in the predator population or only some conflict individuals should be eliminated; meanwhile, the second one determines the importance of livestock in covering the food requirements of the carnivores. While both factors give a good insight into the general feeding habits even separately, their joint information will be decisive in drafting practical measures for human-wildlife conflict mitigation.

Only studies that performed stomach content analyses or scat analyses for the diet composition were included in the statistical analysis (97 papers out of 105). Studies that have not reported these conventional indices (e.g., articles based on direct observations, frequency of depredation, or summarised literature data) were excluded from the statistical evaluation (8 papers out of 105); however, I present them in a summary text as additional results in the discussion chapter. Papers reporting data from multiple sites or repeated measures (N=31 papers out of 97) were analyzed as independent studies. As a result, I extracted 101 unique studies from those 31 papers that conducted repeated research, and together with one-time projects (66 papers), the final amount of available studies became 167.

In each of these studies available for statistical evaluation, each reported predator-livestock pair was handled separately as a unique observation, i.e., a case when one of the prey species of interest was examined about its consumption of any livestock. Consequently, if one study reported wolves' consumption of sheep, goats, and pigs, I considered it as three separate observations regarding wolf predation. Thereby, I could separate 423 observations. If a study directly reported %O or %B as 0 for a livestock species of interest, I assumed that the authors have specifically checked it in

the samples, and they wanted to emphasize that the potential prey species was not consumed at all. Consequently, I also utilized these results in my analyses.

3.1.1.3. Statistical Analyses

A non-parametric Kruskal-Wallis test was performed on the %O or %B data in R (R Development Core Team, 2021), to verify statistical differences in the reported livestock consumption of the studied canid species and to find the most consumed livestock species groups for each carnivore. The overall livestock consumption of canid species was compared by taking the minimum and maximum values of the reported %O data and the summarised %B data per study. In many publications, livestock consumption was reported only broken down to livestock species; no aggregated value was given. Thus, for the %O values, it was unknown whether or not different livestock species were found in the same samples, *i.e.*, whether they were overlapping or their values should be added. Therefore, I could only determine a range for the overall livestock consumption frequency, not a specific value. In this way, I could reveal potential differences among canids regarding the magnitude of livestock remains in their diets.

The "not specified" category (incorporating cases where the exact livestock species was unknown) was excluded when livestock species groups were compared with the test. The Dunn post hoc test was implemented for pairwise comparisons, which is ideal for groups with unequal numbers of observations (Zar, 2010). The p-value adjustment was performed using the Holm-Bonferroni method, and the 95% confidence intervals were calculated for the mean rank differences. When two groups were compared, the Mann-Whitney U test was used.

3.2. Studies Conducted in Georgia

This research was carried out together with and following the technical task by the Wildlife Agency of the Ministry of Agriculture and Environmental Protection of Georgia. For our study, we selected seven regions for the bioacoustics survey and a semi-urbanized park for the camera trap study. The questionnaire among the rural residents was carried out in eleven regions throughout Georgia (Table 1).

Georgia is a part of the Caucasus Ecoregion and is especially rich in endemic plant species and noted as one of the 34 most diverse and threatened biodiversity hotspots, which implies high conservation priorities. The country also contains 24 Natura 2000 habitat types - 18 forest habitat types belong to the European temperate forest region, and the remaining six belong to Mediterranean deciduous forest habitats (Akhalkatsi, 2015). Instead of Natura 2000, Georgia designates Emerald sites as a non-EU state. Based on the Convention On The Conservation Of European Wildlife And Natural Habitats (2024), as of 2024, there are 66 officially designated Emerald sites in Georgia. The regions are divided into plains and mountainous areas according to the natural conditions. The lowlands are characterized mainly by more humid subtropical weather,

which results in moderately hot summers and moderately cool winters. The mountainous area has milder weather, and the climate is characterized by moderately warm summers and moderately cold winters.

Table 1. The area (km²), population density (resident/km²) and percentage cover of major land cover types (%) of the studied administrative regions of Georgia. All regions presented here were subjects to the questionnaire survey. Regions where bioacoustical surveys were conducted are written in bold. Land cover data was obtained from the ESA Worldwide Land Cover Mapping (Zanaga et al., 2022).

	Total area (km²)	Population density	Forest area	Shrubland (%)	Grass- land	Cropland (%)	Built area	Water bodies
		(resident/km ²)	(%)		(%)		(%)	(%)
Adjara	2,880	115.9	82.0	0.0	15.4	0.6	1.2	0.3
Guria	2,033	55.8	80.2	0.1	11.8	3.7	0.7	0.8
Imereti	6,475	82.5	78.2	0.1	15.0	4.5	1.3	0.6
Kakheti	11,311	28.2	35.1	4.4	34.0	21.6	1.1	0.4
Kvemo Kartli	6,072	69.8	28.9	1.2	49.5	16.7	2.5	0.7
Mtskheta- Mtianeti	6,786	13.9	44.2	0.1	40.3	2.8	0.9	0.6
Racha- Lechkhumi & Kvemo Svaneti	4,990	6.4	68.4	0.0	24.3	0.1	0.1	0.6
Samegrelo- Zemo Svaneti	7,440	44.5	59.6	0.2	22.3	4.7	0.7	1.1
Samtskhe- Javakheti	6,413	25	30.2	0.0	59.0	7.8	0.7	1.5
Shida Kartli	3,324	52.4	43.3	0.0	31.0	22.1	2.7	0.5
Tbilisi	502	1,540	29.1	1.2	36.6	4.1	25.5	2.8

3.2.1. Citizen Science

3.2.1.1. Data collection

For research purposes, to understand the presence of large and medium-sized carnivores in Georgia and understand the extent of the Human-Carnivore conflict in Georgia, we conducted a survey among the local communities in 11 regions (Mtskheta-Tianeti; Tbilisi; Guria; Samtskhe-Javakheti; Kakheti; Kvemo Kartli; Adjara; Imereti; Samegrelo, Zemo Svaneti; Racha Lechkhumi; Kvemo Svaneti; Shida Kartli). Total of 2,000 surveys were distributed (181 surveys per region) in paper format to the local authorities and asked to be shared with the residents as the remote residents

have limited or no access to the internet. The respondents were chosen randomly with regard to the demographics, but all living in rural areas, not in the cities.

The survey asked the following ten questions accompanied with instructions to maximize the correct understanding of each question and prevent misinterpretation of the questionnaire. The questions were asked in a multiple-choice format, and the respondents could check either one or multiple answers (possible answers are noted in *Italics*). The questionnaire was conducted in the Georgian language and translated for this study.

- 1. Which carnivore species have you seen most in your region? (Wolf, Golden jackal, Brown bear, other unnamed).
- 2. Which of the carnivore species have you heard or seen attack domestic livestock the most? (Wolf; Golden jackal; Brown bear; other unnamed).
- 3. Which of the carnivore species have you heard or seen to attack or disturb humans the most? (Wolf; Golden jackal; Brown bear; other unnamed).
- 4. During which season(s) are the attacks by carnivore species on domestic livestock (including poultry) most prominent? (*Spring*; *Summer*; *Autumn*; *Winter*).
- 5. Which of the carnivore species would you note as the most problematic species to occur in your region? (Wolf; Golden jackal; Brown bear; other unnamed).
- 6. Which of the carnivore species have you heard of or seen that causes damage to personal property or to personal belongings, for example: car, house, garden, etc.? (Wolf; Golden jackal; Brown bear; other unnamed).
- 7. Once you identify a carnivore-induced disturbance upon your property and/or belongings, what is the typical action you would undertake to deal with the consequence? (*Call the emergency services; filling a complaint to the local authority; self-prevention; no reaction*).
- 8. What is the most frequently noted type of damage that you have either experienced yourself or heard of that was done by the carnivore species? (predation on Domestic animals; predation on Domestic birds; consumption of crops or any local produce; other).
- 9. In your opinion and personal experience, what is the most effective prevention method for the damage induced by carnivore species? (*Electric fencing; guard dogs; hunting; other*).
- 10. Which carnivore species have you sighted the most in the past year? (Wolf; Golden jackal; Brown bear; other unnamed).

3.2.1.2. Data Analyses

I primarily used a descriptive statistical approach to evaluate the demographic distribution of respondents and their attitude toward local carnivores from several aspects. The distributed survey papers were collected back from the regional authorities at the end of the surveying period and the results were manually entered and processed with Microsoft Excel. It is important to note that the final data was only available in regionally aggregated format which in turn limited the capacity of conducting a more detailed statistical analysis of respondent demographics.

Nevertheless, where possible for statistical testing, I used the Chi-Square test for independence to reveal whether there is any association between the location of the respondents by region and their answers to the most crucial questions of the survey. Since peoples' experiences can vary among regions of different attributes and differing pressures of human-wildlife conflicts, this approach is essential to discover the potential hot-spots of conflicts.

3.2.2. Camera Trapping

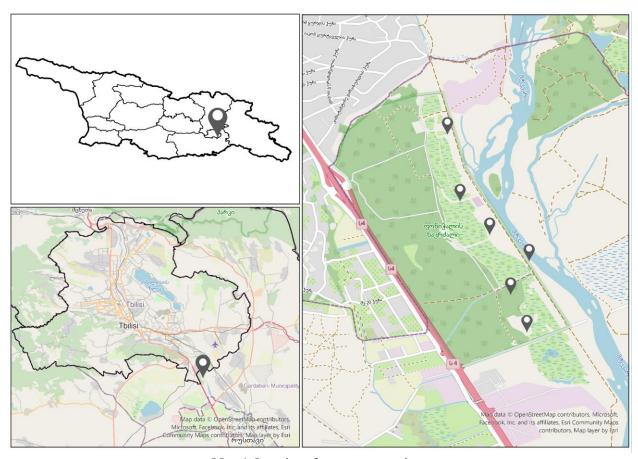
3.2.2.1. Study Site

Ponichala Nature Reserve is a protected area renowned for its ecological importance and recreational opportunities, which people frequently populate throughout the year. The Reserve lies within the boundaries of Tbilisi Municipality and is part of the administrative region of Kvemo Kartli. The reserve is situated close to the settlement of Ponichala, which is a district within Tbilisi itself. The area lies along the banks of the Mtkvari River (also known as Kura River), which occasionally floods the Park area during wet years, creating more of a fragmented habitat. However, during arid years, the river levels are low, providing an easier passage for the animals between the forest patches. The area is diverse in vegetation and landscapes, showcasing a mix of riparian forests, meadows, and semi-arid landscapes. The terrain is predominantly flat to gently undulating, with some areas featuring low hills. The park's proximity to the Mtkvari River contributes to its fertile soils, supporting diverse vegetation. The climate in this region is semiarid, with hot summers and mild winters shaping the park's ecosystem. The reserve is an important biodiversity hotspot, especially for species adapted to riparian and semi-arid conditions. The park has various native trees, such as oak, poplar, willow, and elm. Woody and herbaceous plant species thrive in its diverse habitats. It supports multiple mammals, including foxes, hares, and hedgehogs. Bird species are particularly abundant, with migratory and resident species like herons, ducks, and raptors frequently spotted. Amphibians and reptiles, such as frogs and lizards, are also common due to the park's wetlands and warm climate.

3.2.2.2. Data Collection

The initial step in studying animal populations using camera trapping is to define an appropriate sampling effort by selecting the ideal number of cameras and the spatial design of their locations randomly or systematically. The way cameras are mounted is determined by the goals of the study. For this study, the goals were to define and study mammal presence in the semi-urbanized area of Ponichala Nature Reserve (3.5 km²) in the Kvemo Kartli region and see how wild mammal species coexist with domestic animals and human presence (Map 1), the cameras were set systematically. As the subject of the study is the animal population within a studied area, the cameras were mounted in spots where targeted species are likely to pass. This approach aims to maximize the rate of encounters.

The camera trapping survey was conducted in two study periods, referred to as "Seasons" in the thesis. Season 1 ran from the 1st of December 2020 to the 16th of March 2021 (204 total trap nights), and Season 2 was marked from the 5th of October 2021 to the 15th of December 2021 (218 total trap nights). In total, there were 422 camera trap nights. The reason for these two sampling periods is the assumption that people do not frequently use the park in late autumn and winter; thus, it would provide a more stable detection opportunity. In addition, during the late autumn and winter, the natural food sources are low. Therefore, the animals would accumulate in green areas with denser natural cover.



Map 1. Location of camera trap stations

A total of six passive infrared cameras (RECONYX UXR6) were used to detect mammal species that were previously expected to occur in the area (Table 2). The cameras were mainly set to detect the presence of golden jackals; furthermore, the presence of raccoon, red fox, wild cat (*Felis silvestris* Schreber, 1777), European badger (*Meles meles* Linnaeus, 1758), and stone marten (*Martes foina* Erxleben, 1777) was also anticipated. The cameras were mounted near the river and water bodies next to the dirt roads and passageways where tracks or faeces of these mammals were previously detected. The cameras were placed in a weather-resistant casing that protected the device from harsh conditions and mounted at the stations at an average height of 60-70 cm from the ground. The cameras were operated non-stop after deployment and checked every 4-5 weeks

to download the pictures captured in the previous survey period and replace batteries or SD cards if necessary.

Table 2. Specifications of the utilised cameras.

Reconyx UltraFire XR6				
Night time illumination	NoGlow TM Covert Infrared up to 24m			
Image Resolution	up to 8.0 MP			
Trigger/Recovery Speed	1.08/3.4 sec			
Detection range	up to 21m			
Detection angle	44.8°			
Field of view angle	40.7°			
Battery power consumption (Resting/Daytime/Night time)	0.18mW/4.31Ws/8.22Ws			
source: Reconyx.com and Trailcampro.com				

The cameras were placed, on average, 340 m apart, with minimum and maximum distances of approximately 285-532m. A GARMIN eTrex 25 GPS device recorded the geographic positions of all camera trap locations (Map 1).

3.2.2.3. Data Analyses

Images recorded by the six camera traps were manually labelled by their corresponding time and date extracted from the image metadata. Species were identified after visual inspection of the images; none of the detections were excluded due to false or ambiguous identification. These detections, with their timestamp, related camera ID, and season information were structured in a tabular format for further analysis. A threshold of 30 minutes was used to separate temporally independent detections based on the review of Sollmann (2018), who found high variability among studies in this regard. Still, this timeframe was common in most camera-trap-based studies. Therefore, consecutive images of the same species within 30 minutes were excluded from the dataset. Given that the study aim was to detect species presence, and that the terrestrial mammals are easy to recognise, we did not utilise multiple cameras on the same site and instead established one camera per sampling site. This setup was further favoured due to its cost efficiency.

Most of the analyses were performed in R software (R Development Core Team, 2021) using Chris Beirne's technical material from WildCo Lab (Beirne, 2023). This online book provided an efficient solution to making basic predictions about the densities of the detected mammal species.

For the spatial evaluation, the total number of detections was visualized in a map for each species, which provided an eligible sample size (No. captures) to find potential differences in the space use of those mammals. The efficiency of detections was expressed in a detection rate form: a metric where the number of detections was expressed relative to survey effort (camera trap days), for temporal evaluation we used this detection rate after generalizing it to detections per 100 camera trap days to allow comparisons.

Based on the corresponding timestamps of detections, the diel activity patterns of the occurring species were also visualized using the package *activity* (Rowcliffe 2023) in R. The tool uses a nonparametric kernel density function to estimate species' activity as a continuous distribution over the wrapped 24-hour cycle (Frey et al., 2017). This method allowed intra-species comparisons by evaluating seasonal differences in activity, just as it allowed inter-species comparisons by contrasting the daily activity cycle of a species pair.

3.2.2.4. Statistical Analyses

The activity cycles of a species between seasons and between species are statistically compared by calculating the coefficient of overlap ($\hat{\Delta}_4$), which estimates a symmetrical overlapping coefficient between two kernel density functions using a total variation distance function (Frey et al., 2017). The coefficient ranges from $0 \le \hat{\Delta}_4 \le 1$, where 0 means total temporal segregation, and 1 as complete overlap (Ridout & Linkie 2009).

The spatiotemporal co-occurrence of detected species was evaluated by implementing a joint species distribution model (Tikhonov et al., 2019) under a Bayesian framework with Gibbs Markov chain Monte Carlo (MCMC) sampling using the *Hmsc* package (Tikhonov et al., 2022). The MCMC algorithm is essential to many Bayesian statistical approaches since these models are too complex for classical analytical solutions (Soriano, 2022). This algorithm enables sampling from the so-called posterior distribution which - in broad terms - describes the change of the response variable in function of the explanatory variable(s). The joint species distribution model also provides probability distributions for different species pairs that can be visualized in a species association matrix, where colours denote the magnitude of co-occurrence of a species pair. These values range -1 to 1, where -1 indicates that the species were unlikely to occur in the same time period and place, while 1 means the opposite. By this method, we can get more insight into the habitat use and the potential niche-segregation of the detected mammal species.

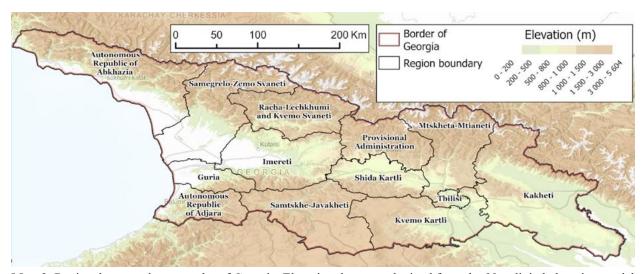
3.2.3. Bioacoustics Survey

3.2.3.1. - Study Site

Bioacoustical surveys were conducted in 7 regions of Georgia to represent all common environmental features in the country, including the variability of land cover and elevation (Map 2 & Table 1).

- Adjara is a relatively small region in Georgia, covering an area of 2,880 km². It has one of the highest population densities in the country, with 115.9 residents per square kilometre. The region is predominantly forested, with 82% of its land primarily composed of Colchic broadleaf forests, dominated by species such as Oriental beech (Fagus orientalis Lipsky), chestnut (Castanea sativa Miller, 1768), and hornbeam species (Carpinus spp.). Grasslands occupy 15.4% of the area, while cropland and built-up areas are minimal, accounting for only 0.6% and 1.2%, respectively. Water bodies are scarce, covering just 0.3% of the region.
- Imereti, one of the larger regions, spans 6,475 km² and has a population density of 82.5 residents per square kilometre. Forests cover 78.2% of the land, mainly in mountainous landscapes up to 2,850 meters above sea level. Imereti's forests are a mix of broadleaf deciduous forests and mixed forests. Oriental beech and several oak species (Quercus spp.) are common in upland areas, while lowlands may feature more diverse deciduous species, including hornbeam and elm species (Ulmus spp.). Grasslands are also significant, comprising 15% of the area, while cropland accounts for 4.5%. Built areas are limited to 1.3%, and water bodies are minimal at 0.6%.
- Kakheti is the largest region in Georgia, covering 11,311 km². Despite its size, it has a relatively low population density of 28.2 residents/km². The region's land cover is diverse with semi-deserts, evergreen forests as well as the subalpine vegetation commonly found throughout the area, with forests making up 35.1%; Kakheti's forests are predominantly oak forests with species like Georgian oak (*Quercus iberica* (Steven ex M.Bieb.) Krassiln., 1968), especially in the drier lowlands and foothills. In higher elevations, there are some areas of beech forests. The region's arid climate limits the extent of forest cover compared to wetter regions. Cropland is also significant, occupying 21.6% of the area, while shrubland accounts for 4.4%. Built-up areas and water bodies are limited, covering 1.1% and 0.4%, respectively.
- **Kvemo Kartli** spans 6,072 km² and has a population density of 69.8 residents per square kilometer. Grasslands dominate the region, covering 49.5% of the area, while forests are less prominent, making up 28.9%. Cropland occupies 16.7%, and the built-up areas account for 2.5%. Water bodies and shrubland are minimal, covering 0.7% and 1.2%, respectively. Kvemo Kartli is characterized by dry oak forests and shrubby woodlands, reflecting the semi-arid climate. Species like Georgian oak dominate the landscape, with junipers (*Juniperus* spp.) occurring in drier and more open areas.

- Racha-Lechkhumi and Kvemo Svaneti is one of the most sparsely populated regions, with a density of just 6.4 residents per square kilometer across its 4,990 km². The region is heavily forested, with forests covering 68.4% of the area. The forests in this region are largely mountain beech forests, transitioning to coniferous forests at higher elevations, including Caucasian fir (*Abies nordmanniana* Spach, 1841) and Caucasian spruce (*Picea orientalis* Link, 1847). These are among the densest and most pristine forests in Georgia. Grasslands make up 24.3%, while cropland and built-up areas are negligible at 0.1% each. Water bodies account for 0.6% of the region.
- Samegrelo is located on the border of the subtropical and temperate zones, where the proximity of the Black Sea greatly influences the air quality. The region holds 7,440 km² and has a population density of 44.5 residents per square kilometer. Forests are the predominant land cover, comprising 59.6% of the area. Oriental beech, chestnut, and oak are common, with dense understory vegetation due to the region's high rainfall. Higher altitudes feature spruce and fir. Grasslands and cropland account for 22.3% and 4.7%, respectively. Built-up areas and water bodies occupy 0.7% and 1.1% of the land, respectively.
- Samtskhe-Javakheti spans 6,413 km² and has a low population density of 25 residents per square kilometer. Grasslands dominate the region, covering 59% of the area, while forests account for 30.2%. Cropland is also significant, occupying 7.8% of the land, while built-up areas and water bodies are minimal, at 0.7% and 1.5%, respectively.



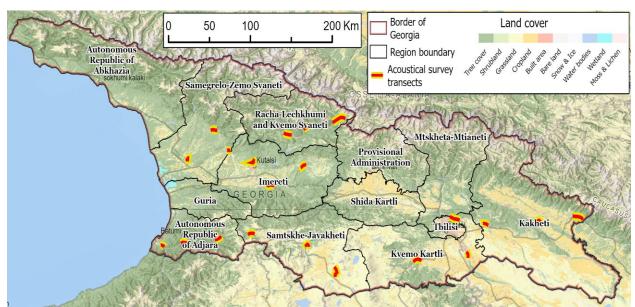
Map 2. Regional map and topography of Georgia. Elevation data was obtained from the 90m digital elevation model of EarthEnv (Robinson et al., 2014). Bioacoustical surveys were conducted in: Adjara, Imereti, Kakheti, Kvemo Kartli, Racha, Samegrelo, and Samtskhe-Javakheti.

3.2.3.2. - Data Collection

The bio-acoustic stimulation has already been successfully used in golden jackal research throughout Europe (e.g., Giannatos et al., 2005; Krofel 2009; Lapini et al., 2009; Szabó et al.,

2009; Banea et al., 2012; Comazzi et al., 2016). The howls are most of the time quite distinguishable from other canids, as a result of which this non-invasive method is a great asset in determining the territorial groups and, indirectly, single individuals. Vagrant individuals are less likely to answer. The golden jackal exhibits complex and diverse types of vocalizations, which can be distinguished either as single or group howls (Jhala & Moehlman 2004) that serve as a tool to reinforce and maintain group cohesion. These howls are vital in finding a mate for reproduction and for territorial defense and become more frequent during the reproductive period (Comazzi et al., 2016). Acosta-Pankov et al. (2018) identified a relationship between the howling occurrence and the season, reporting the highest period of howling between September and December in Europe. However, in the Caucasus, jackals howl more during the paring period in late winter (Dinnik 1914). Giannatos et al. (2005) concluded that solitary individuals tend to excerpt vocalization less frequently compared to adult individuals living in groups. This may be due to their young age or attempt to avoid fights with resident packs.

For this study, seven regions were selected to conduct bioacoustical surveys for the golden jackal (Map 3). The selected areas were Adjara (2,880 km²), Imereti (6,516 km²), Kakheti (11,310 km²), Racha (2,893 km²), Samegrelo (7,468 km²), Samtskhe-Javakheti (6,413 km²) and Kvemo Kartli (6,527 km²). In every region, we established three 10km long transects with five broadcasting points on each to survey for the golden jackal (21 transects and 105 points in total, Map 3).



Map 3. The location of transects for bioacoustical surveys in the seven regions and Georgia's dominant land cover types. Land cover data was obtained from the ESA Worldwide Land Cover Mapping (Zanaga et al., 2022).

There is no actual data for the abundance of golden jackals or wolves in these regions, nor information on the density of other carnivores that may compete for resources in the studied areas. We retrieved the hunting bag statistics from the Ministry of Environmental Protection and Agriculture of Georgia, which gives a vague idea of the carnivore numbers in each region, as presented in Table 3, and indicates a relatively inefficient culling of wolf and golden jackal.

Table 3. The total number of received and granted requests to harvest problematic individuals between 2015 - 2020 in Guria (Ozurgeti, Chokhatauri), Samegrelo (Martvili, Senaki, Khobi, Tsalenjikha), Adjara (Kobuleti), Imereti (Terjola, Zestafoni, Baghdadi). Source: Georgian Ministry of Environmental Protection of Georgia, 2024 records.

	Wolf	Jackal	Fox	Bear
Requested	740	433	8	2
Harvested	134	80	0	0

To provoke jackals' response along the transects of the study area, we used a calling survey method that combined acoustic and visual observations of jackals after stimulation with playback howls by following the methods of (Giannatos et al., 2005). With a mean distance of 1.8 km (min-max: 0.62 to 3.3 km), the broadcasting points were established along these transects where the pre-recorded jackal howls were played using a 50 Watts power megaphone (PULE PMP57LIA) which included a USB, SD and MP3 player software. The call that was used for broadcasting was 30 seconds in duration and was recorded in Eastern Georgia in June 2020 near the town of Telavi. Following every 30-second broadcast, we kept a 3-minute pause to observe potential responses. In case of no response, the procedure of broadcasting and pausing was repeated five times per individual station; once a response was registered, we determined the direction of the call using a compass. The same recording was used throughout all the broadcasting stations. In addition to the howls, we collected data on the weather, and if the wolf responded instead of the golden jackal, we recorded that as well.

The survey was conducted between June and November 2021. The fieldwork aimed to identify only the species present, so the procedure was not repeated over the following months.

3.2.3.3. - Data Analyses

My first goal was to estimate the individual density of golden jackals across the seven regions of Georgia where the surveys were conducted (Table 1). To effectively determine the individual density, a few assumptions were made based on the specialties of bioacoustic stimulation as a method and on the territorial behavior of the species. Since golden jackals typically live in groups, they tend to vocalize in response to nearby calls when they exhibit assertive territorial behavior (Comazzi et al., 2016); each recorded vocal response was interpreted as evidence of a distinct social group within the detection area. A single vocal response represented a single individual, whereas multiple responses were assumed to be a group of four individuals. An average group size of four individuals is the most widely reported group size (Macdonald 1979; Giannatos et al., 2005; Negi 2014; Trbojević et al., 2018). This group-size assumption provides a basis for calculating population density across multiple spatial scales.

Our study design goes in line with that of Acosta-Pankov et al. (2018), who also based their study design on the findings of Giannatos et al. (2005) that determined the maximum human hearing distance on windless nights from a vantage point in open terrain with no background noise at 1.8 – 2 km. In light of this, the population density estimates were calculated at three detection areas around the testing site with a radius of 1 km, 1.5 km, and 2 km buffer areas. By using this three-level approach, we aimed to represent the variation and restrictions in detection ability, which can be intrinsic or originate from environmental barriers such as the relief, the surrounding mountainous area, or other background noise, which can significantly reduce the distance where jackals can be heard from. The density estimates from each of these scales were then extrapolated across the entire area of the sampled region, enabling a broader assessment of the regional population. This extrapolation involved calculating the average density per square kilometer and applying it to the total surveyed area.

To project population growth, based on the extrapolated density estimates, assumptions were made about the sex composition and reproductive behavior of the population.

- For sex ratio, we assumed a balanced sex ratio, with 50% of the individuals of the population female, a common assumption in carnivore population studies (Csányi & Sándor, 2024).
- To model reproductive potential, two reproductive activity levels were assumed: a **Low Reproductive Population Rate** where 35% of the female population was thought to be reproductively active and a **High Reproductive Population Rate** where 65% of the female population was assumed to be reproductively active (Vlasseva et al., 2020).

These assumptions allowed the estimation of potential breeding females, which directly influenced the population growth projections:

- To complete the growth model, it was assumed that each reproductively active female gave birth to an average of five pups per breeding cycle, based on typical litter sizes reported for golden jackals and the pups' 50% survival rate (Moehlman 1987; Stoyanov 2012).
- An estimate of the annual population growth was generated by multiplying the estimated number of active females by five. This value served as the projected increase in population size under each reproductive scenario, providing insight into potential population growth rates over time. It is important to note that hunting pressure was not included in the model for analyses, as the harvest efficiency in Georgia is low, (as shown in Table 1, Appendix 1) which would add further uncertainties to my estimation if the hunting pressure were incorporated.

My second goal was to evaluate and analyze the underlying environmental factors influencing jackal occurrence. For this purpose, detections registered at the broadcasting points (both individual and group responses) were coded into a presence/absence (1/0) form independent of how many jackal howls were heard at each point. I used the widest area of detection with a radius

of 2 km (12.57 km²) to calculate the percentage cover of land cover types, the mean value of elevation, and the terrain ruggedness index, which functioned as covariates. In addition, the sampling points' distance from the nearest settlement and the actual weather conditions (mean daily temperature and total precipitation) were also utilized as explanatory variables, just as the registered wolf howls along the transect (Table 4). Since wolves were also detected during the surveys by "responding" to the calls sometimes, their potential competition with jackals must be considered in jackal occurrence modeling.

Table 4. List of the used covariates to assess golden jackal occurrence.

variable name	description	unit	source
land cover data	Percentage cover of land cover types in the 2km buffer area: 1) Tree cover; 2) Shrubland; 3) Grassland; 4) Cropland; 5) Built area; 6) Bare land; 7) Snow and ice; 8) Water bodies; 9) Wetland.	%	ESA Worldwide Land Cover Mapping 2021 (Zanaga et al., 2022)
elevation data	Rasterized elevation data derived from the smoothed 90m digital elevation model (DEM).	meter	EarthEnv-DEM90 (Robinson et al., 2014)
Terrain Ruggedness Index (TRI)	The amount of elevation difference between adjacent cells of a DEM that quantifies topographic heterogeneity.	Calculated from the DEM raster for each cell by averaging the absolute difference between the center and the surrounding cells.	Riley et al., 1999; QGis Desktop 3.34.10. Raster Analysis toolset
Distance from settlement	The distance of a broadcasting point from the nearest settlement.	meter	OpenStreetMap Foundation (OSMF, CC BY 4.0)
Weather conditions	Registered daily mean temperature and total precipitation data for the actual day and location of the survey.	°C and mm	openmeteo package for R, Open Meteo API (Pisel 2023)

audio signal along a transect.

3.2.3.4. - Statistical Analyses

For modeling golden jackal occurrence in the function of the covariates mentioned above, I implemented a generalized linear mixed model (GLMM) in R with the *glmmTMB* package (Brooks et al., 2017). The presence/absence of jackal (based on responses to playback calls) was used as a dichotomous response variable. In contrast, the set of explanatory variables from Table 4 were selected with a stepwise selection method during model fitting. All explanatory variables were scaled and filtered for multicollinearity. Due to the spatial hierarchy and to handle potential non-independence, survey transects, and their corresponding regions were added as random effects. The best model version was selected with likelihood ratio tests.

After the best model was found, predictions were made by the *sjPlot* package (Lüdecke, 2024) to explain the relationship and magnitude of the suitable explanatory variables on jackal occurrence probability. These predictions were generalized and visualized in a 10 × 10km UTM grid covering Georgia obtained from the Military Grid Reference System (MGRS, 2024). In addition, the predictive process and the created map were updated with the direct visual detections of wolves reported by the Ministry of Environmental Protection and Agriculture of Georgia. These reports functioned as weights when predictions were calculated at a regional scale.

4. RESULTS

The *Results* chapter presents the findings from both the literature review and the fieldwork conducted in Georgia. It summarizes the outcomes of each methodological approach, including citizen science surveys, camera trapping, and bioacoustic monitoring. The chapter provides insights into the spatial and temporal distribution of carnivore species, evaluates patterns of species co-occurrence, and models environmental factors influencing predator presence. Each subsection highlights key observations relevant to the study's objectives and hypotheses.

4.1. Literature Review

Most of the articles were published during the 2000s, reaching a peak after 2010, when studies on wolves and jackals gained more interest (Figure 1). Compared to wolf and golden jackal, stray dog studies were comparatively rare.

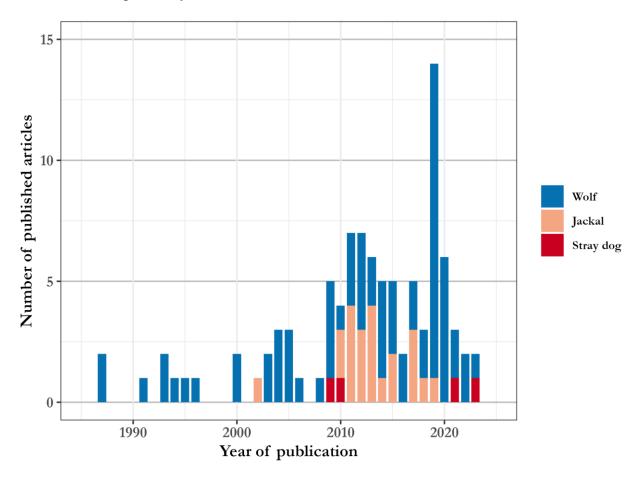
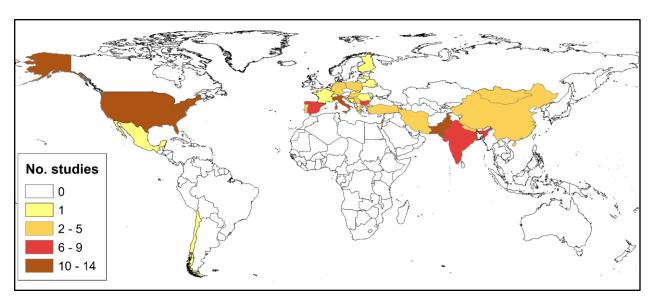


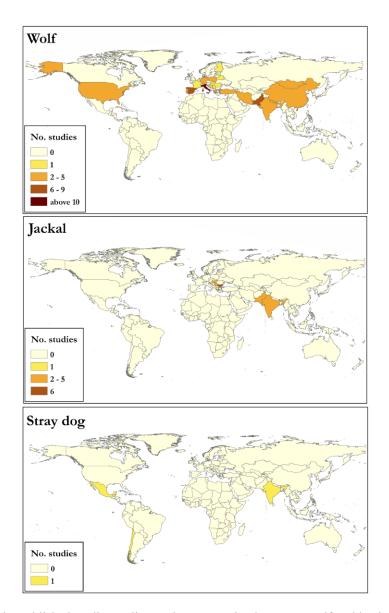
Figure 1. Scientific articles on carnivore livestock predation published yearly (from 1987 to 2023). The figure incorporates articles that were used for statistical analysis (N=97). See Appendix II for the list of used articles.

Most of the studies (84%) were based on scat samples, while the studies based on stomach samples were 16%. Altogether, the 97 studies originated from 29 countries. We found more than 10 studies from Italy and Pakistan and more than five from India, Spain, and Bulgaria (Map 4).



Map 4. Location of the published research performed on livestock consumption by canid predators. (The map is based only on papers included in the statistical analysis).

Approximately 55% of the countries (16 out of 29) were represented by only two or one publication about wild canines vs. livestock interactions.



Map 5. Location of the published studies on livestock consumption by a grey wolf, golden jackal, and a stray dog. (The map is based only on papers included in the statistical analysis).

Considering the analyzed papers, the impact of wolves on livestock was the most studied worldwide among the three canids: 71% of the papers (75 articles out of 105) were related to wolves. Especially Italy (N=13), Spain, and Pakistan (both N=7) gave place for these types of studies. Still, a significant number of articles originated from India, Iran, Poland, Portugal, the USA (all N=4), and Mongolia (N=3). Most jackal studies were conducted in Bulgaria and Pakistan (N=6 and 4, respectively). The query found more than one golden jackal-related study on livestock consumption in Hungary, India, and Serbia (N=3). The stray dog diet was scarcely studied worldwide and almost disappeared in this context (Map 5).

4.1.1. Frequency of Total Livestock Consumption by Canid Species

Considering all observations (N=423), we found that the wolf (N=300 observations) was the most frequently reported canid species that consumed livestock, followed by the golden jackal (N=104) and stray dog (N=19, Figure 2).

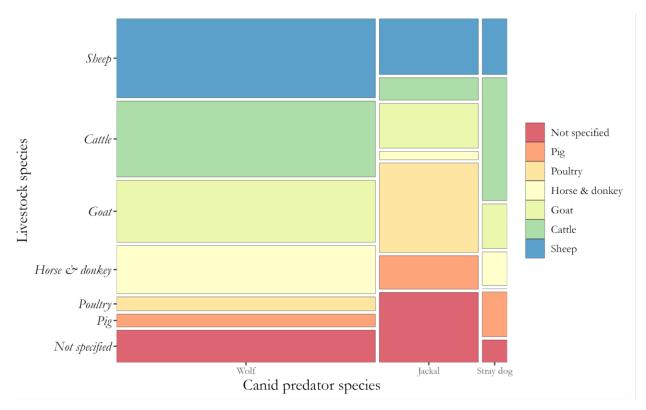


Figure 2. The relative distribution of livestock species reported as consumed by the canid species of interest in the articles. The height and width of each rectangle represent the relative proportion of the contrasting categories, i.e., how many times each livestock-predator pair occurred in the studies (number of observations).

We found that the overall livestock consumption (Figure 3) was significantly different among canid species when maximal consumption rates were compared based on the frequency of occurrence data (Kruskal-Wallis test: H(2)=17.2, p=0.002). The Dunn post hoc test revealed a significant difference between wolf (%O median = 32, interquartile range = 57) and jackal (%O median = 9.9, IQR = 23.4, p=0.002, Table 5).

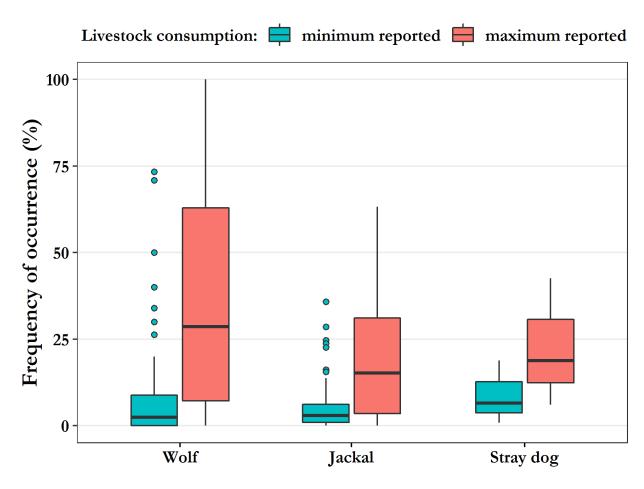


Figure 3. Minimal and maximal livestock consumption of canids based on the reported frequency of occurrence data.

The minimal consumption rates were statistically similar among canids (H(2)=1.4, p=0.8).

Table 5. Mean rank difference and their 95% confidence intervals for the significant pairwise comparisons. %O - frequency of occurrence data; %B - percentage of biomass data. **Bold** text indicates which group had higher mean rank scores in the comparison.

			_	95% Confidence interval		
group	metric	comparison	mean rank differenc e	lower	upper	p
livestock	max. %O	jackal vs. wolf	-28.15	-49.76	-6.53	0.003

wolf	%O	horse/donkey vs. cattle	-44.07	-86.49	-1.64	0.03
wolf	%O	horse/donkey vs. goat	-58.64	102.27	-15.02	0.001
wolf	%B	cattle vs. poultry	51.18	7.79	94.57	0.008
wolf	%B	cattle vs. sheep	31.03	2.53	59.52	0.021
jackal	%O	horse/donkey vs. pig	-49.83	-94.91	-4.76	0.017
jackal	%O	pig vs. sheep	28.37	1.32	55.41	0.031
jackal	%B	pig vs. poultry	22.02	5.48	38.58	0.001

No %B data was reported in the case of stray dogs. Therefore, the comparison was made between wolf and jackal only, but no difference was revealed between them for the total biomass data (Mann-Whitney test: U=394, p=0.51). The median was above 50% for jackals and under 25% for wolves (Figure 4). However, we have to consider that potential scavenging was frequently reported in the relevant studies: 3 out of 5 for jackals (60%) and 14 out of 31 studies for wolves (45%).

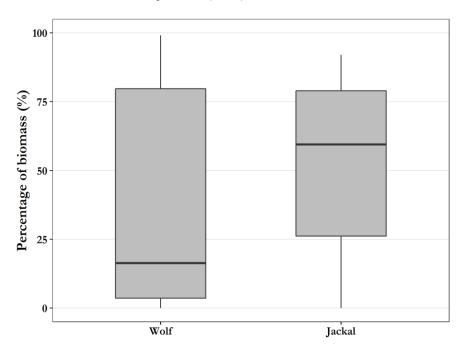


Figure 4. Livestock consumption per carnivore species as shown by the percentage of biomass.

4.1.2. Consumption of Various Livestock Species by Canid Species

Sheep (N=91, 22% of observations) and cattle (N=84, 20% of observations) were the most frequently reported livestock species consumed the most by canids. Goats were the third most reported species (N=77, 18% of observations). Horse and donkey (N=52, 12% of observations), poultry (N=44, 10% of observations), and pigs (N=25, 6% of observations) were less often mentioned (Figure 5).

The reported %O data significantly differed among livestock species groups in the wolf's diet (Figure 5, H(5)=19.42, p=0.002). Based on 300 reported observations, the %O of equines (mostly horse and donkey, median = 3.6, IQR = 11) was significantly less from cattle (median = 12, IQR = 15.6, p=0.03) and goat (median = 10.2, IQR = 23.2, p=0.001, Table 5).

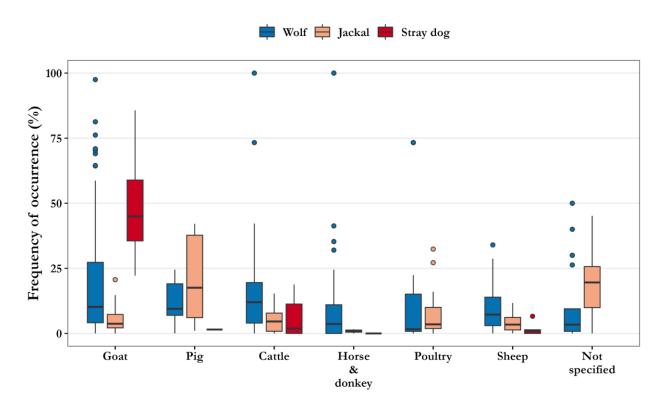


Figure 5. Consumption of livestock species by wolf, golden jackal and stray dog as shown by the frequency of occurrence.

Significant differences were also revealed in the %B data for wolves (Figure 6) based on 129 observations (H(5)=18.3, p=0.003), where the consumed biomass of cattle (median = 16.8, IQR = 46.4) was significantly higher than that of poultry (median = 0.1, IQR = 10.1, p=0.008) and sheep (median = 4.9, IQR = 9.5, p=0.019, Table 5).

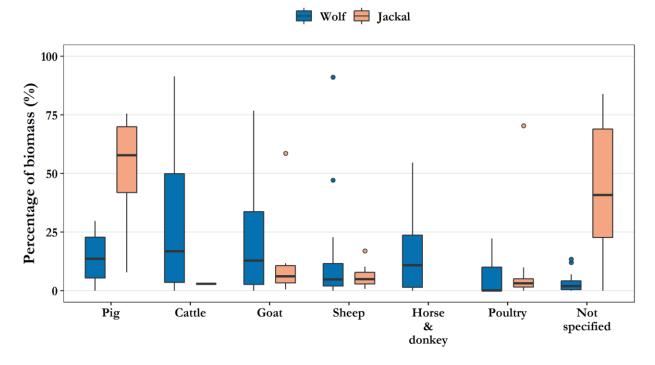


Figure 6. Consumption of livestock species by wolf and golden jackal as shown by the percentage of biomass.

Regarding to jackal (N=104 observations) %O data (H(5)=15.8, p=0.007), the consumption of pig (median = 18, IQR = 31.7) was significantly higher than equines (median = 1, IQR = 0.8, p=0.018) and sheep (median = 3.4, IQR = 4.8, p=0.03) (Figure 5). Pairwise comparisons on %B data (N=45 observations) revealed statistical difference between pig (median = 57.8, IQR = 28.1) vs. poultry (median = 3.2, IQR = 3.5, p<0.001) consumption (H(4)=15.67, p=0.004, Figure 6, Table 5).

The %O data of stray dogs' livestock consumption showed no difference between livestock species. Testing on biomass data was impossible due to the lack of adequate data.

4.2. Citizen Science

Based on voluntary responses, the survey conducted among rural residents revealed significant insights into their experiences with carnivores in the sampled regions. With 2000 individual surveys distributed across the country, we received 947 survey responses (47% response rate) documenting the perspectives of the local communities. The surveys were conducted in Mtskheta-Tianeti (response rate of the region: 25.3%), Tbilisi (36.8%), Guria (98.9%), Samtskhe-Javakheti (31.3%), Kakheti (96.2%), Lower Kartli (85.7%), Adjara (17%), Imereti (81.8%), Svaneti (19.8%), Lower Svaneti (14.3%), and Inner Kartli (13.2%). The majority of the respondents were male (77%) between the age interval of 35-44. Figure 7 shows the distribution of the gender and age of the respondents. The most active age groups of the respondents were 35-44 (28.2%) and 45-54 (26%); the majority of the respondents had a high school degree (34.02%), and only a few were post-graduates (11.49%). It is essential to highlight that since the respondents could select

multiple answers, we expressed the percentages per question based on the total number of answers. Therefore, the results presented are not the reflection of the respondents but of the answers per individual question.

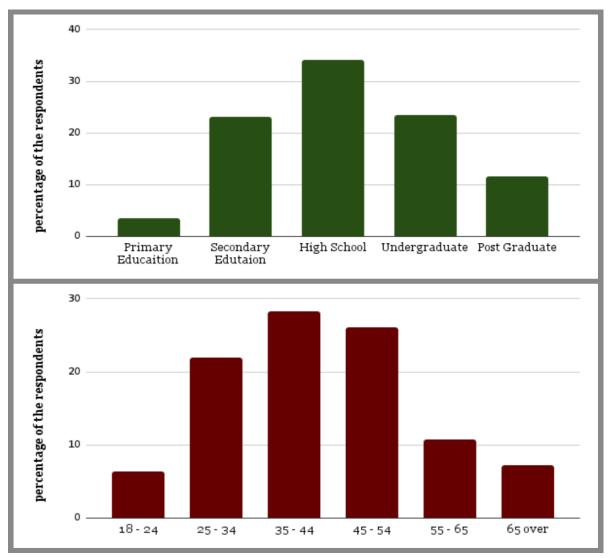


Figure 7: Education level and the age distribution groups of the respondents.

We collected 1,756 answers for **Question 1**, which asked about **the predator species they have sighted the most in their respective regions**. 49% of the answers identified the *golden jackal* as the species that were encountered the most often, followed by the *wolf* (40%), *brown bear* (4%), and *other* carnivore species (6.8%). Similarly, for **Question 10**, for which we collected 1,687 answers and asked **which of the predator species the local respondents have sighted the most in the past year**, 49.7% indicated that the *golden jackal* was the most sighted species, followed by the *wolf* (38.2%), *other* predators (6.3%), and *brown bear* (5.6%).

Question 5, to which we collected a total of 1,713 answers, asked about the most problematic predator species that occur in their respective regions 49.6% of the answers identified the golden jackal as the most problematic predator, followed by 40.5% of the responses identifying the wolf, while only 4.6% noting the brown bear. Similarly, for Question 2, for which we collected 1,725 answers, golden jackals (47%) and wolves (47.3%) were the most noted species the respondents have seen or heard attack domestic livestock in their region. In contrast, the brown bear only accounted for 5% of these attacks. When asked in Question 3 if any of these species were seen to have attacked or in any way disturbed humans, out of 1,359 total answers, 47.3% and 44% noted that golden jackal and wolf, respectively, were the carnivores that disturbed or otherwise caused local communities discomfort.

None of the answers given to the above mentioned questions were independent from the location of the respondents. The generally most sighted predator species, golden jackal was indeed commonly reported in Samegrelo (67%), Guria (54%), Kakheti (52%), Kvemo Kartli (52%); while only 2% of respondents found it problematic in Racha Lechkhumi. Instead, reports about wolves reached the 50% of responses here, just like it was registered in Adjara (56%). This regional variability was also captured by the independence test both for golden jackal ($\chi^2 = 43.6$, df = 10, p < 0.001) and grey wolf ($\chi^2 = 54.9$, df = 10, p < 0.001).

Reported attacks on domestic livestock had higher regional variability for golden jackal (min. 0% in Racha - max. 60% in Adjara) than wolf (min. 29% in Kvemo Kartli - max. 51% in Racha). Answers on both species were non-independent by region (jackal: $\chi^2 = 71.5$, df = 10, p < 0.001; wolf: $\chi^2 = 29$, df = 10, p = 0.001). It is important to note that 49% of the answers reported bears as primary predators of livestock after wolves (51%) in Racha Lechkhumi, and none of the answers reported golden jackal here.

Distribution of answers on Question 3 can be described with almost the same pattern. Observed or known attacks on humans had much higher range regarding golden jackal (min. 0% in Racha - max. 66% in Adjara) than wolf (min. 28% in Adjara - max. 55% in Guria). Racha Lechkhumi also had the highest reported bear attacks (52%) before wolves (48%). The distribution of answers were significantly associated with the regions surveyed (jackal: $\chi^2 = 69.1$, df = 10, p < 0.001; wolf: $\chi^2 = 51$, df = 10, p < 0.001).

To see which season was the most critical for the local communities with large carnivore disturbances (Question 4), we collected 2,416 answers which showed that the most critical season was *Winter* (32.4%), followed by *Autumn* (30.3%), *Spring* (24.6%) and *Summer* (12.7%).

Question 8, for which we collected 2,056 responses, showed that *domestic birds* (39.4%) and *livestock* (38.5%) were the most frequent types of damage inflicted by predators that local respondents had either experienced themselves or heard about from another source. *Harvest destruction* was also noted as damage caused by carnivore species, as indicated by 18% of the responses. However, Question 6 further explored the damage predators inflicted on personal belongings; for example, cars, houses, and gardens. According to the 1,605 responses received, 48.8% indicated damage caused by *golden jackals*, 40.1% by *wolves* and 4.6% by *bears*, while 6.4% of the damages were attributed to *other* carnivore species.

Reports about damages on personal belongings were nearly the same regarding golden jackal (38 - 57%) among regions with one exception: Racha, where only 2% of these damages was connected to the species while bears and wolves had the same frequency of reports (49% for both). Guria had the second highest reports about bears in this regard (11%). Reports on wolves never decreased under 25% regionally (min. 28% in Kvemo Kartli - max. 50% in Guria). Frequencies were not independent by regions for jackal ($\chi^2 = 76.7$, df = 10, p < 0.001) nor wolf ($\chi^2 = 81.2$, df = 10, p < 0.001). Besides these characteristic species, the reported frequency of *other species* was notably high in Tbilisi (20%). Due to the specifications of the questionnaire the exact species can be only assumed in this case, but racoon might be a decent guess in this highly urbanized region (Figure 11).

Afterward, the questionnaire asked what measures the locals undertake once the damage has been inflicted to rid themselves of the disturbance from the large predators in the future. Out of 938 answers we gathered for Question 7, 41.1% of the answers indicated that they take no action against the problem predators. In contrast, 35.1% indicated that they take matters into their own hands to eliminate the individual. Only 12.8% noted that they had filed a report to the local authority, and 11% indicated they had called the emergency services for further assistance. Those responses that chose no action mainly originated from Tbilisi (76%) and Kakheti region (63%); while none of the respondents answered with no action in Adjara, Samegrelo, Racha-Lechkhumi and Shida Kartli. Interestingly, not all of these regions had chosen self prevention as the most common answer as it was anticipated (Adjara - 61%, Samegrelo - 62%, Racha-Lechkhumi - only 6%, Shida Kartli - 60%). For example, filing a report to local authority was the most frequent answer in Racha (94%); while self prevention was dominated in Mtskheta-Tianeti (75%) and Samtskhe-Javakheti (73%).

To further understand the personal opinion of the local communities regarding **the best method to prevent these damages in the future** out of 1,037 answers for **Question 9**, 83.1% of the local communities noted *hunting* to be the most effective method of managing the large carnivore populations followed by *guarding dogs* (14.3%), and *other methods* (2%). *Electric fences* were rarely specified, amounting to 0.5% of the responses. All respondents from Racha-Lechkhumi, Samegrelo and Shida Kartli voted for *hunting* without exception (100%); and even the lowest value in this regard among the regions was way higher than 50% (min. 69% in Adjara). Despite the overwhelming amount of votes for *hunting*, the answers were not independent of the regions ($\chi^2 = 62.3$, df = 7, p < 0.001).

4.3. Camera Trapping

4.3.1. General Observations

Throughout the study, 897 images were taken, and 203 provided a definite and well-identifiable image of at least one individual of the target species of interest. On average, the cameras recorded

25.41 images per day, with 5.81 detections of the target species daily. Due to maintenance and technical details, the number of deployed cameras varied each month, but in the middle periods of each season, 5-6 cameras were ensured to be online (Figure 8 left). This peak of active cameras occurred in February during Season 1 (N=5) and in November during Season 2 (N=6, Figure 8 left). The detections mainly were aligned with the camera trapping effort, i.e., the number of active cameras (Figure 8 right). Consequently, most detections were registered in February for season 1 (58 detections/100 trap days) and in November for season 2 (50 detections/100 trap days). However, on occasions when less than 5 cameras have functioned, the detection rate dropped down seemingly more than expected.

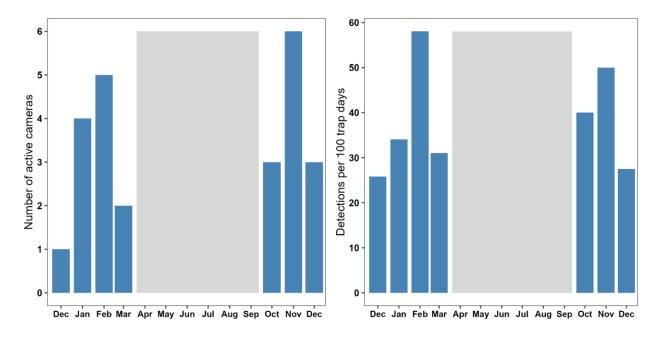


Figure 8: The number of active camera traps (left) and capture rates per month (right). The grey blocks indicate the period when cameras were inactive.

Considering the detection of focal species, the deployed cameras detected six frequently occurring mammal species in the Ponichala Nature Reserve (Figure 9). The majority of them were captured by each one of the cameras. Still, surprisingly, the free-ranging domestic species, namely dogs and cats, were the ones who were only detected by five cameras out of the six deployed (Figure 9 right). Despite some unclear detection, where the detected cats have a similar appearance to wildcats, these detections were identified as domestic cats (*Felis catus* Linnaeus, 1758) or "cat" without any further specification (*Felis* spp.) due to the proximity of the city and the highly urbanized environment. The other four detected mammal species are well known for their tolerance towards anthropogenic disturbances: golden jackal, red fox, raccoon, and stone marten, which appeared in all camera trap sites, achieving a 100% detection rate (Figure 9 right). The golden jackal was the most frequently observed species, recorded on 56 occasions in total (Figure 9 left). The second most common species was the raccoon (36 independent detections), an alien species present throughout Georgia. Free-ranging dogs and cats were only the 3rd (N=31) and 4th

(N=29) most common species, respectively. Elusive and well-adapted species such as the stone marten and red fox were the least common mammals in the study area, with 14 independent detections each (Figure 9 left), however, they still appeared in every camera trap site.

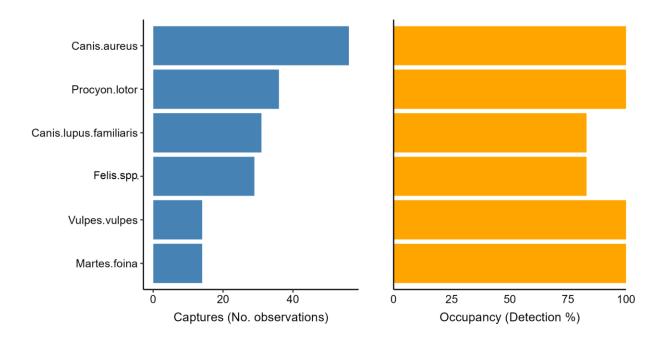


Figure 9: The total count of images per detected species (left) and the occurrence rate of the detected species (right) in the Ponichala Nature Reserve.

4.3.2. Spatial Distribution of Detections

Besides their high detection rate, golden jackals were frequently captured by the camera traps positioned in the northern part of the study area (Figure 10 left). The detections gradually decreased southbound from a maximal detection rate of 19.7 to 6.2 /100 trap days. On the contrary, cameras situated on the southern side of the Nature Reserve registered the bulk of the stray dog detections from a 9.9 to 11.3 detection rate (Figure 10 right), without any detection in the middle area. Dog appearance was much lower in the northern part of the study site (3.9 - 5.5 detection/100 trap days).

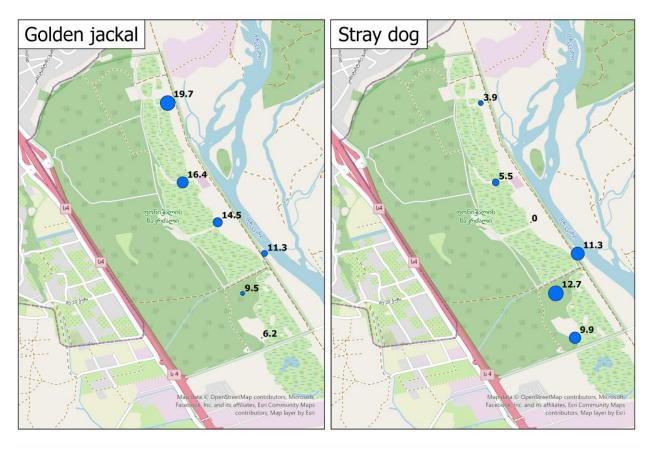


Figure 10: The spatial distribution of golden jackal (left) and stray dog detections (right) in the Ponichala Nature Reserve. The numbers mean the corresponding detection rate values calculated for each camera trap.

The presence of raccoons was the highest at camera 3 (detection rate: 18.3), placed closest to the riverbed (Figure 11 left), while the species appeared less frequently at the other camera trap sites, even though it used the whole area of the Nature Reserve.

Cats actively used the inner-middle parts of the study area (Figure 11 right) but were completely missing from those camera trap images that recorded the highest number of stray dog (Figure 10 right), stone marten (Figure 12 left), and red fox detections (Figure 12 right).



Figure 11: The spatial distribution of racoon (left) and cat detections (right) in the Ponichala Nature Reserve. The numbers mean the corresponding detection rate values calculated for each camera trap.

Stone marten also occurred in every location where camera traps were set up, and they were active in the north (max: 5.3 / 100 trap days) and the southern parts (max: 6.3 / 100 trap days) of the study site (Figure 12 left).

During the study, red fox detections concentrated on the southern side of the study area, with peaking detections at camera 5 (max: 6.3 detection rate); still, they also appeared before all camera traps (Figure 12 right).

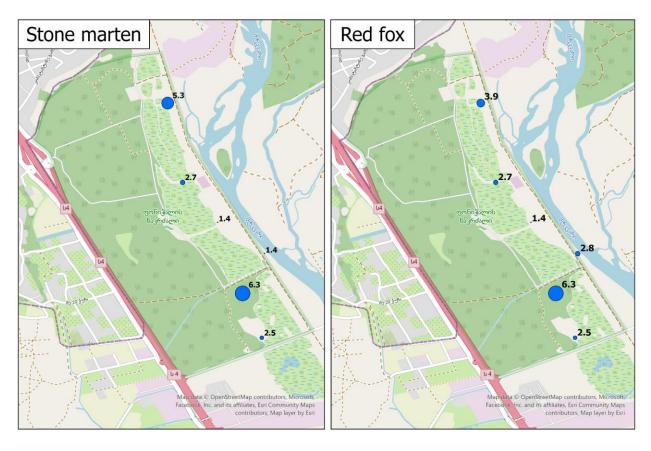


Figure 12: The spatial distribution of stone marten (left) and red fox detections (right) in the Ponichala Nature Reserve. The numbers mean the corresponding detection rate values calculated for each camera trap.

4.3.3. Temporal Distribution of Detections

Monthly detections

Considering the monthly detections of the species, the camera trapping effort (see Figure 8 left) is mostly represented in the case of the red fox (Figure 13 right) and the cat (Figure 14 left) since the intensity of their detections was notably increased when all camera traps operated in the area. Cameras recorded almost the same number of individuals of foxes in both seasons (6 vs. 8 individuals in total); while cat detections were much higher in the second season (11 vs. 25 individuals in total). There were months without any detections regarding these species: Specifically March and December 2021 for red foxes and December 2020 and October 2021 for cats.

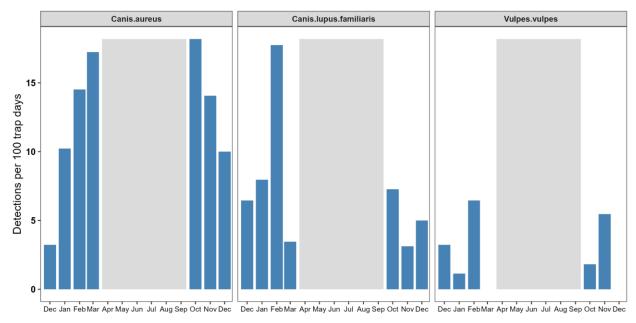


Figure 13: Monthly detection rates of golden jackal (left), dog (middle), and red fox (right) during the camera trapping in the Ponichala Nature Reserve. The grey blocks indicate the period when cameras were inactive.

The most common species, the golden jackal, provided an exceptional trend during the study, differing from any other registered species (Figure 13 left). Due to the technical pause of the camera trapping, the continuously increasing detection rate could not be monitored in the spring and summer of 2021. However, a peak in their activity can undoubtedly be presumed during that period, which could be the highest among the detected mammals (Figure 13 left). Altogether, 27 independent detections were registered in season 1 and 35 detections in season 2.

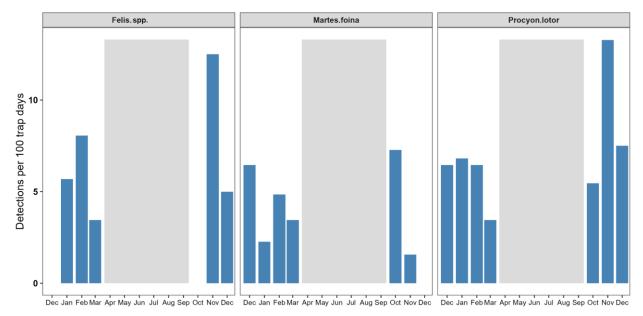


Figure 14: Monthly detection rates of cat (left), stone marten (middle) and racoon (right) during the camera trapping in the Ponichala Nature Reserve. The grey blocks indicate the time period when cameras were inactive.

Since free-ranging dogs primarily occupied different parts of the study area than golden jackals (see Figure 10), their monthly detection rates remained seemingly unaffected in season 1 (21 independent detections) than in season 2 (15 individuals). The proportion of group detections among all was highest in dogs, accounting for 23% of stray dog detections when 2 or 3 individuals were detected simultaneously.

Stone marten and raccoon had nearly random or stagnating detection rates in season 1. They became more variable in season 2, resulting in a complete decline in stone marten detections (Figure 14 middle) and indicating the highest registered peak in raccoon's temporal activity (Figure 14 right). This increase provided the third highest registered detection rate (13.3 detection /100 trap days) after golden jackals and stray dogs. It is also worth noting that cat activity was also high in November 2021 (Figure 14 left) when cameras detected several raccoons. Furthermore, their space use was similar in the study area (see Figure 11).

Daily activity

Based on the above-mentioned spatiotemporal aspects of detections, I focused on analyzing those species' diel activity cycles whose presence caused notable differences or similarities with others. These were the contrasting space use of golden jackal and dog (Figure 10) and the similar monthly detection rates and space use of racoon and cat (Figure 11). The activity patterns were demonstrated by kernel density functions and statistically evaluated using the coefficient of overlap ($\hat{\Delta}_4$) as described by Ridout and Linkie (2009) excluding December 2021 from the comparison to avoid duplicated months.

Contrasting the diel activity cycles of golden jackal and free-ranging dogs, an apparent shift can be observed between them (Figure 15). The highest activity of golden jackal was registered between 6 a.m. and 12 a.m. with an elongated peak activity. Dog detections got more intensive when jackal presence decreased, in the early afternoon from 1 p.m. to 5 p.m. Another but less intensive peak period was registered in the first half of night-time, just right after the jackal detections started to decrease, indicating an approximately 1-1.5 hour lag in peak activities between the two species.

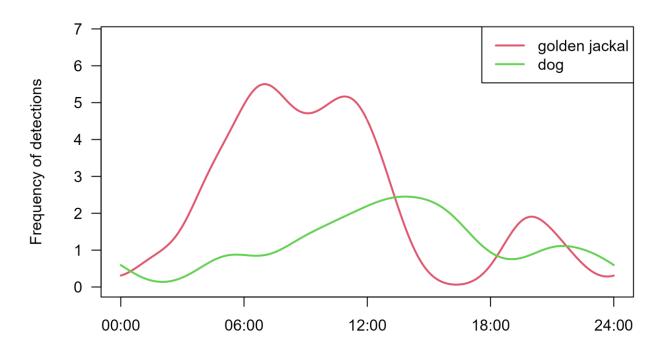


Figure 15: Kernel density estimation of the diel activity of golden jackal and free ranging dogs based on camera trap data.

The $\hat{\Delta}_4$ coefficient confirmed a significant but low overlap between the activity cycles ($\hat{\Delta}_4 = 0.6$, p = 0.001), since the probability of encounters between the species gradually increased during the first half of the day (Figure 15), and only the peak activity periods were segregated.

Based on the seasonal daily activity patterns, golden jackals were primarily active during twilight hours and early in the morning, with reduced activity in the afternoon and early evening. In season 1, they became active again around sunset and into the late evening. The same pattern was observed in season 2 with an approximately 2-3 hour delay (Figure 16).

Canis aureus

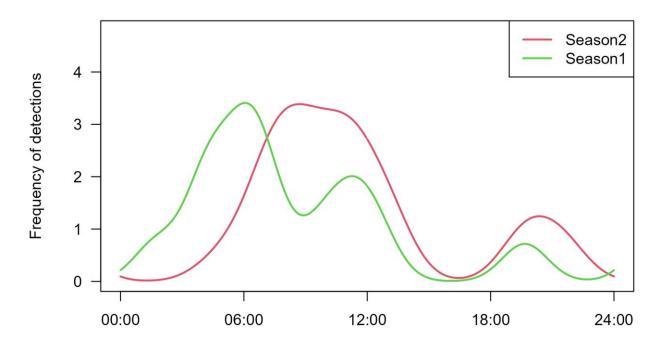


Figure 16. Kernel density estimation of the seasonal diel activity of golden jackal based on camera trap data.

In contrast, stray dogs were most frequently observed around noon in season 1 and became active again after sunset (Figure 17). In season two, their peak activity was shifted to later hours, between 3 and 4 p.m., when almost no golden jackals were sighted (see Figure 16). In the midnight and late night hours, stray dog activity reached its minimum (Figure 17).

Canis lupus familiaris

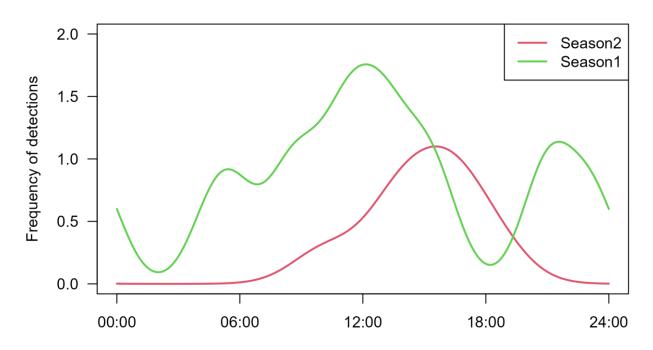


Figure 17: Kernel density estimation of the seasonal diel activity of free ranging dogs based on camera trap data.

By comparing the raccoon and cat activity cycles, the $\hat{\Delta}_4$ coefficients of overlap confirmed a significant but weak overlap between them ($\hat{\Delta}_4 = 0.59$, p = 0.006). The most distinct pattern of their activity is related to the specific and differing nocturnal behaviour (Figure 18) which was registered by the camera traps. Namely, raccoons were the most active during the night around 2 a.m. and 5 a.m. and their frequency of detection peaked around max. 1 individual during daylight. Cats appeared at the highest rate around 7 a.m. and 1 p.m. at the cameras, and their activity was dropped before nightfall (Figure 18), suggesting a rather diurnal behavior. However, their co-occurrence cannot be excluded considering their spatial (Figure 11) and temporal habitat use (Figure 18), which assumes potential encounters of the individuals from the two species.

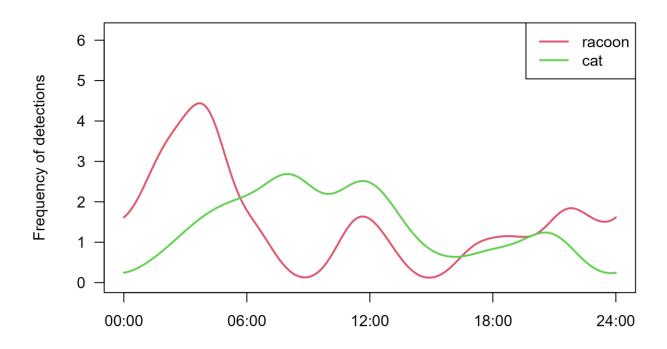


Figure 18. Kernel density estimation of the diel activity of racoon and cat based on camera trap data.

Despite the potential co-occurrence, a very specific activity cycle was registered for both species when each season's Kernel density estimation of their diel activity was calculated. This was depicted by a multimodal curve varying between the trapping seasons. It seemed when one member of this species pair followed a consistent and stable activity cycle (like a raccoon in season 1 - Figure 19), the other one's presence was quite disturbed (like a cat in season 1 - Figure 20) and vice versa.

Procyon lotor

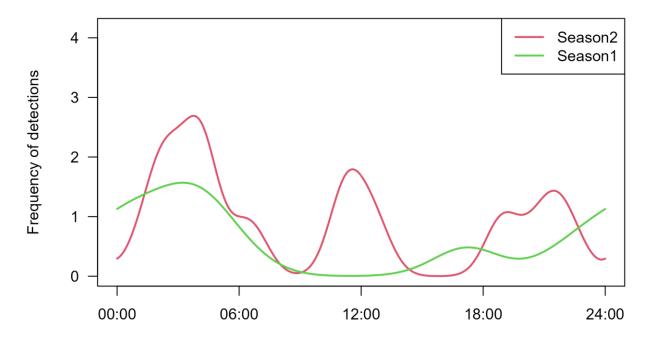


Figure 19: Kernel density estimation of the seasonal diel activity of raccoon based on camera trap data.

In season 2, raccoon even appeared around noon (Figure 19), when the cat's activity started dropping after a peak (Figure 20). However, it is also true that more raccoons were detected in season 2 than in season 1.

Felis spp.

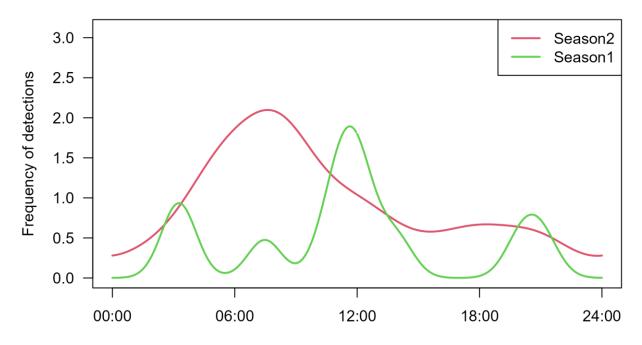


Figure 20. Kernel density estimation of the seasonal diel activity of cat based on camera trap data.

4.3.4. Species Co-occurrence

The species-to-species association matrix highlights patterns of co-occurrence and negative association among the detected species (Figure 21) in temporal and spatial dimensions. Based on the joint species distribution model, the association strength was the highest for the dog-racoon pair (r = 0.33). At the same time, it remained positive but rather indifferent for the dog-red fox (r = 0.16) and the golden jackal-stone marten pairs (r = 0.12). The spatiotemporal contrasts between golden jackal and dog occurrence were also emphasized in the matrix (r = -0.29), predicting that these two species are likely to avoid each other.

random effect level: station

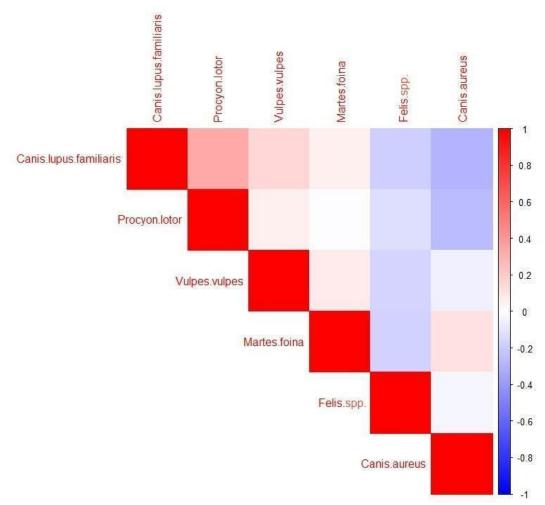


Figure 21: Species co-occurrence in the study area at both study seasons, based on the joint species distribution model. The color gradient ranges from red (positive association/co-occurrence) to blue (negative correlation/avoidance). White cells indicate indifferent relationship. The scale on the right shows values from -1 to 1, where 1 (deep red) indicates a strong positive association (species tend to appear together). In contrast, -1 (deep blue) notes strong negative association (species tend to avoid each other) than expected under the independence hypothesis.

The cat was generally the most reluctant species based on the model's predictions ($r_{mean} = -0.14$), avoiding interactions with other species. Namely, it likely used different, less frequented parts of the study area when other species were around or appeared in those short periods when other species temporarily disappeared, generating a multimodal activity curve (see Figure 20 Season 1). Its lowest association was predicted with a stray dog (r = -0.18), while surprisingly, the highest value was estimated with another canid, the golden jackal (r = -0.04), indicating an indifferent relationship towards this species.

Considering the estimated association values of other species pairs, many remained near to r = 0, primarily due to insufficient observations.

4.4. Acoustic Survey

4.4.1. Response Intensity and Estimated Population Parameters

The survey was conducted from June to November 2021 in the seven regions of Georgia. With three transects per region, each made of five calling stations, we had a total of 105 calling points. We had four scenarios emerging after the playback of the jackal howling. We recorded the responses of *individual jackals*; responses from multiple individuals that were classed as *group responses*, and *no responses*. On occasion, we also recorded the responses from wolves, which were also included in the analyses (Figure 22). The distribution of responses varies across regions, with some showing higher responses from individuals, while in others, we recorded high group responses. When comparing across all areas, the mean number of individual responses was 3.42 ± 1.9 , while the mean number of no responses was 3.14 ± 2.54 . Group responses were higher, averaging 6.85 ± 4.56 . Wolf responses were lower than those of the target species, the golden jackal, with an overall mean of 1.5 ± 2.29 .

The highest number of individual responses was recorded in Adjara (7 responses), and the lowest was observed in Kakheti (1). However, in Kakheti there were the highest number of group responses (12), whereas Racha and Samckhe Javakheti had the lowest group participation, with only one response each. The highest number of wolf responses was recorded in Racha (6), which is much higher than other regions, where wolf responses ranged from 0 to a maximum of 3. There were some occasions where we did not hear any responses after playing the recorded jackal howling. The highest number of no responses was found in Samckhe Javakheti (7) and Racha (6) regions.

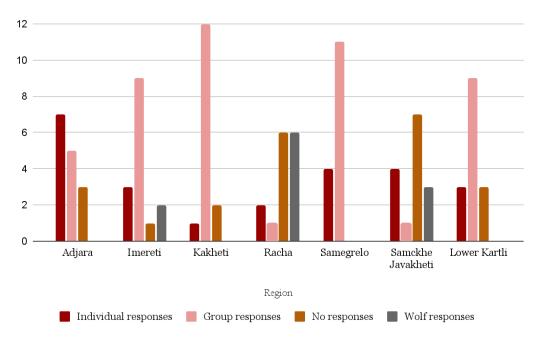


Figure 22: Number of detected responses per region in all calling stations of each transect.

Population density estimates were reflected over the three different detection radii (1 km, 1.5 km, and 2 km) around the calling stations within the transects and notably varied between the seven regions. I generally expressed this metric for the buffer zone of 1.5 km and provided estimates for the 1 and 2 km buffers in parentheses, indicating that there is some uncertainty in detection distance (± 500 m). Kakheti was shown to have the highest estimated density of 0.46 individuals per km² (1.04 for 1 km and 0.26 for 2 km buffer zones). Similarly, the regions of Samegrelo displayed relatively high density estimates of 0.45 (1.02 - 0.25) individuals per km². However, Racha showed the lowest estimated density with 0.06 (0.13 - 0.03) individuals per km², indicating a much lower presence of jackals in this region. In other regions, such as Kvemo Kartli and Imereti, results noted an intermediate density estimate, while Samtskhe-Javakheti demonstrated relatively low densities (Table 6).

Based on these density estimates, population growth under two reproductive scenarios were estimated where the females exhibit a low reproductive rate (35% of females reproducing) and a high reproductive rate (65% of females reproducing). In both scenarios, an average of five pups per female was assumed, with a 50% pup survival rate. Based on these assumptions, under the low reproductive rate scenario, Kakheti showed the population growth potential with 2286 (5148 - 1286) juveniles, respectively. Racha, being one of the most mountainous regions, showed the least population growth potential, with only 72 (161 - 40) pups across the three buffer zones. The same conclusion holds true for the scenario with high reproduction rate of the females. Kakheti and Samegrelo are the regions with highest potential population density while Racha and Samtskhe Javakheti are the lowest (Table 6).

Table 6: Estimated population density and reproductive projections for golden jackals in the seven study regions

Region	_	observed individuals	population density (individual /km²)		35% reproduction rate (No. of pups)			65% reproduction rate (No. of pups)		
			1km 1.5km	2km	1km	1.5km	2km	1km	1.5km	2km
Adjara	2880	27	0.57 0.25	0.14	722	321	180	1341	596	335
Imereti	6516	39	0.83 0.37	0.21	2361	1048	590	4384	1947	1095
Kakheti	11310	49	1.04 0.46	0.26	5148	2286	1286	9560	4246	2388
Kvemo Kartli	6527	39	0.83 0.37	0.21	2365	1050	591	4391	1950	1097
Racha	2893	6	0.13 0.06	0.03	161	72	40	299	133	75
Samegrelo	7468	48	1.02 0.45	0.25	3330	1479	832	6184	2746	1545

4.4.2. Modeling Golden Jackal Occurrence in Function of Environmental Variables

As it can be seen from Figure 22, the absolute values of jackal responses were seemingly lower in those regions where wolves responded to the playback calls. This negative relationship can be better illustrated with response rates, indicating that the average jackal response rates were much lower in regions where wolves also responded to the calls (Figure 23). These areas were mainly mountainous regions like Racha (jackal: 0.2 ± 0.41 , wolf: 0.4 ± 0.51 , elevation: 1110 ± 430 m) and Samtskhe Javakheti (jackal: 0.33 ± 0.49 , wolf: 0.2 ± 0.41 , elevation: 1553 ± 282 m).

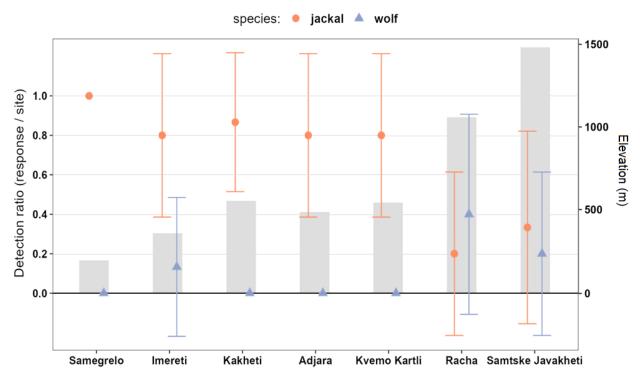


Figure 23. Detection ratio (broadcasting points with response divided by all broadcasting points) of the golden jackal (orange circle) and grey wolf (blue triangle) in different regions of Georgia based on the bioacoustic survey. Grey bars represent the mean elevation of sampling sites per region arranged in an ascending order.

Forest and related woody vegetation was the dominant land cover type on most broadcasting sites throughout the sampled regions (Figure 24). Its mean cover was similar independent of jackal response within the 2 km surrounding area (12.6 km²) around the broadcasting points (with response: $65 \pm 28\%$; without response: $62 \pm 35\%$). Grassland and meadow was the second most common land cover category; its cover was less variable around sites with jackal responses (17 ± 15%) than without it (26 ± 25%). Cropland area cover was highly variable by the actual region and degree of urbanization (with response: 9 ± 17%; without response: 8 ± 16%); while the other

land cover types remained under 5% in the buffer area of the broadcasting stations most of the time (Figure 24).

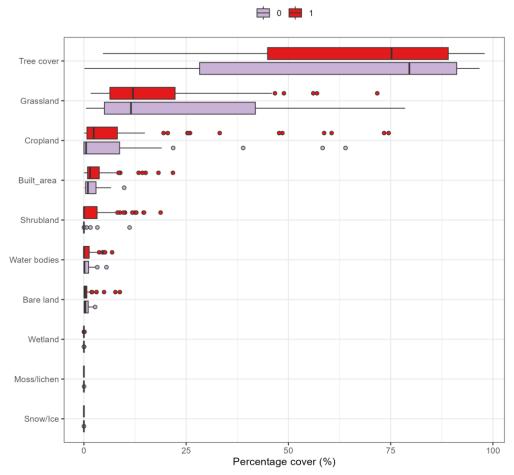


Figure 24. Percentage cover of land-cover types on the surrounding 2 km buffer area of the broadcasting points associated with the presence (1) and absence (0) of responding golden jackals. Land cover data was obtained from the ESA Worldwide Land Cover Mapping (Zanaga et al., 2022).

During data preparation, a high negative correlation was revealed between tree cover vs. grassland (r = -0.73, p < 0.001) and tree cover vs. cropland (r = -0.74, p < 0.001); therefore, these variables were excluded from the generalized linear mixed model. Transects that incorporated the 5-5-5 broadcasting points per region significantly enhanced model performance (likelihood ratio test: χ^2 = 14.9, p < 0.001) as random effects; the same was true for the areas sampled (χ^2 = 6.1, p = 0.01).

However, none of the remaining land cover variables was eligible to provide significant explanatory power to the fitted model in predicting jackal occurrence. The likelihood ratio test results were $\chi^2 = 2.6$, p = 0.11 for grassland; $\chi^2 = 0.02$, p = 0.89 for cropland; $\chi^2 = 2.9$, p = 0.09 for shrubland; $\chi^2 = 1.4$, p = 0.24 for water bodies; $\chi^2 = 0.31$, p = 0.58 for bare land; $\chi^2 = 1.5$, p = 0.22 for wetland.

Among environmental variables, neither the Terrain Ruggedness Index ($\chi^2 = 0.6$, p = 0.43) nor the distance from the nearest settlement ($\chi^2 = 0.2$, p = 0.67) and the actual weather conditions (total daily precipitation: $\chi^2 = 0.4$, p = 0.5, daily mean temperature: $\chi^2 = 1.1$, p = 0.3) were considered significant.

Only elevation (likelihood ratio test: $\chi^2 = 17.1$, p < 0.001) and the detected wolf presence on transects provided adequate significance levels in the model. The latter one only had a weak association, but the likelihood ratio test indicated that wolf detections can still have adequate explanatory power ($\chi^2 = 3.4$, p = 0.05) that resulted in the final model below (Table 7).

Table 7. The results of the generalized linear mixed model examining the effects of elevation and wolf presence on golden jackal responses to the bio-acoustical survey. Variables were scaled before fitting. The coefficients and their corresponding confidence intervals are expressed in odds ratios, the exponentiated form of the default log of the odds output of the model. Transect and region were added as random effects to the model.

			nfidence rval				
	Estimate	lower	upper	z value	р		
Intercept	2.94**	1.46	5.95	3	0.002		
Elevation	0.31**	0.13	0.7	-2.8	0.005		
Wolf presence on transect	0.52	0.25	1.09	-1.73	0.084		
Variance of random effects: by transect = 1.001; by region = 1.717 ** p<							

The model predicted a gradual decrease in the occurrence probability in the elevation increase function (Figure 25). The relationship is almost linear, increasing uncertainty at higher elevations, indicating that other latent variable(s) may also affect jackal presence.

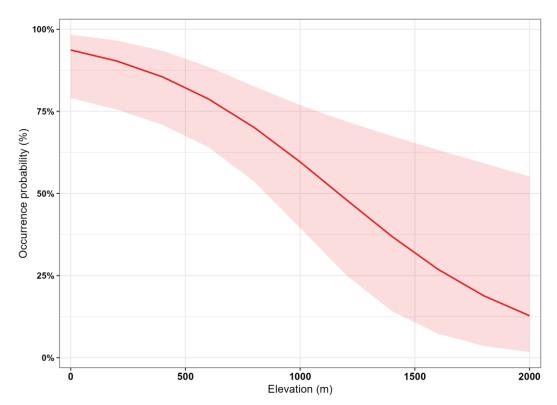


Figure 25. The estimated occurrence probability of golden jackal in function of elevation predicted by the fitted model.

One of these could be the presence—more precisely, the co-occurrence—of wolves in these habitats (Figure 26), which negatively affected jackal occurrence, but the errors gave high uncertainty to this factor. On the other hand, its effects were more pronounced in mountainous areas (see Figure 23), where it can significantly alter the habitat use of the golden jackal.

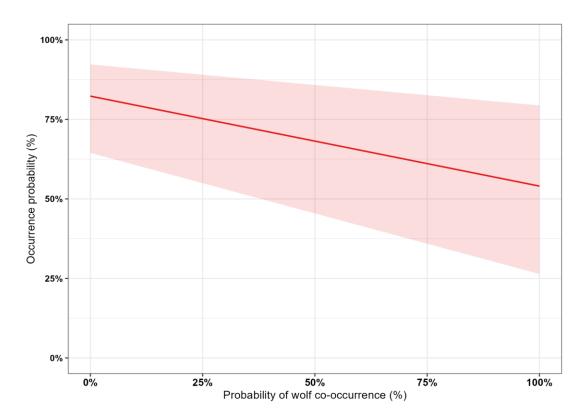


Figure 26. The estimated occurrence probability of golden jackal in function of wolf presence predicted by the fitted model.

By combining the elevation data obtained from the Digital Elevation Model (Robinson et al., 2014) and data from the Agency of Wildlife on the direct observations of wolf presence in Georgia 2021, the fitted model (Table 7) was used to predict and extrapolate golden jackal occurrence throughout the country (Figure 27). Extrapolations were created at the 10×10 km UTM grid scale (MGRS, 2024).

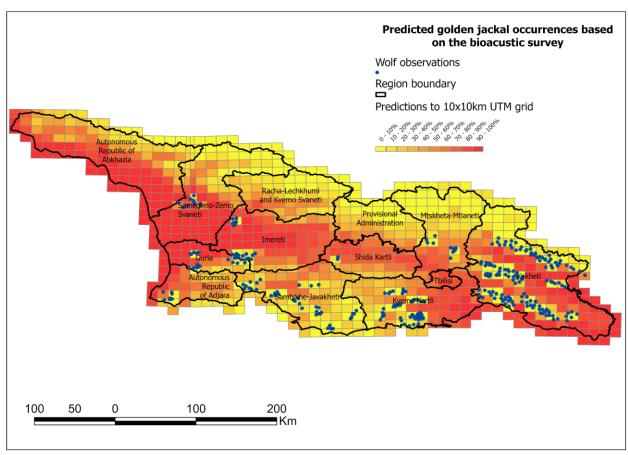


Figure 27. The estimated occurrence probability of golden jackal in Georgia based on the fitted model. Elevation and wolf presence, as significant variables, were used to create model predictions which were generalized onto the 10×10 km UTM grid.

5. DISCUSSION

The *Discussion* chapter analyzes and interprets the results within the broader ecological and conservation context. The chapter compares findings with existing literature, explores the implications of species presence and abundance in human-dominated landscapes, and evaluates the effectiveness of monitoring methods. The chapter also addresses the role of native and invasive species in ecosystem dynamics and human-wildlife conflict and reflects on management strategies suitable for the Georgian context.

5.1. Literature Review

The literature review sought to address Research Objectives 1. and 2. which aimed to investigate the general impact of canids on livestock damages and understand the impacts of increasing predator population on domestic prey. The results of the systematic review align with H_1 and find that wolves consume the highest proportion of livestock and prefer larger domestic animals (like cattle and goats). Golden jackals, having more omnivorous feeding habits, primarily target medium- or small-sized domestic species and showed the highest consumption of pigs. H_1 goes further to say that stray dogs consume the least livestock, as their diet primarily consists of anthropogenic food sources due to their close association with human settlements. While I could not prove this statement statistically due to the low number of scientific publications on stray dogs, it is evident from the scientific literature that most of the food found in the stray dog diet is anthropogenic as they inhabit areas closest to the human settlements (Voslářová & Passantino, 2012; Vanak & Gompper, 2009; Carrasco-Román et al., 2021).

Overall, the predation and/or consumption of domestic livestock by canid species strongly depends on the region, wild prey availability, and livestock management practices. For example, most livestock species in the wolf diet were observed in Southern European countries like Greece and Portugal, where natural prey availability is considerably low (Papageorgiou et al., 1994; Vos, 2000; Torres et al., 2015; Capitani et al., 2015; Janeiro-Otero et al., 2020). Prey vulnerability is one of the most critical factors that promotes livestock depredation. Blanco et al. (2021b) found that the highest cattle damage caused by wolves occurs in Spain. After a large number of areas that belonged to the Cantabrian Mountains, sheep and goats (which were the dominant type of livestock until the late 1900s) were replaced by free-ranging beef cattle, it was falsely assumed by the farmers that the cattle are less vulnerable to predation compared to sheep and goats, given its size and behavior. As a result, farmers dedicated less time and effort to cattle protection and, in turn, made them compatible with other activities (e.g. tourism) which had been supplementing the economy of the areas. However, since the year 2000, once the wolves recolonized the centralwestern territories of Spain, such as the province of Ávila, wolves would kill more than 1,600 calves each year. This was mainly because simple prevention methods like fencing and guard dogs were ineffective against wolf predation since Avila held an extremely high densities of beef cattle and low densities of wild ungulates.

Similarly, in Portugal, free-ranging husbandry systems, where cattle graze far from shelters, experience more wolf attacks than semi-confined systems near shelters (Pimenta et al., 2018). Reporting on cattle damages caused by wolf predation has also risen in countries like the USA and Italy, increasing nearly 1.5 times in recent years (Breck et al., 2004; Dondina et al., 2015). It is interesting to consider the reasons for this increased reporting. While it reflects the increasing population of wolves, there may also be an element of heightened awareness of compensation programs and, therefore, increased observations of wolf attacks. In certain regions this may also be due to the decrease in numbers of alternative livestock species to cattle, such as sheep and goats. The significance of high livestock vulnerability and mismanagement is also illustrated in countries like Portugal (Torres et al., 2015) and Greece (Iliopoulos, 2009), where wolves tend to show preference for goats over sheep. In this case, the preference is strongly influenced by regional factors. Firstly, goats typically graze in remote hilly areas farther from human settlements, often accompanied by few or no shepherds, making it challenging to deter predators (Torres et al., 2015). Additionally, goats are commonly managed under a free-grazing regime, increasing their vulnerability to predation. In contrast, sheep usually graze closer to villages and stay in tightly grouped flocks, making them less susceptible to predators like wolves (Torres et al., 2015).

Additionally, in response to the outbreak of bovine spongiform encephalopathy, the EU sanitary regulation 1774/2002 until 2011 required the elimination of livestock carcasses from the field. This regulation was later repealed by Regulation (EC) No 1069/2009 of the European Parliament and of the Council of 21 October 2009 laying down health rules as regards animal by-products and derived products not intended for human consumption and repealing Regulation (EC) No 1774/2002 (Animal by-products Regulation) This may have reduced food resources for the predators and encouraged the diet shift towards predating on living individuals of domestic species (Lagos & Bárcena, 2015). Adapting livestock management practices to livestock grazing behavior would be an important factor to consider to minimize predator damage.

Regional variation and prey availability also play an essential role in determining the golden jackal diet. Interestingly, the diet variability also depends on the social structure of the golden jackal. For example, when hunting individually, jackals primarily pursue smaller-sized prey, such as rodents, hares, and birds. However, their hunting efficiency increases during breeding season when they form small social groups. This enables them to hunt medium- to large-sized wild ungulates and domestic animals (Mahmood et al., 2013; Jhala & Moehlman, 2004).

Golden jackals showed the highest preference for pigs. This was most noticeable in countries like Serbia, where the consumption is the highest during winter. This coincides with the period when the slaughter of domestic pigs increases for meat production, and the remains of these animals are discarded near settlements (Ćirović et al., 2014; Penezic, 2015). Similar scenarios are reported in some areas in Greece (Giannatos et al., 2005) and Israel (Rotem et al., 2011), where illegal waste dumps are located near human settlements. With cold winter temperatures preserving the remains

for longer periods, predators like golden jackals have access to reliable food, which draws them closer to villages, increasing the potential for conflict.

In contrast to Serbia, golden jackals in Greece primarily feed on goats in addition to pigs (Lanszki et al., 2009; Giannatos et al., 2010). Meanwhile, in Israel, poultry constitutes the most common livestock in their diet (Lanszki et al., 2010). In the case of medium-sized carnivores like golden jackals, cattle and equines are generally too large and dangerous to target. Seasonal changes and habitat variations also influence their diet (Jhala & Moehlman, 2004), with their broad dietary preferences closely tied to the local availability of different food sources (Macdonald, 1979). This adaptability may explain their overall low reliance on livestock. It is also essential to consider that golden jackals and stray dogs typically tend to consume alternative food sources, such as plant matter, reptiles, amphibians, smaller rodents, and garbage, resulting in a lower proportion of domestic animal remains in their diet (Lanszki et al., 2006, 2010; Giannatos et al., 2010).

Unlike the predation habits of wolves and golden jackals, livestock predation by stray dogs is poorly studied. Stray dogs primarily scavenge human-generated waste, a pattern observed in most free-ranging or feral dog populations in regions such as Italy (Macdonald & Carr, 1995), North America (Daniels & Bekoff, 1989; Lantis, 1980), India (Oppenheimer & Oppenheimer, 1975), Southeast Asia, and Australia (Corbett, 1995). Some research suggests that stray dogs may consume more livestock than wolves (Echegaray & Vilà, 2010). However, unlike wolves and other canid predators, stray dogs are closely associated with human settlements and typically live near farms. This proximity to humans explains why most of their diet consists of anthropogenic food sources (Vanak & Gompper, 2009; Silva-Rodríguez et al., 2010; Carrasco-Román et al., 2021).

5.2. Citizen Science

The citizen questionnaire addressed Research Objective 3 which aimed to understand the extent of the Human-Carnivore conflict in Georgia. The results align with **H**₂ and find that human-carnivore conflict in Georgia is most severe in rural areas, where livestock depredation and crop raiding are prevalent, leading to increased reliance on lethal control methods such as trapping and shooting.

A study by Kikvidze and Tevzadze (2014) showed that throughout history, Georgian rural communities developed an elaborate understanding and set of practices that effectively reduced conflicts with predator species, enabling a relatively peaceful coexistence. This knowledge encompassed livestock management techniques, methods to deter predators, and community-based monitoring systems, all passed down through generations and helped maintain a balance between human activities and wildlife. However, given that Georgia has experienced some significant socio-economic changes concerning urbanization, agricultural practices shifts, and rural economy transformations, traditional knowledge essential for coexistence gradually declined. With younger generations migrating to the cities and rural lifestyles evolving, the transmission of

ecological knowledge has diminished. Consequently, this loss has left rural communities less prepared to manage interactions with predators, resulting in increased livestock predation and more frequent conflicts.

To gather insight on Research Question 3.1 (Are the studied species a nuisance to the local communities? If so, what type of problems are they causing?), survey question Q8 (2056 answers in total) showed that the most damage done by the carnivores is on poultry and livestock. Kopaliani et al. (2009) suggest that the lack of wild prey species, substantial encroachment of human settlements into predator's habitat, and lack of natural and artificial barriers for predator resettlement causes a high degree of adaptation and habituation to the presence of people in the vicinity. Similarly, Q1 (1756 responses) and Q10 (1688 responses) gave an insight into the most sighted carnivore species. Jackals and wolves have been noted to be the species most sighted by the residents. Similar answers were provided in Q2 (1725 responses) regarding predator attacks. While it is easy to assume that these frequent sightings are due to the increased population numbers of these carnivores, Kopaliani et al. (2009) suggest that in Georgia, the frequency of wolf attacks on livestock is caused not so much by the increase in wolf population, but by the rise in the number of synanthropic (ecologically associated with humans) wolves specializing in predating on domestic livestock. The study showed that the synanthropization of the wolf in Georgia was facilitated by both ecological and socio-economic factors.

In researching the causes of synanthropization of wolves, Kopaliani et al. (2009) concluded that the waste problem, which is created in many regions of Georgia, is an essential factor in predator adaptation to humans. Landfills located near human settlements are a source of food for both wild and domestic animals (as well as a source of infection) and attract predators like jackals and wolves. Our camera trap study also proved this concerning the golden jackal (see Chapter 5.3). The change in the type of economic activity is another factor strongly contributing to the predator adaptation to the human settlements. Kikvidze (2014) and Kopaliani et al. (2009) note that the rural population lacks the tradition and relevant knowledge of domestic livestock care and protection. In light of the scarcity of wild prey, the presence of less protected and more vulnerable livestock in the area becomes an important factor in attracting wolves and other predators. It should be noted that there has been no intensification of wolf attacks on livestock in areas where the type of farming has not changed, and the population follows the traditional farming rules. It is also interesting to highlight that these less disturbed areas are adjacent to places where the population is disturbed by synanthropic wolves.

It is worth noting that certain environmental factors encourage human-wildlife interaction and synanthropization. For example, in Mtskheta-Tianeti, Guria, and Adjara the socio-economic change is promoted by changes in the landscape. Notably, the restoration of the Katsvi forest near the villages in Mtskheta-Tianeti (area of Kazbegi), and the wilding of tea bushes in Guria and Adjara due to land abandonment and climate change. These factors contribute to the synanthropization of wolves and other predators as these new landscapes act as corridors

connecting the forest and the villages. At the same time, as they are remote and wild, they are less accessible to humans but provide an adequate refuge for predators. These can be one of the many reasons why Q5 (1713 responses), Q2 (1725 responses), and Q6 (1606 responses) indicated jackals and wolves to be the most problematic species for the local communities.

After investigating Research Question 3.2 (What is the most common method used by the local communities to mitigate and prevent the damages?) it was clear that while survey question Q9 (1037 responses) did not have a high response rate, it showed that the most common methods of predation prevention are hunting and using guard dogs. In their questionnaire study, Kikvidze (2014) noted that most respondents who recently switched to livestock farming owned small-sized dogs. This showed to be a problem when the wolf attacks in the villages frequently took place at night, and small-sized dogs could not defend livestock against the predators. Furthermore, small dogs tend to hide if they sense danger, follow their owners at all times, and cannot protect the livestock at night. Therefore, the degree of protection afforded by dogs depended greatly on their breed and size. In comparison, large dogs tend to be kept at home during the day, but they protect the farm and livestock at night.

To address Research Question 3.3 (What are the major factors that need to be considered in management effort in relation to these carnivore species?), it is first important to understand the timing of the conflict. Winter and autumn were shown to be when the highest damage occurred, as shown by the Q4. This question was also the most answered one out of all ten (2416 answers - 14.8%), showing that the local communities are the most vulnerable during winter. Singer et al. (2022) aimed to investigate the seasonal distribution of wolf conflicts. The study concluded that the period between July and October was when most of the incidents occurred - 48.7% of total incidents occurring within these months. This was especially clear for sheep (55.2%), cattle (43.4%), and goats (40.9%). The low number of damages in winter months in Europe is mainly because the livestock species are kept indoors during these months with more intensive husbandry systems. Therefore, more research is needed to understand what factors in the winter months lead to higher damages in Georgia and how to best address them.

It was noticeable that some of the questions that were asked by the questionnaire resulted in fewer answers. It can be that these specific questions were either considered irrelevant by the respondents or rather uncomfortable to answer. One such case was Q7, which aimed to gain insight into actions taken by the respondents to mitigate the predator damage and was the least answered question (938 responses - 5.8%). Comparing the 938 answers to the total of 947 respondents who sent back the questionnaire, it is possible that all respondents picked only one answer out of the 4, while a certain number of people haven't answered at all. Interestingly, the most selected answer to the question on prevention methods is either *no reaction* or *self-prevention*. Only a few answers indicated that the respondents called a hotline (10%) or filed an official complaint (12%). This can be because the rural residents do not trust their local authorities to take action against the predators.

Furthermore, only 18% of requested harvests were fulfilled for wolves and golden jackals over the five years (2015-2020) in the Georgian regions, as indicated by Table 3.

To effectively address the issue of human-wildlife conflict in rural Georgia, it is essential to investigate the golden jackal's adaptability to urban areas, as Hatlauf (2024) documented the species appearing in the capital city of Austria. In the more rural context, blending traditional knowledge with modern scientific techniques could provide a viable solution to reduce these incidents. Reviving traditional practices through community education programs and engaging local elders could restore some of the lost knowledge. In addition, incorporating modern wildlife management methods, such as improved livestock enclosures, the use of guard animals, and technological innovations like GPS tracking and automated deterrents, could enhance conflict mitigation strategies.

5.3. Camera Trapping

The results of the camera trapping study addressed Research Objective 4, which sought to understand the coexistence between wild canids, domestic animals, and humans in semi-urbanized areas. The results partially align with H₃ and indicate that golden jackals are indeed found in semi-urbanized areas. However, there was no detection of wolves in the study area. While the wolf did not appear in the Ponichala Nature Reserve based on my camera trap data, their occurrence in other semi-urbanized areas cannot be excluded, and more research is needed in other semi-urban zones to understand their occurrence patterns since wolves were also reported as problem species in the citizen questionnaire. The results also partially align with H₄, noting that alien species like raccoons exist in semi-urban areas and have potential conflicts with similar-sized animals. While the results show a particular disturbance between raccoons and cats based on their seasonal activity cycles, the coexistence between a raccoon and golden jackal, as well as with other non-target species, is well documented by the study and offers rich insights about their spatiotemporal activities.

The direct observations with the camera traps allowed insights into Research Question 4.1 (*What are the possible factors that encourage their occurrence in the semi-urban area?*). The study found that golden jackals were the most frequently detected species, consistent with their adaptability to anthropogenic landscapes (Šálek et al., 2014; Tsunoda & Saito, 2020). The detection rates of golden jackals were highest in the northern region of the study area; this pattern may be attributed to the proximity of a deserted land patch located approximately 1 km from the northernmost camera. This deserted land patch was an abandoned ditch filled in previous years. It can be assumed that this patch is an abundant food source, enabling the jackals to use it as a feeding site while relying on the Forest-Park area for breeding and mating activities. This type of spatial preference aligns with findings from other studies that suggest golden jackals thrive in semi-natural habitats where resources are abundant and human presence is moderate (Ćirović et al., 2014; Šálek et al., 2014; Tsunoda & Saito, 2020).

One of the other factors that can influence the occurrence of golden jackals in the semi-urbanized areas is the area's topography. For example, the area of Ponichala Nature Reserve lies along the banks of the Mtkvari River (also known as River Kura) and is surrounded by urbanized environments from the North and the West while being bordered by waters from the East and North-East. Over the years, the river has occasionally flooded the park area during wet years, creating more of a fragmented habitat. In contrast, during arid years, the river levels are low and provide an easy passage for the animals between the forest patches. While jackals can disperse from the southern rural area into the Nature Reserve, the roads and highways pose a significant risk of vehicle collisions. Therefore, swimming across the river cannot be ruled out as a possible way into the park, especially during severe droughts with low water levels. However, golden jackals still occurred in the park areas in the year 2021, which was the wet year when the river flooded the passageways. This again highlights their high adaptability, and due to the abandoned land patch, jackals found a way to establish a stable population here. This could illustrate a clear example of the realized niche of the golden jackal due to competition with larger species such as the wolf.

Contrary to jackals, raccoons demonstrated widespread presence across the entire reserve. However, much higher detection rates of raccoons were noticed near the riverbed. This underlines the species' preference for more aquatic and riparian habitats (Sanderson 1987). As raccoons are an alien species in Georgia, this raises a potential worry about their overexploitation of resources and their potential impacts on native biodiversity.

The study also offered insights into Research question 4.2 (How do large and medium-sized carnivores interact and coexist with domestic animals and humans in semi-urbanized areas in Georgia?). The study showed that stray dogs predominantly occupied the southern regions of the park and rarely overlapped with golden jackals. Several reasons can be assumed for this type of avoidance. For example, inevitable dietary overlay can lead to competition for food resources, especially in areas where resources are limited. Both golden jackals and stray dogs are opportunistic feeders with overlapping diets that include small mammals, carrion, and anthropogenic feed (Vanak & Gompper, 2009; Giannatos et al., 2010; Ćirović et al., 2014; Tsunoda & Saito, 2020). This avoidance behavior minimizes direct confrontation and potential injury during disputes over food. Moreover, both species exhibit territorial behavior (Font, 1987; Comazzi et al., 2016). The pictures showed that stray dogs often occurred in groups of 2 or 3 individuals and may have defended their territories, whereas jackals appeared alone or in pairs. Jackals, typically monogamous and forming smaller family groups during the breeding season, may avoid areas dominated by larger or more aggressive dog packs to reduce conflict. The results also indicate a significant difference in the measured overlap of temporal activity. This suggests that dogs and jackals primarily appeared at the same locations at different times. However, when active during the same period, they tended to occupy different areas within the park.

Racoon was the second most observed species after the golden jackal (Figure 9). It is worth noting that raccoon activity was highest in November 2021 when cameras also detected the highest number of cats and highlighted similar space use activities. While the space use was rather similar between the two species, they differed in their temporal activities. The results confirmed raccoons' nocturnal activity, whereas cats were mainly detected around 7 a.m. and 1 p.m., and their activity dropped before nightfall (Figure 18). This suggests a rather diurnal behavior. This type of diurnal activity peak could indicate that these were domestic (home) cats, but more research is needed to identify the exact nature of these cats. It occurred as one of these species followed a consistent and stable activity cycle (like a raccoon in season 1 - Figure 19), the other one's presence was quite disturbed (like cats in season 1 - Figure 20) and vice versa. It is possible that the species behaved in a way that first probed for the presence of others and then decided if they would stay in the area (like cats in season 1 - Figure 20). The statistical analyses proved no significant competition between stone marten and raccoons. It is possible to conclude that the increase in raccoon detection was due to their adaptation to the area as a highly effective generalist species.

Cats were detected to actively use the inner parts of the study area and were completely absent from those camera trap images, which recorded the highest stray dog, stone marten and red fox detections. This may be due to competition between cats and other species for resources. Stone martens and cats may compete for similar food resources, such as small rodents or birds. Cats may avoid encounters to reduce the likelihood of competition or aggression. Foxes and cats often share overlapping territories in suburban, rural, or semi-natural environments. Cats avoid areas where foxes are known to hunt to reduce risks. In addition, if the cats have kittens nearby, they would likely avoid the territories that overlap with other potential predator species to protect their young (Krauze-Gryz et al., 2012; Rodríguez et al., 2020).

The technical pause in camera trapping prevented monitoring of the steadily increasing detection rate of golden jackals during the spring and summer of 2021. However, the results still offered valuable insights into Research Question 4.3 (Are there seasonal differences in the occurrence of large and medium-sized canids in semi-urban areas?). It is reasonable to assume that a peak in golden jackal activity during this period is likely the highest among the detected mammals. This assumption is supported by the abundance of food resources in spring and the increased presence of people in the Natural Reserve during favorable weather, which may have contributed to more anthropogenic resources. It is important to note that the park is an open public space, making it impossible to control or accurately track the number of visitors per seasons. It can only be assumed that usage increases during the summer months due to favorable weather conditions. Golden Jackal, unlike the wolf, is unique in its high tolerance towards anthropogenic disturbance, which has allowed populations to become established in human-modified landscapes (Šálek et al., 2014; Tsunoda & Saito, 2020), where they show high utilization of anthropogenic foods (Ćirović et al., 2014). The seasonal daily activity patterns revealed that golden jackals were predominantly active during twilight hours and early mornings, with reduced activity in the afternoons and early evenings. Activity resumed around sunset and continued into the late evening during season 1. A

similar pattern was observed in season 2, but with a delay of approximately 2–3 hours, likely due to the longer daylight hours.

The detection rates of stone martens and raccoons were nearly random or stagnant during season 1 but became more variable in season 2 (Figure 14). This resulted in a complete decline in stone marten detections, while raccoons exhibited their highest recorded peak in temporal activity. This increase in raccoon detections represented the third-highest recorded rate, following golden jackals and stray dogs. Elusive and well-adapted species such as the stone marten and red fox appeared less in the study area. This may be due to the low number of these species in the area or the cameras themselves. Authors like Gompper et al. (2006) and Pirie et al. (2016) argue that tack plates are more effective and have higher Probability of Detection (POD) for observing and studying smaller mammal species like martens and weasels than camera traps. However, Gompper et al. (2006) found for mid-sized carnivores, for example, raccoon, fisher (*Pekania pennanti* Erxleben, 1777), opossum (*Didelphis virginiana* Linnaeus, 1758), and domestic cat, camera traps and plate tracks had a very similar detection efficiency, this is also confirmed by the study done by Shamoon et al. (2017) that investigated medium-sized carnivores in Mediterranean agricultural areas. However, since small-sized carnivores were not the initial target species of the study, the track plates were not installed at the testing sites.

It is important to highlight that the estimated association values of those species pairs that emerged as near to r=0 should be evaluated with care, as it is due mainly to insufficient observations (Figure 21).

5.4. Bioacoustic Survey

The bioacoustic survey aimed to address Research Objective 5 and investigate the population size of golden jackals in Georgia. The results partially align with H₅, which predicted that environmental variables and interspecific competition significantly influence the distribution and occurrence of the golden jackal. Specifically, golden jackals preferentially inhibit lower elevation areas and related landscape features due to potentially high resource availability while actively avoiding areas with high competition from larger carnivores.

In addressing Research Question 5.1 (What is the minimum population size of the golden jackal at the county and country level?), the reproduction growth model showed that under the assumption of low reproductive rates in golden jackal females and an assumption of 50% pup survival rate, the estimated population within a 2 km radius buffer zone would be 3,638 individuals across the seven surveyed regions. In contrast, assuming high reproductive rates, the population could reach 6,756 individuals. However, these projections should be interpreted cautiously, as additional population assessment research is necessary to accurately determine the minimum population size which ultimately enables to determine population density data to appropriately connect it to the actual magnitude of the related ecological index, and to "fine-tune" the adaptive management

plans. However, various ecological and environmental factors significantly influence reproductive success and must be considered for more precise predictions.

In further addressing Research Question 5.1 (What are the factors influencing golden jackal occurrence in different regions of Georgia?), we did not find that any of the land cover variables, such as forest cover, grasslands, and croplands defined jackal occurrence in any specific region despite initial expectations. This aligns with the international literature that suggests that jackals exhibit considerable ecological plasticity, adapting to various habitats (Šálek et al., 2014; Tsunoda & Saito, 2020). While the specific land cover was not revealed as a significant factor, the elevation was shown to be a significant factor that influenced the distribution of the golden jackals.

The Generalized Linear Mixed Model (GLMM) (see Figure 22) showed reduced occurrence of jackals at higher elevations. The results showed that the probability of golden jackal occurrence – the frequency of potential golden jackal encounters - is the highest along Georgia's NW - SE central line (Figure 27). These areas are between 0 and 1200 m above sea level with a mean of 415 ± 323 m elevation (see Map 2), dominated by a mix of land types, mostly croplands, and grasslands, which are divided by forests or less dense woody vegetation near to waterfowls (Map 3). While the lack of jackal occurrence at higher elevations can be attributed to the reduced availability of prey, it may also be due to the less suitable habitat. While we cannot directly say that any of the land cover was preferred, the observed preference for lower elevations may indirectly suggest a preference for lowland habitats, which typically support higher prey availability and lower predation risk.

Interestingly, UTM cells (Figure 27) with more than a 70% probability of golden jackal occurrence contained various land cover types and were mainly near the rivers. Furthermore, river Rioni, which runs in the West of Georgia, River Kura in the middle, and River Alazani in the East, all create a somewhat mixed environment that breaks the continuity of homogeneous forest cover, increasing the golden jackal presence (Map 3). It can be assumed that one or two vegetation types never dominated these areas but were somewhat mixed habitats. While this study cannot confirm the preferred types of vegetation of the golden jackals, international literature noted that the mixed habitats are most occupied by the golden jackals (Stoyanov, 2012; Šálek et al., 2014; Tsunoda & Saito, 2020).

While investigating the land cover preferences was not the initial goal of the thesis, it emerged as one of the needs for more fine-scale habitat analysis. Research incorporating prey availability, interspecific competition with wolves, and effects of human disturbance is needed to suggest conservation policies based on the broader predator-prey dynamics within these ecosystems.

In further investigating the factors that could affect golden jackal distribution, the results of the bioacoustics survey show rather interesting variations in golden jackal and wolf presence in the surveyed regions. The distinct response rates between individual and group responses to the playbacks highlighted the territorial and social structures of jackal populations. Adjara had the

highest number of individual responses, while Kakheti had the highest group response rates, suggesting that regions like Kakheti may likely support more cohesive social groups and experience higher growth rates. Higher growth rates in jackal populations have been observed by Moehlman (1987), where forming social groups increases the survival rate of the pups.

The estimated population densities suggest that Kakheti and Samegrelo, the lowest-lying regions of Georgia (Figure 2), have the highest jackal densities. In contrast, Racha and Samtskhe-Javakheti, both high-elevation regions, exhibit the lowest jackal occurrence. This variability across habitats may stem from differences in climatic conditions, environmental factors, and prey availability (Acosta-Pankov et al., 2018). The fact that Racha, the region with the highest elevation, exhibited the lowest growth potential of golden jackals could suggest that wolves may be preying on juvenile individuals, especially since this region had the highest mean wolf detection rate (Figure 23). The current bioacoustics survey also indicated that golden jackals occurred significantly less in highly elevated places, mainly when wolves were found nearby. While reproductive projections provide insight into potential growth scenarios, these results should be interpreted cautiously and warrant further investigation. A broader range of factors influencing jackal population growth must be considered.

One of the most important findings is the negative relationship between golden jackal and wolf responses (see Figure 23), which was also indicated by the fitted model (Table 7 and Figure 26). It is interesting to explore why wolves responded to the jackal howl playbacks in certain areas and why they ignored it in others. For example, wolves were present in the region of Imereti where the average elevation was less than in Racha or Samckhe Javakheti; it is plausible to assume that wolves also occur in the other areas of lower elevations that did not respond to the jackal howl playbacks. However, wolf spatial presence needs further investigation. While it is reasonable to conclude that the lack of wolf responses is due to low numbers or absence of wolves from the area, assuming some aspects of competition is also sensible. For example, regions with higher wolf detections, such as Racha and Samtskhe-Javakheti, corresponded to lower jackal detections. Jhala and Moehlman (2004) suggest an interspecific competition, where wolves, as apex predators, may suppress jackal populations through direct predation or competitive exclusion in the shared habitats. The only exception is the Kakheti region, where the significant number of wolf detections strongly modified the predicted occurrence of golden jackals (Figure 27). Any other regions outside of this axis got gradually decreasing estimates of occurrence due to the lack of acoustical surveys in the northern side of the country on the one hand (see Map 3) and the high reported direct observations of wolves along the southern border on the other hand.

It has been observed in many areas that jackals generally tend to avoid wolves. For example, its range in Europe has significantly and quickly expanded from the Balkan Peninsula to central and western countries (Arnold et al., 2012; Rutkowski et al., 2015) in which the wolf, acting as a dominant competitor, is absent (Newsome et al., 2017; Tsunoda & Saito, 2020). The jackal range expansion is often mirrored with the decline in wolf distribution (Krofel et al., 2017). However,

the opposite is true in other regions, where jackals benefit from scavenging on wolf kills (Boitani et al., 2018) and successfully coexist with wolves. A similar relationship is seen with red foxes and coyotes in North America (Levi & Wilmers, 2012; Wikenros et al., 2017). The distribution area overlap of wolves and jackals increased from about 7.1% during 1950–1970 to 22.7% in central Europe after 2000, with wolves reclaiming historical ranges and jackals colonizing new areas (Krofel et al., 2017).

No proof of a specific environment was found regarding Research Question 5.2 (What regions do these species occupy, and what type of habitats are they mostly found in?). Further research is needed to investigate the environmental factors that encourage and promote golden jackal occurrence in Georgia and its implications for the interaction with human settlements.

6. CONCLUSIONS AND RECOMMENDATIONS

The literature review revealed a few shared conclusions about livestock damage and human-wildlife conflict in Europe (H₁). This study highlights that the dietary habits of wolves, golden jackals, and stray dogs are heavily affected by regional variations, especially aspects such as prey availability, livestock management practices, and anthropogenic factors. Wolves in Southern Europe, where natural prey is less abundant, rely more on domestic livestock, leading to increased conflicts with farmers. Furthermore, free-ranging livestock is the most difficult to protect and it is the most vulnerable to wolf predation. This is particularly evident in countries like Spain, Portugal, and Italy, where free-ranging husbandry practices make cattle and goats more susceptible to predation. In the EU, there are many fine-scale differences in human-wildlife conflict. A few large carnivore individuals can produce great damage when the environmental, social, and economic systems predispose to it, whereas large populations can make a limited impact in different circumstances. The availability of natural prey, landscape characteristics, and protection measures shape the incidence of damage to livestock, making it crucial to develop region-specific management strategies.

The study found that the local communities struggle to coexist with the large carnivores (H₂) and face continuous damage during winter and autumn. The local communities, who frequently experience damage to their livestock and poultry by golden jackals and wolves, often reserve the opportunity to eliminate the problem individually due to the lack of trust in the local authorities. Incorporating large-sized dogs and bulls in the herds is an effective way to reduce damage to livestock significantly; however, introducing more modern techniques, such as electric fences and other physical barriers, is also effective in helping mitigate the risks associated with increased cattle numbers. By addressing these management gaps, it may be possible to reduce the impact of wolf predation and enhance the sustainability of livestock husbandry in the region. Moreover, some baseline recommendations have been made to address the issues of predators. Firstly, it is essential to agree on defining the "problem causing" predators and then document every case of such individuals. Secondly, removing any possible attractants and implementing preventive measures is crucial. Personally, conducting a lethal removal of problem individuals should be the last resort. Thirdly, communication regarding predator management needs to be adequately established and performed with the local communities and the general public. It is imperative to highlight the necessity of not feeding and approaching the predators, as this action creates the risk of predators becoming accustomed to humans.

The findings of this study have important implications for the management of golden jackal populations in semi-urban areas as well. The observations showed that the urbanized environment doesn't negatively affect the golden jackal's presence but instead provides them with an ideal refuge to establish viable populations (H₃). In addition, given the lower social tolerance towards wolves, the urbanized areas can keep the wolves away from the vicinity, facilitating a higher appearance of the golden jackals. The camera trap survey can also confirm this assumption, where

the golden jackals were the most commonly detected species in an area close to the capital city. High priority needs to be attributed to managing the golden jackal population in urban areas as there is a high possibility for interference with humans. Further, raccoons were found to prefer more riparian habitats (H₄). This raises concerns over their effect on the native species and habitats. More research is needed to investigate the impact of alien species on native ecosystems and develop a dedicated management plan before alien species become invasive.

Based on the population growth predictions, the highest densities observed in Kakheti and Samegrelo suggest that these regions may require more active management to mitigate potential human-wildlife conflicts, particularly in agricultural areas (H₅). Conversely, in regions with low densities, such as Racha and Samtskhe-Javakheti, conservation strategies should focus on maintaining habitat connectivity and minimizing competitive pressures from wolves. It is still important to note that the predictions should be handled carefully in areas where no bioacoustics surveys were made, especially in Abkhazia, South Ossetia, and North-Mtianeti.

Georgia has an active need for effective policy frameworks that support the preservation and integration of traditional ecological knowledge in wildlife management. Encouraging policymakers to consider the socio-cultural dimensions of wildlife conservation and involve local communities in developing and implementing management plans is essential. This inclusive approach could lead to more sustainable and effective solutions for addressing wolf-human conflicts. Consequently, a multifaceted approach is the only way to address these human-wildlife conflict cases effectively. Education and outreach programs are crucial elements that help improve the understanding of wolf behavior and ecology, potentially reducing unfounded fears and misconceptions.

Most importantly, authorities need to foster coexistence, which, for it to be successful, needs to involve collaborative efforts between wildlife conservationists, local communities, and government authorities. Through this process, policies need to be developed to consider the needs of both human and wolf populations. Tackling the underlying causes of conflict and fostering collaborative, well-informed strategies may alleviate tensions, paving the way for a more balanced coexistence between humans and predators.

7. NEW SCIENTIFIC RESULTS

- Livestock Predation (Research Objectives 1 & 2): Wolves strongly prefer larger domestic livestock, specifically cattle and goats. Golden jackals primarily target medium-or small-sized domestic species, with a notable preference for pigs. Stray dogs consume the least livestock, as their diet relies heavily on anthropogenic food sources, but more research is needed to understand livestock consumption by stray dogs.
- Species Distribution and Damage (Research Objective 3): Golden jackals and wolves are the most sighted species in remote rural areas. During the winter and autumn, these species cause the most damage to livestock and domestic fowl.
- Conflict Mitigation (Research Objective 3): Based on the surveys, guard dogs and lethal control methods are the most widely utilized methods to prevent predator conflicts. In spite of their widespread use, the effectiveness of these methods requires further research to develop effective mechanisms to respond to human-carnivore conflict and promote coexistence.

• Golden Jackal Ecology:

- Golden jackals do not avoid semi-urban areas, as these locations offer refuge with abundant food and minimal predator presence. They can disperse regardless of natural barriers such as rivers (*Research Objectives 4*).
- The occurrence of golden jackals is negatively correlated with elevation. Golden jackals are most abundant in regions with lower elevations, like Kakheti and Samegrelo, and least abundant in areas of higher elevations, like Racha and Samtskhe-Javakheti (*Research Objective 5*).
- Areas with a more than 70% probability of golden jackal occurrence contained various land cover types, mainly near rivers. Jackal populations form more substantial social groups in certain areas (e.g., Kakheti), possibly leading to higher reproductive success (*Research Objective 5*).

• Species Interactions and Habitat:

- Of Golden jackals and wolves exhibit spatial separation: high wolf density regions have lower jackal presence. Wolf responses to jackal playbacks varied, suggesting potential competitive interactions or territorial avoidance in some areas (*Research Objective 5*). The camera trap study revealed an absence of wolves in the semi-urbanized area where jackals were present in high numbers, suggesting jackals are more adaptive to urbanized environments (*Research Objective 5*).
- Similar avoidance was observed between golden jackals and stray dogs, as well as between raccoons and cats, likely due to dietary overlap and territorial disputes. Raccoons prefer riverine habitats, raising concerns about competition with native species. Raccoons and cats showed particular avoidance in their seasonal activity cycles (Research Objective 4)

8. SUMMARY

Since wildlife management is a relatively new field in Georgia, there is a significant lack of scientific research on carnivore management. However, having a sound scientific base is instrumental in developing mechanisms that adequately address the human-wildlife conflict in rural areas, which is an active topic of complaint from the local communities. Despite the many attempts by the local authorities to mitigate the conflict, unfortunately, the conflict still prevails today. Understanding carnivore distribution, population sizes, and interaction with other species are essential information. The main aim of the research was to understand the ecology of the species in local conditions and, where possible, estimate the minimum population of native and introduced species of large and medium-sized predators, namely the wolf, golden jackal, and raccoon in Georgia. The thesis further aimed to investigate the public presentation about the predator species and the extent of the human-predator conflict that is taking place in rural environments. To achieve this, we divided the research into two types of analyses: analytical work that included a General Systematic Literature Review and fieldwork conducted in Georgian regions that included citizen questionnaires, camera trap studies, and bioacoustics monitoring.

For the General Systematic Literature Review, I aim to reveal the general impact of canid species on livestock damage and the effect of increasing predator populations on domestic prey. The systematic review based on 167 papers evaluated two indices expressing the diet composition of the canid species: the frequency of occurrence (%O) and the percentage of biomass (%B). The study revealed that wolves generally consume more livestock and prefer large-sized species like cattle. In contrast, golden jackals tend to favor consuming more medium-sized species. Golden jackals generally consume fewer livestock species as they rely on alternative food sources such as plant matter and anthropogenic foods. Given the lack of publications on stray dogs, it was only possible to give a descriptive conclusion regarding their livestock consumption. Because stray dogs live close to human settlements, they tend to rely on anthropogenic food provided by the rural residents. The literature review also showed that factors like wild prey availability and vulnerability of domestic livestock significantly influence predation patterns of wolf and golden jackals. In addition, waste management also emerged as one of the most important factors to consider when trying to minimize wolf and golden jackal occurrence close to human settlements. All of these factors highlighted the need to develop region-specific management strategies.

For the citizen questionnaire, we aim to investigate the human-wildlife conflict in rural areas of Georgia and see the most common damage done by the carnivore species. To achieve this, 2,000 paper surveys were distributed across 11 regions of Georgia. Based on 47% of returned surveys, the results showed that human-carnivore conflict in Georgia is the most severe in rural areas, where livestock depredation and crop raiding are prevalent, leading to increased reliance on lethal control methods such as trapping and shooting. The residents indicated that golden jackals and wolves are the most sighted species in remote rural areas, causing the most damage to domestic birds and livestock in winter and autumn. Consequently, guard dogs and lethal control methods are the most

widely utilized methods for preventing conflict with predators. More research is needed to evaluate these methods' effectiveness and refine their response actions to human-wildlife cases. There is an active need for an effective mechanism to respond to the human-carnivore conflict and promote coexistence. Additionally, the study found that merging traditional knowledge with modern scientific techniques could effectively provide a viable solution to reduce conflicts.

We deployed a camera trap study to understand the coexistence between wild canids, domestic species, and humans in the semi-urbanized area. We established six cameras in the Ponichala Nature Reserve (3.5 km²), which operated for two seasons (1st of December 2020 to 16th of March 2021 and 5th of October 2021 to 15th December 2021). The cameras gathered 203 images over the two seasons and revealed effective coexistence between the species, primarily spatio-temporal avoidance. This was shown by the absence of wolves in the semi-urbanized area where jackals were present in high numbers, indicating that jackals are more adaptive to urbanized environments. However, wolves can potentially occur in semi-urban areas, as noted in the citizen questionnaire, and further research is needed in other semi-urban regions to understand their occurrence patterns. Another spatiotemporal avoidance was observed between jackals and stray dogs, likely due to dietary overlap and territorial disputes. We found that golden jackals do not avoid semi-urban areas, as these places act as ideal refugees with abundant food resources and minimal predator presence.

Furthermore, golden jackals can disperse regardless of natural barriers such as rivers and establish populations in urban areas. However, further research is needed to understand the environmental factors influencing golden jackal distribution in Georgia and specific implications for the human-wildlife conflict. The results showed that raccoons prefer riverine habitats, raising concerns about competition with native species.

Lastly, to reveal the population size and country-wide distribution of golden jackals in Georgia, we conducted a bioacoustics survey in seven regions of Georgia. We established three 10km long transects with five broadcasting points on each to survey for the golden jackal per region. Based on the results, we found that golden jackal occurrence is negatively correlated with elevation, meaning that golden jackals are most abundant in the areas with lower elevations like Kakheti and Samegrelo and least abundant in regions of higher elevation like Racha and Samtskhe -Javakheti. While no specific land cover was found to be significantly preferable for the golden jackal, areas that had more than 70% probability of golden jackal occurrence contained a variety of land cover types and were mostly near to the rivers. Further research is needed to understand the habitat and land cover preferences of golden jackals in Georgia. Golden jackals and wolves also exhibit spatial separation: high wolf density regions (e.g., Racha, Samtskhe-Javakheti) have indicated lower jackal presence.

Additionally, we noticed that jackal populations form more substantial social groups in certain regions (e.g. Kakheti), possibly leading to higher reproductive success. Wolf responses to jackal

playbacks varied, suggesting potential competitive interactions or territorial avoidance in some areas. Based on these results we aimed to estimate the minimal population size of golden jackals in the seven tested regions of Georgia. We found that the highest densities are observed in Kakheti and Samegrelo, which suggests that these regions may require more active management to mitigate potential human-wildlife conflicts, particularly in agricultural areas. Conversely, in regions with low densities, such as Racha and Samtskhe-Javakheti, conservation strategies should focus on maintaining habitat connectivity and enhancing long term coexistence with wolves.

9. ÖSSZEFOGLALÓ

Mivel a vadgazdálkodás viszonylag új terület Grúziában, a ragadozók kezelésével kapcsolatos tudományos kutatások jelentősen hiányosak. Ugyanakkor a szilárd tudományos alapok elengedhetetlenek ahhoz, hogy olyan mechanizmusokat lehessen kidolgozni, amelyek megfelelően kezelik a vidéki területeken az emberek és a vadon élő állatok közötti konfliktusokat, amelyek a helyi közösségek aktív panaszainak tárgyát képezik. A helyi hatóságok számos kísérlete ellenére, amelyek célja a konfliktus enyhítése volt, sajnos a konfliktus ma is fennáll. A ragadozók elterjedésének, populációjának méretének és más fajokkal való interakciójának megértése alapvető fontosságú információ. A kutatás fő célja az volt, hogy felmérjük a nagy és közepes méretű emlős ragadozók, nevezetesen a farkas, az aranysakál és a mosómedve jelenlétét, és ahol lehetséges, megbecsüljük a grúziai őshonos és betelepített fajok minimális populációját. A disszertáció további célja az, hogy vizsgálja a ragadozó fajokról szóló nyilvános megjelenéseket és a vidéki környezetben zajló ember-ragadozó konfliktus mértékét. Ennek elérése érdekében a kutatást kétféle elemzésre osztottuk: analitikai munkára, amely magában foglalta az általános szisztematikus irodalomáttekintést, és grúz régiókban végzett terepmunkára, amely magában foglalta az érintett lakosság körében végzett kérdőíves felmérést, a kameracsapdás vizsgálatokat és bioakusztikai módszeren alapuló felméréseket.

A szakirodalom szisztematikus áttekintésének célja, hogy feltárja a kutyafélék által az állatállományra gyakorolt általános hatást, valamint a ragadozók populációjának növekedése által a háziállatokra, mint zsákmányra gyakorolt hatását. A 167 tanulmányon alapuló szisztematikus áttekintés két, a kutyafélék táplálkozási összetételét kifejező mutatót értékelt: az adott táplálék forrás előfordulási gyakoriságát (O%) és a biomassza százalékos arányát (B%). A tanulmány kimutatta, hogy a farkasok általában több háziállatot fogyasztanak, és inkább a nagy testű fajokat, például a szarvasmarhákat preferálják. Ezzel szemben az aranysakálok inkább a közepes testű fajokat fogyasztják. Az aranysakálok általában kevesebb háziállatot fogyasztanak, mivel alternatív táplálékforrásokra, például növényi anyagokra és antropogén táplálékra is támaszkodnak. A kóbor kutyákról szóló publikációk hiánya miatt csak leíró jellegű következtetést lehetett levonni háziállatok fogyasztásukról. Mivel a kóbor kutyák emberi települések közelében élnek, inkább a vidéki lakosok által biztosított antropogén táplálékforrásokat fogyasztják. A szakirodalom áttekintése azt is kimutatta, hogy olyan tényezők, mint a vadon élő zsákmányok elérhetősége és a háziállatok sebezhetősége jelentősen befolyásolják a farkasok és az aranysakálok ragadozási szokásait. Ezenkívül a hulladékgazdálkodás az egyik legfontosabb tényezőnek bizonyult, amelyet figyelembe kell venni, ha minimalizálni szeretnénk a farkasok és az aranysakálok előfordulását emberi települések közelében. Mindezek a tényezők rávilágítottak arra, hogy régió-specifikus gazdálkodási stratégiákat kell kidolgozni.

Az érintettek körében végzett kérdőíves felméréssel a célunk az volt, hogy vizsgáljuk a grúziai vidéki területeken előforduló ember-vadállat konfliktusokat, és meghatározzuk a ragadozó fajok által okozott leggyakoribb károkat. Ennek érdekében 2000 papír alapú kérdőívet osztottunk szét

Grúzia 11 régiójában. A visszaküldött kérdőívek 47%-a alapján az eredmények azt mutatták, hogy Grúziában az ember és a ragadozók közötti konfliktus a vidéki területeken a legsúlyosabb, ahol gyakoriak az állatállomány elleni támadások és a termésben okozott kár is. A károk miatt leggyakrabban halálos módszerekkel, csapdázással és fegyveres vadászattal védekeznek az érintettek. A lakosok jelezték, hogy a távoli vidéki területeken a leggyakrabban megfigyelt fajok az aranysakál és a farkas. A ragaozók télen és ősszel okozzák a legnagyobb károkat a háziállat állományokban. A károk csökkentésére a már említett halálos módszereket alkalmazzák, a megelőzés legismertebb módja pedig az őrzőkutyák alkalmazása. További kutatásokra van szükség ezeknek a módszereknek a hatékonyságának értékeléséhez és az ember és vadállatok közötti konfliktusokra adott válaszintézkedések finomításához. Mindenképpen szükség lenne egy aktív és hatékony mechanizmusra az ember és a ragadozók közötti konfliktusokra való reagáláshoz és az együttélés elősegítéséhez. Ezenkívül megállapítottam, hogy a hagyományos tudás és a modern tudományos technikák ötvözése hatékony megoldást jelenthet a konfliktusok csökkentésére.

Kameracsapdás vizsgálatot végeztem, hogy megértsük az emlős ragadozó fajok, a háziasított fajok és az emberek együttélését félig urbanizált területen. Hat kamerát helyeztünk el a Ponichala Természetvédelmi Területen (3,5 km2), amelyek két évszakon át működtek (2020. december 1-jétől 2021. március 16-ig és 2021. október 5-től 2021. december 15-ig). A kamerák a két évszak alatt 203 képet rögzítettek, és feltárták a fajok közötti hatékony együttélés módját, elsősorban a térbeli és időbeli elkülönölést. Ezt bizonyította a farkasok hiánya a félig urbanizált területen, ahol nagy számban voltak jelen sakálok, ami arra utal, hogy a sakálok jobban alkalmazkodnak az urbanizált környezethez. A farkasok azonban potenciálisan előfordulhatnak félig városiasodott területeken, amint az a kérdőív adataiból látszik. Mindenképpen további kutatásokra van szükség más félig városiasodott régiókban, hogy megértsük az előfordulás mintázatát. Térbeli és időbeli elkerülést figyeltünk meg a sakálok és a kóbor kutyák között, valószínűleg az étrend átfedése és a fajok közötti területi kizárás miatt. Megállapítottuk, hogy az aranyszakálok nem kerülik a félig városiasodott területeket, mivel ezek a helyek ideális menedékhelyként szolgálnak, bőséges táplálékforrásokkal és minimális ragadozó jelenléttel.

Ezenkívül az aranysakálok a természetes akadályoktól, például a folyóktól függetlenül is elterjedhetnek. Városi területeken is képesek populációkat létrehozni. Azonban további kutatásokra van szükség annak megértéséhez, hogy milyen környezeti tényezők befolyásolják az aranysakálok elterjedését Grúziában, és milyen konkrét következményei vannak ennek az ember és a vadon élő állatok közötti konfliktusra. Az eredmények azt mutatták, hogy a mosómedvék a folyóparti élőhelyeket kedvelik, ami aggodalmakat vet fel a őshonos fajokkal való versengés tekintetében.

Végül, hogy feltárjuk az aranysakálok populációjának méretét és országos elterjedését Grúziában, bioakusztikai felmérést végeztünk Grúzia hét régiójában. Három 10 km hosszú transzekmentén, két kilométerenként, azaz öt-öt felmérési ponttal dolgoztunk, minden egyes régióban. Az

eredmények alapján megállapítottuk, hogy az aranysakálok előfordulása negatívan korrelál a tengerszint feletti magassággal, ami azt jelenti, hogy az aranysakálok leginkább az alacsonyabb tengerszint feletti magasságú területeken, mint Kakheti és Samegrelo, és legkevésbé a magasabb tengerszint feletti magasságú régiókban, mint Racha és Samtskhe-Javakheti, fordulnak elő. Bár nem találtunk olyan konkrét növényzetet, amelyet az aranysakál kifejezetten preferált volna, az aranysakál előfordulásának 70%-os valószínűséggel rendelkező területek különböző növényzetűek voltak, és többnyire folyók közelében helyezkedtek el. További kutatásokra van szükség a sakálok élőhely- és talajborítás-preferenciáinak megértéséhez Grúziában. A sakálok és a farkasok között is térbeli elválasztottság figyelhető meg: a farkasok sűrűségének magas régióiban (pl. Racha, Samtskhe-Javakheti) alacsonyabb a sakálok előfordulása.

Ezenkívül azt is észrevettük, hogy a sakálpopulációk bizonyos régiókban (pl. Kachetiban) nagyobb csoportokban élnek, ami valószínűleg magasabb szaporodási sikerhez vezet. A farkasok reakciói a sakálhangok lejátszására változatosak voltak, ami egyes területeken potenciális versengésre vagy területi elkerülésre utal. Ezen eredmények alapján megpróbáltuk becsülni az aranysakálok minimális populáció nagyságát Grúzia hét vizsgált régiójában. Megállapítottuk, hogy a legnagyobb sűrűség Kakheti és Samegrelo régiókban figyelhető meg, ami arra utal, hogy ezeken a területeken aktívabb gazdálkodásra lehet szükség a potenciális ember-ragadozó konfliktusok enyhítése érdekében, különösen a mezőgazdasági területeken. Ezzel szemben az alacsony sűrűségű régiókban, mint például Racha és Samtskhe-Javakheti, a védelmi stratégiáknak az élőhelyek összeköttetésének fenntartására és a farkasok által jelentett versengés minimalizálására kell összpontosítaniuk.

10. LIST OF PUBLICATIONS

Publications

Kalandarishvili, A., Feher, A., Katona, K. (2024). Differences in livestock consumption by grey wolf, golden jackal, coyote and stray dog revealed by a systematic review. Hystrix, the Italian Journal of Mampalogyo. 35(1)4/10ystrix-D0672-2023

Kalandarishvili, A., & Heltai, M. (2023). Camera traps as a research method for carnivore population estimation: strength, weaknesses, opportunities and threats, analyses and improvements. *COLUMELLA – Journal of Agricultural and Environmental Sciences*, 10(2), 13-24. DOI: 10.18380/SZIE.COLUM.2023.10.2.13

Kalandarishvili, A., & Heltai, M. (2019). The colonization of raccoon (Procyon lotor L. 1758) in Georgia – The beginning of the invasion? *Columella : Journal of Agricultural and Environmental Sciences*. 10.18380/SZIE.COLUM.2019.6.2.17

Posters

Kalandarishvili, A., & Heltai, M. (2024). Monitoring the Occurrence and Distribution of Large and Medium-Sized Predators in Georgia – Preliminary results. *Pathways Europe - A Part of the Pathways: Human Dimensions of Wildlife Conference*. 13-16 October 2024, Córdoba, Spain.

Conferences

Kalandarishvili, A., & Heltai, M. (2023). Monitoring the occurrence and distribution, and studying the feeding habits of large and medium sized predators in Georgia. 3rd International Jackal Symposium. 2 – 4 November 2022. Gödöllő, Hungary.

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References

- Acosta-Pankov, I. & Spassov N., & Banea, O. (2018). Seasonal Differences in Howling Response of Golden Jackals Canis aureus L., 1758 (Mammalia: Canidae) in Eastern Bulgaria. *Acta Zoologica Bulgarica*. 70. 539-545.
- Akçakaya, H. Resit, Mills, Gus and Doncaster, C. Patrick (2007). The role of metapopulations in conservation. In, Macdonald, David W. and Service, Katrina (eds.) *Key Topics in Conservation Biology*. Oxford, UK. Blackwell Publishing, pp. 64-84.
- Akhalkatsi, M., (2015). Forest Habitats restoration in Georgia. Clean up Georgia. Tbilisi, Georgia. https://orkisi.ge/wp-content/uploads/2023/02/tyishabitatebisagdgenasakartveloshi-GEO.pdf (In Georgian).
- Aliev, F. F., & Sanderson, G. C. (1966). Distribution and Status of the Raccoon in the Soviet Union. *The Journal of Wildlife Management*, 30(3), 497–502. https://doi.org/10.2307/3798740.
- Apollonio, M., Andersen, R., & Putman, R. (2010). European Ungulates and their Management in the 21st Century | Natural resource management, agriculture, horticulture and forestr. Cambridge University Press.
- Arnold, J., Humer, A., Heltai, M., Murariu, D., Spassov, N., & Hackländer, K. (2012). Current status and distribution of golden jackals Canis aureus in Europe. *Mammal Review*, 42(1), 1–11. https://doi.org/10.1111/j.1365-2907.2011.00185.x.
- Balčiauskas, L. (2008). Wolf numbers and distribution in Lithuania and problems of species conservation. *Annales Zoologici Fennici*, 45(4), 329–334.
- Balme, G. A., Slotow, R., & Hunter, L. T. B. (2009b). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (Panthera pardus) population. *Biological Conservation*, 142(11), 2681–2690.
- DOI: 10.1016/j.biocon.2009.06.020 Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009a). Evaluating Methods for Counting Cryptic Carnivores. Journal of Wildlife Management, 73(3), 433–441. doi:10.2193/2007-368
- Banea O. C., Krofel M., Červinka J., Gargarea P. & Szabó L. (2012). New records, first estimates of densities and questions of applied ecology for jackals in Danube Delta Biosphere Reserve and hunting terrains from Romania. *Acta Zoologica Bulgarica 64*: 353–366.
- Bart, J., S. Droege, P. Geissler, B. Peterjohn, & C. J. Ralph. (2004). Density estimation in wildlife surveys. *Wildlife Society Bulletin 32:1242–1247*.
- Bartoszewicz, M. (2011). Invasive Alien Species Fact Sheet Procyon lotor From: Online Database of the European Network on Invasive Alien Species NOBANIS www.nobanis.org.
- Beirne, C. (2023). An introduction to camera trap data management and analysis in R. Wildlife Coexistence Lab, Faculty of Forestry, The University of British Columbia.; WildCam Network https://wildcams.ca.
- Bela, G., Peltola, T., Young, J. C., Balázs, B., Arpin, I., Pataki, G., Bonn, A. (2016). Learning and the transformative potential of citizen science. *Conservation Biology*, *30*, *990–999*. https://doi.org/10.1111/cobi.12762.
- Bennett J, Sjölander-Lindqvist A, Sandström C and Larsson S (2022). Addressing the Swedish Large Carnivore Controversy: Identifying Roadblocks in Collaborative Governance to Reduce Conflict. *Front. Conserv. Sci. 3:952242.* doi: 10.3389/fcosc.2022.952242.

- Beschta, R., & Ripple, W. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142(11), 2401–2414. https://doi.org/10.1016/j.biocon.2009.06.015.
- Bijl, H., Schally, G., Márton, M. 1., Heltai, M. s. and Csányi, S. (2024). From invaders to residents: The golden jackal (Canis aureus) expansion in Hungary since the mid-1990s. *PLoS ONE*, *19* (7): e0306489.
- Bisi, J., Kurki, S., Svensberg, M., & Liukkonen, T. (2007). Human dimensions of wolf (Canis lupus) conflicts in Finland. *European Journal of Wildlife Research*, *53(4)*, *304–314*. https://doi.org/10.1007/s10344-007-0092-4.
- Blanco, J.C., Herraiz, P., Barroso, A., & Olmeda, C. (2021). Extensive beef cattle grazing and wolf damage in Ávila province (Spain). The search for solutions. Report for the Regional Platform of the European Union on the wolf in Ávila. Istituto di Ecologia Applicata, Roma.
- Blanco, C., & Cortes, Y. (2023). Mastiff Dogs Protect Livestock from Wolves in Spain | International Wolf Center. Retrieved 29 September 2024, from https://wolf.org/wolf-info/mastiff-dogs-protect-livestock-from-wolves-in-spain/.
- Blanco, C., & Sundseth, K. (2023). The situation of the wolf (canis lupus) in the European union: An in depth analysis. Publications Office of the European Union. https://data.europa.eu/doi/10.2779/187513.
- Blanco, J. (2019). Aspectos esenciales del lobo y su gestión LIFE15 GIE/ES/000962 SOUTHERN WOLVES.
- Blaney, R., Jones, G., Philippe, A., & Pocock, M. (2016). Citizen Science and Environmental Monitoring: Towards a Methodology for Evaluating Opportunities, Costs and Benefits. Final Report on behalf of UKEOF.
- Boitani, L., Kaczensky, P., Alvares, F., Andrén, H., Balys, V., Blanco, J. C., Chapron, G., Chiriac, S., Cirovic, D., Drouet-Houguet, N., Groff, C., Huber, D., Illppoulos, Y., Ionescu, O., Kojola, I., Krofel, M., Kutal, M., Linnell, J., Majic, A., & Patko, L. (2022). Assessment of the conservation status of the Wolf (Canis lupus) in Europe.
- Boitani, L., Phillips, M., & Jhala, Y. (2018). Canis lupus (errata version published in 2020). *Conservation Biology, 7(4), 874–881.*
- Boitani, L. & Powell, R. A. (2012). Carnivore ecology and conservation: a handbook of techniques. *Oxford University Press* 2012.
- Breck, S.W., Meier, T., (2004). Managing wolf depredation in the United States: past, present, and future. *Sheep Goat Res. J. 19 (Special Issue: Predation)*, 41–46.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M. (2017). glmm TMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal 9, 378–400*. https://doi.org/10.3929/ethz-b-000240890.
- Bubnicki, J. W., Churski, M., Schmidt, K., Diserens, T. A., & Kuijper, D. P. (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *eLife*, 8, e44937. https://doi.org/10.7554/eLife.44937.
- Burbaitė, L., & Csányi, S. (2009). Roe deer population and harvest changes in Europe. *Estonian Journal of Ecology, 58, 169–180*. https://doi.org/10.3176/eco.2009.3.02.
- Carrasco-Román, E., Medina, J.P., Salgado-Miranda, C., Soriano-Vargas, E., Sánchez-Jasso, J.M. (2021). Contributions on the diet of free-ranging dogs (Canis lupus familiaris) in the

- Nevado de Toluca Flora and Fauna Protection Area, Estado de México, Mexico. *Revista Mexicana de Biodiversidad*, *92*. https://doi.org/10.22201/ib.20078706e.2021.92.3495.
- Capitani C., Chynoweth M., Kusak J., Coban E., Sekercioglu C. H. (2015). Wolf diet in an agricultural landscape of north-eastern Turkey. *Mammalia* 80, 329-334.
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., ... Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517–1519. DOI: 10.1126/science.1257553
- Choate, D. M., M. L. Wolfe, & D. C. Stoner. (2006). Evaluation of cougar population estimators in Utah. *Wildlife Society Bulletin 34:782–799*
- Ćirovic, D., Penezic, A., & Krofel, M. (2016). Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biological Conservation*, 199, 51–55. https://doi.org/10.1016/j.biocon.2016.04.027.
- Ćirović, D., Penezic, A., Milenkovic, M., & Paunovic, M. (2014). Winter diet composition of the golden jackal (Canis aureus L., 1758) in Serbia. *Mammalian Biology*, 79(2), 132–137. https://doi.org/10.1016/j.mambio.2013.11.003.
- Ciucci, P., & Boitani, L. (1998). Wolf and dog depredation on livestock in central Italy. *Wildlife Society Bulletin.* 26(3), 504-514. https://iris.uniroma1.it/handle/11573/104887.
- Ciucci, P., (2015). All's well that ends well? Wolf recovery and conservation in Italy. *Int. Wolf.* 25, 24–25.
- Comazzi C., Mattiello S., Friard O., Filacorda S. & Gamba M. (2016). Acoustic monitoring of golden jackals in Europe: setting the frame for future analyses. *Bioacoustics 25 (3): 267–278.* DOI:10.1080/09524622.2016.1152564.
- Convention On The Conservation Of European Wildlife And Natural Habitats. (2024). pdated list of officially adopted Emerald Network sites (December 2024). 44th Standing Committee, Strasbourg, 2-6 December 2024. https://www.coe.int/en/web/bern-convention/emerald-network
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital., *Nature*, 387(6630), 253–260. https://doi.org/10.1038/387253a0.
- Corbett, L. K. (1995). The dingo in Australia and Asia. Sydney: University of New South Wales Press.
- Cortés Y, Ribeiro S, Petrucci-Fonseca F, Blanco J., C. (2020). A decade of use of damage prevention measures in Spain and Portugal. *Carnivore Damage Prevention News 20: 32-47.*
- Croose, E., Birks, J. D. S., Martin, J., Ventress, G., MacPherson, J., & O'Reilly, C. (2019). Comparing the efficacy and cost-effectiveness of sampling methods for estimating population abundance and density of a recovering carnivore: the European pine marten (Martes martes). *European Journal of Wildlife Research*, 65(3). doi:10.1007/s10344-019-1282-6
- Csányi, E., & Sándor, G. (2024). Sexual dimorphism in the Hungarian golden jackal population: analysing body and skull size and shape. *Mamm Biol 104*, 647–660

 DOI: 10.1007/s42991-024-00436-0

- Dalerum, F., Selby, L. O. K., & Pirk, C. W. W. (2020). Relationships Between Livestock
 Damages and Large Carnivore Densities in Sweden. *Frontiers in Ecology and Evolution*,
 7. DOI: 10.3389/fevo.2019.00507
- Daniels, T. J., Bekoff, M. (1989). Population and social biology of free-ranging dogs, Canis familiaris. *J. Mammal.* 70: 754–762.
- DBBW, Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf (2022): Wolfsverursachte Schäden, Präventions- und Ausgleichszahlungen in Deutschland 2021. 41 S.
- DBBW, Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf, (2018). https://www.dbb-wolf.de/Wolfsvorkommen/territorien/karte-der-territorien,
- Delisle Z. J., Flaherty E. A., Nobbe M. R., Wzientek C. M., & Swihart R. K. (2021). Next-Generation Camera Trapping: Systematic Review of Historic Trends Suggests Keys to Expanded Research applications in Ecology and Conservation. *Front. Ecol. Evol.* 9:617996. doi: 10.3389/fevo.2021.617996.
- Dinnik N. J. (1914). Zveri Kavkaza. Tbilisi (In Russian).
- Di Minin, E., Slotow, R., Hunter, L. T. B., Montesino Pouzols, F., Toivonen, T., Verburg, P. H., Leader-Williams, N., Petracca, L., & Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Scientific Reports*, 6(1), 23814. https://doi.org/10.1038/srep23814.
- Dolrenry, S., L. Hazzah, and L.G. Frank. (2016). Conservation and monitoring of a persecuted African lion population by Maasai warriors. *Conservation Biology 30: 467–475*. https://doi.org/10. 1111/cobi.12703
- Dondina, O., Meriggi, A., Dagradi, V., Perversi, M., Milanesi, P., (2015). Wolf predation on livestock in an area of northern Italy and prediction of damage risk. Ethol. *Ecol. Evol. 27:* 200–219.
- Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., & Ritchie, E. G. (2015). Incorporating anthropogenic effects into trophic ecology: Predator—prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: *Biological Sciences*, 282(1814), 20151602. https://doi.org/10.1098/rspb.2015.1602
- Echegaray J, Vilà C. (2010). Noninvasive monitoring of wolves at the edge of their distribution and the cost of their conservation. *Animal Conservation* 13: 157–161.
- Ericsson, G., Heberlein, T. A., Karlsson, J., Bjärvall, A. &Lundvall, A. (2004). Support for hunting as a means of wolf Canis lupus population control in Sweden. *Wildlife Biology*, 10: 269-276
- 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., ... Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. *Science*, 333(6040), 301–306. DOI: 10.1126/science.1205106
- Ferna'ndez-Llamazares, A'., R.A. Garcia, I. Dı'az-Reviriego, M. Cabeza, A. Pyha"la", and V. Reyes-Garcı'a. (2017). An empirically tested overlap between indigenous and scientific knowledge of a changing climate in Bolivian Amazonia. *Regional Environmental Change 17: 1673–1685*. https://doi.org/10.1007/s10113-017-1125-5.

- Findo, Slavomir & Gallay, Igor & Mikušová, Miriama & Skuban, Michaela & Bučko, Jozef. (2023). The impact of large carnivore population density on sheep and goat losses in Slovakia. 10.21203/rs.3.rs-3771757/v1.
- Figueiredo, A. M., Valente, A. M., Barros, T., Carvalho, J., Silva, D. A. M., & Fonseca, C. (2020). What does the wolf eat? Assessing the diet of the endangered Iberian wolf (Canis lupus signatus) in northeast Portugal | *PLOS ONE. 15 (3)*. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0230433.
- Font, E. (1987). Spacing and social organization: Urban stray dogs revisited, *Applied Animal Behaviour Science*, 17(3-4) 319-328. https://doi.org/10.1016/0168-1591(87)90155-9.
- Frey, S., Fisher, J. T., Burton C. A., Volpe J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sensing in Ecology and Conservation 3(3): 123-132*. https://doi.org/10.1002/rse2.60
- Frigerio D, Pipek P, Kimmig S, et al., Citizen science and wildlife biology: Synergies and challenges. Ethology. (2018). *Ethology*. 124: 365–377. https://doi.org/10.1111/eth.12746
- Fuller, T.K. and Sievert, P.R. (2001). Carnivore Demography and the Consequences of Changes in Prey Availability. In: Gittleman, J.L., et al., Eds., Carnivore Conservation, Cambridge University Press, Cambridge, 163-168.
- Galov, A., Fabbri, E., Caniglia, R., Arbanasić, H., Lapalombella, S., Florijančić, T., Bošković, I., Galaverni, M., & Randi, E. (2015). First evidence of hybridization between golden jackal (Canis aureus) and domestic dog (Canis familiaris) as revealed by genetic markers. *Royal Society Open Science*, *2*(12). DOI: 10.1098/rsos.150450
- Gandiwa, E. (2013). Top-down and bottom-up control of large herbivore populations: a review of natural and human-induced influences. *Tropical Conservation Science* 6(4): 493-505. DOI 10.1177/194008291300600404
- Ganz, T. R., DeVivo, M. T., Wirsing, A. J., Bassing, S. B., Kertson, B. N., Walker, S. L. & Prugh, L. R. (2024). Cougars, wolves, and humans drive a dynamic landscape of fear for elk. *Ecology:* e4255
- Garvey, J.E., & Whiles, M. (2016). Trophic Ecology (1st ed.). *CRC Press*. https://doi.org/10.1201/9781315367804
- Gazzola A, Capitani C, Mattioli L, Apollonio M. (2008). Livestock damage and wolf presence. *J. Zool.*, 274(3): 261–269. https://doi.org/10.1111/j.1469-7998.2007.00381.x
- Giannatos, G., Karypidou, A., Legakis, A., & Polymeni, R. (2010). Golden jackal (Canis aureus L.) diet in Southern Greece. *Mammalian Biology 75, 227–232*. https://doi.org/10.1016/j.mambio.2009.03.003.
- Giannatos, G., Marinos, Y., Maragou, P., & Catsadorakis, G. (2005). The status of the Golden Jackal (Canis aureus L.) in Greece. *Belgian Journal of Zoology*, 135, 145–149.
- Glen, A. S., Dickman, C. R., Soule, M. E., & Mackey, B. G. (2007). Evaluating the role of the dingo as a trophic regulator in Australian ecosystems—GLEN 2007—*Austral Ecology*—*Wiley Online Library. 32, 492–501*. https://doi.org/10.1111/j.1442-9993.2007. 01721.x.
- Gompper M. E; Kays R. W; Ray J. C; Lapoint S. D; Bogan D. A.; Cryan J. R. (2006). A Comparison Of Noninvasive Techniques To Survey Carnivore Communities In Northeastern North America. *Wildlife Society Bulletin.* 34(4) 1142-1151. https://doi.org/10.2193/0091-7648(2006)34[1142:ACONTT]2.0.CO;2

- Grichik, V. V., Prakapchuk, V. V., Grebenchuk, A. E., Rabtsava, A. A., & Tsybovsky, I. S. (2018). Шакал (Canis aureus L., 1758) новый вид в териофауне Беларуси. *Experimental Biology and Biotechnology, 3, Article 3.*
- Hatlauf, J. (2024). Urban encounter: First confirmed record of a golden jackal (Canis aureus) in Vienna, Austria. Die Bodenkultur: *Journal of Land Management, Food and Environment.* 75. 1-7. 10.2478/boku-2024-0001.
- Hayama, H., Kaneda, M., & Tabata, M. (2006). Rapid range expansion of the feral raccoon (Procyon lotor) in Kanagawa Prefecture, Japan, and its impact on native organisms.
- Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, 139(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018.

 Hayward, G. D., D. G. Miquelle, E. N. Smirnov, & C. Nations. (2002). Monitoring Amur tiger populations: characteristics of track surveys in snow. *Wilidlife Society Bulletin* 30:1150–1159.
- Hoffmann, M., Arnold, J., Duckworth, J. W., Jhala, Y., Kanler, J. F., & Krofel, M. (2018). IUCN Red List of Threatened Species: Canis aureus. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en.
- Iliopoulos, Y., Antoniadi, E., Kret, E., Zakkak, S., & Skartsi, T. (2021). Wolf-Hunting Dog Interactions in a Biodiversity Hot Spot Area in Northern Greece: Preliminary Assessment and Implications for Conservation in the Dadia-Lefkimi-Soufli Forest National Park and Adjacent Areas. Animals: *An Open Access Journal from MDPI*, 11(11), 3235.

 DOI: 10.3390/ani11113235
- Iliopoulos, Y., Sgardelis, S., Koutis, V., & Savaris, D. (2009). Wolf depredation on livestock in central Greece. *Acta Theriol.*, *54*: *11–22*.
- Ivanova GI, (1962). Comparison of the diets of the red fox, badger and raccoon dog in Voronez national Park. *Institut im. V. I. Lenina 186: 210–256* (In Russian).
- Janeiro-Otero, A., Newsome, T. M., Van Eeden, L. M., Ripple, W. J., & Dormann, C. F. (2020). Grey wolf (Canis lupus) predation on livestock in relation to prey availability. *Biological Conservation*, 243: 108433. doi:10.1016/j.biocon.2020.108433
- Jędrzejewski, W., Niedziałkowska, M., Hayward, M. W., Goszczyński, J., Jędrzejewska, B.,
 Borowik, T., Bartoń, K. A., Nowak, S., Harmuszkiewicz, J., Juszczyk, A., Kałamarz, T.,
 Kloch, A., Koniuch, J., Kotiuk, K., Mysłajek, R. W., Nędzyńska, M., Olczyk, A., Teleon,
 M., & Wojtulewicz, M. (2012). Prey choice and diet of wolves related to ungulate
 communities and wolf subpopulations in Poland. *Journal of Mammalogy*, 93(6), 1480–1492.
 DOI: 10.1644/10-MAMM-A-132.1
- Jhala Y. V., & Moehlman P. D. (2004). Golden jackal Canis aureus Linnaeus, 1758, least concern. In: Sillero–Zubiri C, Hoffmann M, Macdonald DW, editors. Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan. Gland (Switzerland) and Cambridge (UK): IUCN/SSC Canid Specialist Group. p. 156–161. x + 430pp.
- Jiménez, J., Nuñez-Arjona, J., Rueda, C. et al. (2017). Estimating carnivore community structures. *Sci Rep 7, 41036*. https://doi.org/10.1038/srep41036
- Jirků, M., Dostál, D., Robovský, J., & Šálek, M. (2018). Reproduction of the golden jackal (Canis aureus) outside current resident breeding populations in Europe: Evidence from the Czech Republic. Mammalia, 82(6), 592–595. https://doi.org/10.1515/mammalia-2017-0141

- Joubert, C.J. (2020). A baited-camera trapping method for estimating the size and sex structure of African leopard (Panthera pardus) populations, *MethodsX*, 7, p. 101042. doi:10.1016/j.mex.2020.101042.
- Kaczensky, P., Ranc, N., Hatlauf, J., Payne, J. C. et al. (2024). Large carnivore distribution maps and population updates 2017 2022/23. Report to the European Comission under contract N° 09.0201/2023/907799/SER/ENV.D.3 "Support for Coexistence with Large Carnivores", "B.4 Update of the distribution maps". IUCN/SSC Large Carnivore Initiative for Europe (LCIE) and Istituto di Ecologia Applicata (IEA).
- Kalandarishvili, A., & Heltai, M. (2019). The colonization of raccoon (Procyon lotor L. 1758) in Georgia The beginning of the invasion? *Columella : Journal of Agricultural and Environmental Sciences, 6, 17–28.* https://doi.org/10.18380/SZIE.COLUM.2019.6.2.17.
- Karamanlidis, A. A., Hernando, M. de G., Avgerinou, M., Bogdanowicz, W., Galanis, K., Kalogeropoulou, S., Krambokoukis, L., Panagiotopoulos, N., & Taklis, C. (2023). Rapid expansion of the golden jackal in Greece: Research, management and conservation priorities. *Endangered Species Research*, *51*, *1–13*. https://doi.org/10.3354/esr01238.
- Kauhala, K, (2009). Diet of the omnivorous raccoon dog in Europe and in the Far East. *Suomen Riista 55: 45–62* (In Finnish with English summary).
- Kays, R. et al. (2009). Camera Traps as Sensor Networks for Monitoring Animal Communities. *The 34th IEEE Conference on Local Computer Networks. 1, 811–818.* https://doi.org/10.1109/lcn.2009.5355046.
- Khorozyan, I., Ghoddousi, A., Soofi, M., & Walter, M. (2015). Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation*, 192, 268–275. DOI: 10.1016/j.biocon.2015.09.031
- Khorozyan, I., & Heurich, M. (2022). Large-Scale Sheep Losses to Wolves (Canis lupus) in Germany Are Related to the Expansion of the Wolf Population but Not to Increasing Wolf Numbers. *In Frontiers in Ecology and Evolution (Vol. 10). Frontiers Media SA*. https://doi.org/10.3389/fevo.2022.778917.
- Kie, J. G. (1999). Optimal Foraging and Risk of Predation: Effects on Behavior and Social Structure in Ungulates. *Journal of Mammalogy*, 80(4), 1114–1129. https://doi.org/10.2307/1383163.
- Kikvidze, Z., & Tevzadze, G. (2014). Loss of traditional knowledge aggravates wolf–human conflict in Georgia (Caucasus) in the wake of socio-economic change. *Ambio*, 44. https://doi.org/10.1007/s13280-014-0580-1.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. d, Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E., Tscharntke, T., & Verhulst, J. (2008). On the relationship between farmland biodiversity and land-use intensity in Europe. Proceedings of the Royal Society B: *Biological Sciences*, 276(1658), 903–909. https://doi.org/10.1098/rspb.2008.1509.
- Kobylińska, J. (1996). The red fox and raccoon dog in wetlands of the Biebrza River Valley: Food composition and burrow use. *Eur. J. Wildl. Res.: 186–189*.
- Kojola, I., Henttonen, H., Heikkinen, S., & Ranc, N. (2024). Golden jackal expansion in northernmost Europe: Records in Finland. *Mammalian Biology*, 104(1), 101–105. https://doi.org/10.1007/s42991-023-00382-3.
- Kopaliani, N., Gurielidze, Z., Tevzadze, G., Murtskvaladze, M., Rcheulishvili, K., Kurkhuli, T., & Shaqarashvili, M. (2009). Human-Wildlife Conflict: Report. Ilia State University.

- Kopaliani, N., Shakarashvili, M., Gurielidze, Z., Qurkhuli, T., & Tarkhnishvili, D. (2014). Gene flow between wolf and shepherd dog populations in Georgia (Caucasus). *The Journal of Heredity*, 105(3), 345–353. https://doi.org/10.1093/jhered/esu014
- Kossak, S. (1998). Wolf predator of domestic animals? Guide to recognizing causes of death of animals pasturing without supervision. Advertising and Publishing Agency A. Gregorczyk, Warsaw (in Polish with an english summary).
- Kowalczyk, R., Kołodziej-Sobocińska, M., Ruczyńska, I., & Wójcik, J. M. (2015). Range expansion of the golden jackal (Canis aureus) into Poland: First records. *Mammal Research*, 60(4), 411–414. https://doi.org/10.1007/s13364-015-0238-9.
- Krauze-Gryz, D., Gryz, J.B., Goszczyński, J., Chylarecki, P., & Zmihorski, M. (2012). The good, the bad, and the ugly: space use and intraguild interactions among three opportunistic predators—cat (Felis catus), dog (Canis lupus familiaris), and red fox (Vulpes vulpes)—under human pressure. *Canadian Journal of Zoology.* 90(12): 1402-1413. https://doi.org/10.1139/cjz-2012-0072.
- Krofel, M., Berce, M., Berce, T., Kryštufek, B., Lamut, S., Tarman, J., & Fležar, U. (2023). New mesocarnivore at the doorstep of Central Europe: Historic development of golden jackal (Canis aureus) population in Slovenia. *Mammal Research*, 68(3), 329–339. https://doi.org/10.1007/s13364-023-00686-2.
- Krofel, M., Giannatos, G., Ćirovič, D., Stoyanov, S., Newsome, T. M. (2017). Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution?. *Hystrix, the Italian Journal of Mammalogy, 28(1), 9-15.* https://doi.org/10.4404/hystrix-28.1-11819.
- Kuijper, D. P. J., Diserens, T. A., Say-Sallaz, E., Kasper, K., Szafranska, P. A., Szewczyk, M., Stepniak, K. M., & Churski, M. (2024). Wolves recolonize novel ecosystems leading to novel interactions *Journal of Applied Ecology—Wiley Online Library*. https://doi.org/10.1111/1365-2664.14602.
- Kuijper, D.P.J., Churski, M., Trouwborst, A., Heurich, M., Smit, C., Kerley, G.I.H., & Cromsigt, J.P.G.M. (2019). Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes? *Biological Conservation*, 235(), 102–111. doi:10.1016/j.biocon.2019.04.004.
- Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 283(1841), 20161625. https://doi.org/10.1098/rspb.2016.1625.
- Kutz, S., & M. Tomaselli. (2019). "Two-eyed seeing" supports wildlife health. *Science 364:* 1135–1137. https://doi.org/10.1126/science.aau6170.
- Lagos, L., & Barcena, F. (2018). Spatial variability in wolf diet and prey selection in Galicia (NW Spain). *Mamm Res.* 63, 125–139. https://doi.org/10.1007/s13364-018-0352-6.
- Lange, P. N., Lelieveld, G., & De Knegt, H. J. (2021). Diet composition of the golden jackal Canis aureus in south-east Europe a review. *Mammal Review*, 51(2), 207–213. https://doi.org/10.1111/mam.12235.
- Lanszki, J., Giannatos, G., Dolev, A., Bino, G., & Heltai, M. (2010). Late autumn trophic flexibility of the golden jackal Canis aureus. *Acta Theriologica*, *55*, *361–370*. https://doi.org/10.1007/BF03193239

- Lanszki, J., Giannatos, G., Heltai, M., & Legakis, A. (2009). Diet composition of golden jackals during cub-rearing season in Mediterranean marshland, in Greece. *Mammalian Biology Zeitschrift Fur Saugetierkunde*, 74, 72–75. https://doi.org/10.1016/j.mambio.2008.03.004
- Lanszki, J., Hayward, M. W., & Nagyapáti, N. (2018b). Feeding responses of the golden jackal after reduction of anthropogenic food subsidies. *PLoS ONE*, 13(12), e0208727. https://doi.org/10.1371/journal.pone.0208727
- Lanszki, J., & Heltai, M. (2002). Feeding habits of golden jackal and red fox in south-western Hungary during winter and spring. *Mammalian Biology*, 67(3), 129–136. https://doi.org/10.1078/1616-5047-00020
- Lanszki, J., & Heltai, M. (2010). Food preferences of golden jackals and sympatric red foxes in European temperate climate agricultural area (Hungary). *Mammalia*. 74(3), 267–273. https://doi.org/10.1515/mamm.2010.005.
- Lanszki, J., Heltai, M., & Szabó, L. (2006). Feeding habits and trophic niche overlap between sympatric golden jackal (Canis aureus) and red fox (Vulpes vulpes) in the Pannonian ecoregion (Hungary). *Canadian Journal of Zoology*, 84(11), 1647–1656. https://doi.org/10.1139/z06-147
- 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. *Annales Zoologici Fennici*, *52(4)*, *243–255*. https://doi.org/10.5735/086.052.0403
- Lanszki, J., Schally, G., Heltai, M., & Ranc, N. (2018a). Golden jackal expansion in Europe: First telemetry evidence of a natal dispersal., *Mammalian Biology*, 88, 81–84. https://doi.org/10.1016/j.mambio.2017.11.011
- Lantis, M. (1980). Changes in the Alaskan Eskimo relation of man to dog and their effect on two human diseases. *Arctic Anthropol.*, 17: 2–24.
- Lapini, L., Conte, D., Zupan, M., & Kozlan, L. (2011). Italian Jackals 1984-2011: An Updated Review (Canis Aureus: Carnivora, Canidae). 62, 219–232.
- Lapini L., Molinari P., Dorigo L., Are G. & Beraldo P. (2009). Reproduction of the golden jackal (Canis aureus moreoticus I. Geofroy Saint Hilaire, 1835) in Julian Pre-Alps with new data on its range-expansion in the High-Adriatic Hinterland (Mammalia, Carnivora, Canidae). *Bollettino del Museo civico di storia naturale di Venezia 60: 169-186*.
- Laundre, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P. and Browning, D. M. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, 95 (5): 1141-1152.
- Lavrov, N. P. (1971). Results of raccoon dog introductions in different parts of the Soviet Union. *Trudy Kafedry Biologii MGZPI 29: 101–160* (In Russian).
- Levi, T., & Wilmers, C., C. (2012). Wolves–coyotes–foxes: A cascade among carnivores. *Ecology*, *93*(4), *921*–*929*. https://doi.org/10.1890/11-0165.1.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., & Sand, H., (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proc. Roy. Soc. B.* 279, 910–915.
- Linnell, J., Cretois, B., Nilsen, E., Rolandsen, C., Solberg, E. J., Veiberg, V., Kaczensky, P., Moorter, B., Panzacchi, M., Rauset, G. R., & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*, 244, 108500. https://doi.org/10.1016/j.biocon.2020.108500.

- Linnell, J.D., Promberger, C., Boitani, L., Swenson, J.E., Breitenmoser, U., & Andersen, R. (2004). The Linkage between Conservation Strategies for Large Carnivores and Biodiversity: The View From the "Half-Full" Forests of Europe.
- Louppe, V., Leroy, B., Herrel, A., & Veron, G. (2019). Current and future climatic regions favourable for a globally introduced wild carnivore, the raccoon Procyon lotor. Scientific *Reports*, 9(1), 9174. https://doi.org/10.1038/s41598-019-45713-y
- Lüdecke, D.,(2024). sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.16. https://CRAN.R-project.org/package=sjPlot
- Macdonald, D. W. (1979). The flexible social system of the golden jackal, Canis aureus. *Behavioral Ecology and Sociobiology*, *5*(1), 17–38. https://doi.org/10.1007/BF00302692
- Macdonald, D.W., Chiaverini, L., Bothwell, H.M. et al. (2020). Predicting biodiversity richness in rapidly changing landscapes: climate, low human pressure or protection as salvation?. *Biodivers Conserv* 29, 4035–4057. https://doi.org/10.1007/s10531-020-02062-x
- Mahmood, T., Niazi, F., & Nadeem, M. S. (2013). Diet composition of Asiatic Jackal (Canis aureus) in margallah hills Naitonal Park, Islamabad, Pakistan. *The Journal of Animal and Plant Sicences*, 2(23) 444-456.
- Markov, G., & Lanszki, J. (2012). Diet composition of the golden jackal, Canis aureus in an agricultural environment. *Folia Zoologica*, 61(1), 44–48. https://doi.org/10.25225/fozo.v61.i1.a7.2012
- Marquard-Petersen, U. (1998). Food Habits of Arctic Wolves in Greenland | Journal of Mammalogy | Oxford Academic. 79(1), 236–244. https://doi.org/10.2307/1382859
- Mayer, M., Olsen, K., Schulz, B., Matzen, J., Nowak, C., Thomsen, P. F., Hansen, M. M., Vedel-Smith, C., & Sunde, P. (2022). Occurrence and Livestock Depredation Patterns by Wolves in Highly Cultivated Landscapes. *In Frontiers in Ecology and Evolution (Vol. 10)*. Frontiers Media SA. https://doi.org/10.3389/fevo.2022.783027
- Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey. *University of Chicago Press*. https://press.uchicago.edu/ucp/books/book/chicago/W/bo20145329.html
- Meriggi, A., & Lovari, S. (1996). A Review of Wolf Predation in Southern Europe: Does the Wolf Prefer Wild Prey to Livestock? *Journal of Applied Ecology*, 33(6), 1561–1571. https://doi.org/10.2307/2404794
- Meuret, M., Moulin, C.-H., Bonnet, O., Garde, L., Nozières-Petit, M.-O., & Lescureux, N. (2021). Missing shots: Has the possibility of shooting wolves been lacking for 20 years in France's livestock protection measures? *The Rangeland Journal*, 42(6), 401–413. https://doi.org/10.1071/RJ20046
- Migli, D., Youlatos, D., & Iliopoulos, Y. (2005). Winter food habits of wolves in central Greece. *Journal of Biological Research, 4, 217–220.* Military Grid Reference System, University of Florida, GeoPlan Center. https://mgrs-data.org/about/
- Miranda, I. (2024). Watch as first golden jackals are spotted in the wild in Spain as experts say there is 'no doubt' more will arrive. https://www.surinenglish.com/spain/watch-first-golden-jackals-are-spotted-the-20240311115641-nt.html
- Moehlman, P. D. (1987). Ecology of Cooperation in Canids. *Ecological Aspects of Social Evolution*, 64–86. doi:10.1515/9781400858149.64
- Mols, B., Lambers, E., Cromsigt, J. P. G. M., Kuijper, D. P. J., & Smit, C. (2022). Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos*, 2022(1). https://doi.org/10.1111/oik.08448

- Moura, A., Tsingarska, E., Dabrowski, M., Czarnomska, S., Je drzejewska, B., & Pilot, M. (2014). Unregulated hunting and genetic recovery from a severe population decline: The cautionary case of Bulgarian wolves Supplementary resources [Dataset].
- Navine, A. K., Camp, R. J., Weldy, M. J., Denton, T., & Hart, P. J. (2024). Counting the chorus: A bioacoustic indicator of population density. *Ecological Indicators*, *169*, *112930*. https://doi.org/10.1016/j.ecolind.2024.112930
- Negi., T., (2014) Review On Current Worldwide Status, Distribution, Ecology And Dietary Habits Of Golden Jackal, Canis Aureus. Oct. *Jour. Env. Res. Vol.* 2(4): 338-359.
- Newsome, T. M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C. R., Dellinger, J. A., López-Bao, J. V., Peterson, R. O., Shores, C. R., Wirsing, A. J., & Ripple, W. J. (2016). Food habits of the world's grey wolves. *Mammal Review*, 46(4), 255–269. https://doi.org/10.1111/mam.12067
- Newsome, T. M., Greenville, A. C., Ćirović, 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. *Nature Communications*, 8(1), 15469. https://doi.org/10.1038/ncomms15469
- Ninausz, N., Fehér, P., Csányi, E., Heltai, M., Szabó, L., Barta, E., Kemenszky, P., Sándor, G., Jánoska, F., Horváth, M., Kusza, S., Frank, K., Varga, L., & Stéger, V. (2023). White and other fur colourations and hybridization in golden jackals (Canis aureus) in the Carpathian basin. *Scientific Reports*, 13(1), 21969. https://doi.org/10.1038/s41598-023-49265-0
- Nowak, S., Mysłajek, R.W., Szewczyk, M., Tomczak, P., Borowik, T., Jędrzejewska, B., (2017). Sedentary but not dispersing wolves Canis lupus recolonizing western Poland (2001–2016) conform to the predictions of a habitat suitability model. *Divers. Distrib. 23, 1353–1364*.
- O'Connell, A. F., Nichols, J. D. & Karanth, K. U. (2010). Camera traps in animal ecology: methods and analyses. *Springer Science & Business Media*.
- Oliveira, T., Treves, A., López-Bao, J. V., & Krofel, M. (2021). The contribution of the LIFE program to mitigating damages caused by large carnivores in Europe. *Global Ecology and Conservation*, *31*, e01815. https://doi.org/10.1016/j.gecco.2021.e01815
- Oppenheimer, E. C. & Oppenheimer, J. R. (1975). Certain behavioral features in the pariah dog (Canis familiaris) in West Bengal. *Appl. Anim. Ethol. 2: 81–92*.
- Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., et al. (2021). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews BMJ 2021; 372:n71 doi:10.1136/bmj.n71
- Papageorgiou, N., Vlachos, C., Sfougaris, A., & Tsachalidis, E. (1994). Status and diet of wolves in Greece. *39*, *411–416*. https://doi.org/10.4098/AT.arch.94-48
- Passilongo, D., Mattioli, L., Bassi, E. et al. (2015). Visualizing sound: counting wolves by using a spectral view of the chorus howling. *Front Zool 12, 22*. https://doi.org/10.1186/s12983-015-0114-0
- Penezić, A., & Ćirović, D. (2015). Seasonal variation in diet of the golden jackal (Canis aureus) in Serbia. *Mammal Research*, 60(4), 309–317. https://doi.org/10.1007/s13364-015-0241-1
- Persson, J., Rauset, G. R., & Chapron, G. (2015). Paying for an Endangered Predator Leads to Population Recovery. *Conservation Letters*, 8(5), 345–350. https://doi.org/10.1111/conl.12171

- Peterson, R. O., & Ciucci, P. (2003). The wolf as carnivore. *Wolves: Behavior, Ecology, and Conservation*, 104–130.
- Pilot, M., Dąbrowski, M. J., Hayrapetyan, V., Yavruyan, E. G., Kopaliani, N., Tsingarska, E., Bujalska, B., Kamiński, S., & Bogdanowicz, W. (2014). Genetic Variability of the Grey Wolf Canis lupus in the Caucasus in Comparison with Europe and the Middle East: Distinct or Intermediary Population? *PLOS ONE*, *9*(4), *e93828*. https://doi.org/10.1371/journal.pone.0093828
- Pimenta, V., Barroso, I., Boitani, L., & Beja, P. (2018). Risks a la carte: Modelling the occurrence and intensity of wolf predation on multiple livestock species. *Biological Conservation*, 228, 331–342. DOI: 10.1016/j.biocon.2018.11.008
- Pisel T. (2023). openmeteo: Retrieve Weather Data from the Open-Meteo API. R package version 0.2.4. https://CRAN.R-project.org/package=openmeteo
- Podgórski, T., Acevedo, P., Apollonio, M., Berezowska-Cnota, T., Bevilacqua, C., Blanco, J., Borowik, T., Garrote, G., Huber, D., Keuling, O., Kowalczyk, R., Mitchler, B., Michler, F., Olszańska, A., Scandura, M., Schmidt, K., Selva, N., Sergiel, A., Stoyanov, S., Vada, R. &Vicente, J. (2020). Guidance on estimation of abundance and density of wild carnivore population:methods, challenges, possibilities. *EFSA Supporting Publications*, 17(11). https://doi.org/10.2903/sp.efsa.2020.en-1947
- Prefete de la region auvergne rhone alpes. La lettre d'information sur le loup et les activités d'élevage. (2022). www.auvergne-rhone-alpes.developpement-durable.gouv.fr
- QGIS Geographic Information System, (2024). QGIS Association.
- R Development Core Team, (2021). A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.r-project.org/
- Ridout, M. S., &M. Linkie. (2009). Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat. 14, 322–337*.
 - DOI: 10.1198/jabes.2009.08038
- Riley, S., J., Degloria, S., D., Elliot, S., D. (1999): A Terrain Ruggedness Index that Quantifies Topographic Heterogeneity. *Intermountain Journal of Sciences*, 5(1-4): 23-27.
- Ripple, W. J., & Beschta, R. L. (2004). Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience*, *54*(8), *755*–766. https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2
- Ripple, W. J., & Beschta, R. L. (2012). Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research*, *58*(4), *733*–742. https://doi.org/10.1007/s10344-012-0623-5.
- 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(6167), 1241484.
 - DOI: 10.1126/science.1241484
- Robinson, N., Regetz, J., &Guralnick, R. P. (2014). EarthEnv-DEM90: A nearly-global, void-free, multi-scale smoothed, 90m digital elevation model from fused ASTER and SRTM data. ISPRS *Journal of Photogrammetry and Remote Sensing*, 87:2014, 57-67.
- Rodríguez, A., Urra, F., Jubete, F., Román, J., Revilla, E., & Palomares, F. (2020). Spatial Segregation between Red Foxes (Vulpes vulpes), European Wildcats (Felis silvestris) and Domestic Cats (Felis catus) in Pastures in a Livestock Area of Northern Spain. *Diversity*, 12(7), 268. https://doi.org/10.3390/d12070268

- Røskaft, E., Händel, B., Bjerke, T., & Kaltenborn, B. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, *13*(2), *172–185*. https://doi.org/10.2981/0909-6396(2007)13[172:HATLCI]2.0.CO;2
- Rotem, G., Berger, H., King, R., Kutiel, P.B., & Saltz, D. (2011). The effect of anthropogenic resources on the space-use patterns of golden jackals. *J. Wildlife Manage*. 75, 132–136.
- Rowcliffe M. (2023): activity: Animal Activity Statistics. R package version 1.3.4. https://CRAN.R-project.org/package=activity
- Rutkowski, R., Krofel, M., Giannatos, G., Ćirović, D., Männil, P., Volokh, A. M., Lanszki, J., Heltai, M., Szabó, L., Banea, O. C., Yavruyan, E., Hayrapetyan, V., Kopaliani, N., Miliou, A., Tryfonopoulos, G. A., Lymberakis, P., Penezić, A., Pakeltytė, G., Suchecka, E., & Bogdanowicz, W. (2015). A European Concern? Genetic Structure and Expansion of Golden Jackals (Canis aureus) in Europe and the Caucasus. *PLOS ONE*, 10(11), e0141236. https://doi.org/10.1371/journal.pone.0141236
- Šálek, M., Červinka, J., Banea, O. C., Krofel, M., Ćirović, D., Selanec, I., Penezić, A., Grill, S., & Riegert, J. (2014). Population densities and habitat use of the golden jackal (Canis aureus) in farmlands across the Balkan Peninsula. *European Journal of Wildlife Research*, 60(2), 193–200. https://doi.org/10.1007/s10344-013-0765-0
- Salgado, I. Is the raccoon (Procyon lotor) out of control in Europe?. (2018). *Biodivers. Conserv.* 27, 2243–2256. https://doi.org/10.1007/s10531-018-1535-9
- Salvatori, V., Godinho, R., Braschi, C., Boitani, L., & Ciucci, P. (2019). High levels of recent wolf × dog introgressive hybridization in agricultural landscapes of central Italy. European Journal of Wildlife Research, 65(5), 73. https://doi.org/10.1007/s10344-019-1313-3
- Sanderson G. C. (1987). Wild Furbearer management and conservation in North America. Ontario Trapper's Association, North Bay, pp. 486-499.
- Scalera, Riccardo & Genovesi, Piero & Essl, Franz & Rabitsch, Wolfgang. (2012). The impacts of invasive alien species in Europe. *European Environment Agency*. 10.2800/65864.
- Selva, N., Jędrzejewska, B., Jedrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology-Revue Canadienne De Zoologie CAN J ZOOL*, 83, 1590–1601.

 DOI: 10.1139/z05-158
- Shamoon, H., Saltz, D., & Dayan, T. (2017). Fine-scale temporal and spatial population fluctuations of medium sized carnivores in a Mediterranean agricultural matrix. *Landscape Ecology*. doi:10.1007/s10980-017-0517-8
- Shirk, J. L., Ballard, H. L., Wilderman, C. C., Phillips, T., Wiggins, A., Jordan, R., ... Bonney, R. (2012). Public participation in scientific research: A framework for deliberate design. *Ecology and Society, 17, 1–29.* https://doi.org/10.5751/ES-04705-170229
- Sharma, S., Y. Jhala, & V. Sawarkar. (2005). Identification of individual tigers Panthera tigris from their pugmarks. *Journal of Zoology 267:9–18*.
- Sillero-Zubiri, C., & Laurenson, M. (2001). Interactions between carnivores and local communities: Conflict or co-existence? (Vol. 5). https://ora.ox.ac.uk/objects/uuid:80adf08f-f601-4a74-b62a-7a38772f4942
- Silveira L., Jácomo A.T.A., Diniz-Filho J.A.F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biol. Conserv.* 114(3), 351-355.
- Singer, L., Wietlisbach, X., Hickisch, R., Schöll, E., Broek, A., Désalme, M., Driesen, K., Lyly, M., Marucco, F., Kutal, M., Pagon, N., Papp, C.-R., Milioni, P., Uzdras, R., Zihmanis, I.,

- Zimmermann, F., Marsden, K., Hackländer, K., López-Bao, J. V., & Wegmann, D. (2022). The spatial distribution and temporal trends of livestock damages caused by wolves in Europe. *Biological conservation 282*.
 - DOI: 10.1101/2022.07.12.499715
- Skroblin, A., T. Carboon, G. Bidu, N. Chapman, M. Miller, K. Taylor, W. Taylor, E.T. Game, and B.A. Wintle. (2019). Including Indigenous knowledge in species distribution modelling for increased ecological insights. *Conservation Biology*. https://doi.org/10.1111/cobi.13373.
- Smith, L. M., Hartmann, S., Munteanu, A. M., Dalla Villa, P., Quinnell, R. J. and Collins, L. M. (2019). The Effectiveness of Dog Population Management: A Systematic Review. *Animals (Basel)*, 9 (12)
- Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56(4): 740-749. https://doi.org/10.1111/aje.12557
- Soriano Joshua (2022). What is Bayesian statistics? A complete guide for beginners. https://quantmatter.com/what-is-bayesian-statistics-a-complete-guide-for-beginners/
- Spassov, N., & Acosta-Pankov, I. (2019). Dispersal history of the golden jackal (Canis aureus moreoticus Geoffroy, 1835) in Europe and possible causes of its recent population explosion. *Biodiversity Data Journal*, 7, e34825.

 DOI: 10.3897/BDL7.e34825
- Stoyanov, S. (2012). Golden jackal (Canis aureus) in Bulgaria. Current status, distribution, demography and diet. International symposium on hunting, »Modern aspects of sustainable management of game population«Zemun-Belgrade, Serbia
- Stephens, P. A., O. Y. Zaumyslova, D. G. Miquelle, A. I. Myslenkov, & G. D. Hayward. (2006). Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Pereleshin formula. *Animal Conservation* 9:339–348
- Suter, S. M., Giordano, M., Nietlispach, S., Apollonio M., & Passilongo, M. (2017). Non-invasive acoustic detection of wolves. *Bioacoustics*, 26 (3): 237-248
- Szabó, L.; Heltai, M.; Lanszki, J. (2009). The growth of the distribution area and the population of the golden jackal in Hungary in the last decade. *Journal of Veterinary Behaviour 4 (2):* 64–65.
- Szabo, Laszlo & Heltai, Miklós & Lanszki, Jozsef & Szűcs, E. (2009). An indigenous predator, the golden jackal (Canis aureus L. 1758) spreading like an invasive species in Hungary. Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca. Animal Science and Biotechnologies. 64.
- Szewczyk, M., Łepek, K., Nowak, S., Witek, M., Bajcarczyk, A., Kurek, K., Stachyra, P., Mysłajek, R. W., & Szewczyk, B. (2021). Evaluation of the Presence of ASFV in Wolf Feces Collected from Areas in Poland with ASFV Persistence. *Viruses*, *13(10)*, *2062*. https://doi.org/10.3390/v13102062
- Tanner, E., White, A., Acevedo, P., Balseiro, A., Marcos, J., & Gortázar, C. (2019). Wolves contribute to disease control in a multi-host system. *Scientific Reports*, *9*(1), 7940. DOI: 10.1038/s41598-019-44148-9
- Tikhonov G., Opedal H. O., Abrego N., Lehikoinen A., Jonge M.J.M., Oksanen J., Ovaskainen O. (2019). Joint species distribution modelling with the R package Hmsc. Methods in *Ecology and Evolution*. 11: 442-447. https://doi.org/10.1111/2041-210X.13345
- Tikkunen, M., & Kojola, I. (2020). Does public information about wolf (Canis lupus) movements decrease wolf attacks on hunting dogs (C. familiaris)? *Nature Conservation*, 42, 33–49. DOI: 10.3897/natureconservation.42.48314

- Tikkunen M (2023). Wolf attacks on dogs in Finland and a potential solution to mitigate the conflict. Oral Presentation in *Wolves across Borders Conference*. 8-11 May 2023, Stockholm, Sweden.
- Tikhonov G., Ovaskainen O., Oksanen J., Jonge M., Opedal O., Dallas T. (2022): Hmsc: Hierarchical Model of Species Communities. R package version 3.0-13. https://CRAN.R-project.org/package=Hmsc
- Torres, T. R., Silva, N., Brotas, G., Fonseca, C. (2015). To eat or not to eat? The diet of the engangered Iberian wolf (Canis lupus signatus) in a hunman-dominated landscape in central Portugal. *PLoSONE10(6): e0129379*. doi:10.1371/journal.pone.0129379
- Treves, A., & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, 17(6), 1491–1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x
- Trbojević, I., Trbojević, T., Malešević, D. (2018). The golden jackal (Canis aureus) in Bosnia and Herzegovina: density of territorial groups, population trend and distribution range.

 Mamm Res 63, 341–348.

 DOI: 10.1007/s13364-018-0365-1
- Trouwborst, A., Boitani, L., & Linnell, J.D.C., (2017a). Interpreting 'favourable conservation status' for large carnivores in Europe: how many are needed and how many are wanted? *Biodivers. Conserv.* 26, 37–61.
- Trouwborst, A., Fleurke, F.M., & Linnell, J.D.C., (2017b). Norway's wolf policy and the Bern Convention on European Wildlife: avoiding the "manifestly absurd". *J. Intern. Wildl. Law Policy 20, 155–167*
- 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. *Biodiversity and Conservation*, 24(10), 2593–2610. https://doi.org/10.1007/s10531-015-0948-y
- Tsunoda, H., & Saito, M. U. (2020). Variations in the trophic niches of the golden jackal Canis aureus across the Eurasian continent associated with biogeographic and anthropogenic factors. *Journal of Vertebrate Biology*, 69(4), 20056.1. https://doi.org/10.25225/jvb.20056
- Vlasseva, Albena & Chassovnikarova, Tsenka & Mitkovska, Vesela & Dimitrov, Hristo. (2020). Compensatory Increase of the Reproductive Capacity of the Red Fox Vulpes vulpes (L., 1758) in Sympatric Coexistence with the Golden Jackal Canis aureus L., 1758. *Acta Zoologica Bulgarica*. *Supplement*. 217-222.
- Valente, A., Acevedo, P., Figueiredo, A., Fonseca, C., & Tinoco Torres, R. (2020). Overabundant wild ungulate populations in Europe: Management with consideration of socio-ecological consequences. *Mammal Review*, 50. https://doi.org/10.1111/mam.12202
- Vanak, A.T., & Gompper M.E. (2009). Dogs Canis familiaris as carnivores: their role and function in intraguild competition *Mammal Rev.* 39: 265–283.
- Van Beeck Calkoen, S., Kuijper, DPJ., & Apollonio, M. (2023). Numerical top-down effects on red deer (Cervus elaphus) are mainly shaped by humans rather than large carnivores across Europe. *Journal of Applied Ecology, 60 (12): 2625-2635* https://doi.org/10.1111/1365-2664.14526
- Van Eeden, L. M., Crowther, M. S., Dickman, C. R., Macdonald, D. W., Ripple, W. J., Ritchie, E. G., & Newsome, T. M. (2017). Managing conflict between large carnivores and livestock. *Conserv Biol.* 2018 Feb;32(1):26-34. doi: 10.1111/cobi.12959.

- Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal., *Journal of Zoology—Wiley Online Library. 251, 457–462.*
- Voslárová, E., & Passantino, A. (2012). Stray dog and cat laws and enforcement in Czech Republic and in Italy. *Annali Dell'Istituto Superiore Di Sanita*, 48(1), 97–104. https://doi.org/10.4415/ANN 12 01 16
- Wandeler, A. I., Matter, H. C., Kappeler, A., & Budde, A. (1993) The ecology of dogs and canine rabies: a selective review. *Rev Sci Tech. Mar;12(1):51-71*. doi: 10.20506/rst.12.1.663.
- Wierboska, IA., Hedrzak, M., Popczyk, B., Okarma, H., & Crooks, K. (2016). Predation of wildlife by free-ranging domestic dogs in Polish hunting grounds and potential competition with the grey wolf. *Biological Conservation*, 201, 1–9. https://doi.org/10.1016/j.biocon.2016.06.016
- Wilson, G.J., and R.J. Delahay. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research 28: 151–164*. https://doi.org/ 10.1071/WR00033.
- Winnie, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function, *Food Webs*, 12, 88-94, https://doi.org/10.1016/j.fooweb.2016.09.002.
- Wikenros, C., Aronsson, M., Liberg, O., Jarnemo, A., Hansson, J., Wallgren, M., Sand, H., & Bergström, R. (2017). Fear or food—Abundance of red fox in relation to occurrence of lynx and Wolf. *Scientific Reports*, 7. https://doi.org/10.1038/s41598-017-08927-6
- Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, 4(7), 170052. DOI: 10.1098/rsos.170052.
- Zanaga, D., Van De Kerchove, R., Daems, D., De Keersmaecker, W., Brockmann, C., Kirches, G., Wevers, J., Cartus, O., Santoro, M., Fritz, S., Lesiv, M., Herold, M., Tsendbazar, N.E., Xu, P., Ramoino, F., & Arino, O., (2022). ESA WorldCover 10 m 2021 v200. doi:10.5281/zenodo.7254221.
- Zar, J.H. (2010). Biostatistical Analysis, 5th edit. Pearson Prentice Hall: Upper Saddle River, NJ, USA, 960 pp.
- Zazanashvili, N. & Mallon, D. (2009). Status and Protection of Globally Threatened Species in the Caucasus. *Tbilisi: CEPF, WWF. Contour Ltd., 232 pp.*
- Zscheischler, J. and Friedrich, J. (2022). The wolf (Canis lupus) as a symbol of an urban-rural divide? Results from a media discourse analysis on the human-wolf conflict in Germany. *Environmental Management*, 70 (6): 1051-1065

Appendix I - Carnivore Harvesting Effort in Georgia

Region (Municipality)	Number of golden jackal harvested	Number of wolf harvested	Golden jackals harvested / km ²	Golden jackals harvested / km ²	
Guria (Ozurgeti, Chokhatauri)	75	23	0.0253	0.0078	
Samegrelo (Martvili, Senaki, Khobi, Tsalenjikha)	38	30	0.0038	0.0030	
Adjara (Kobuleti)	1	5	0.00034	0.00171	
Imereti (Terjola, Zestafoni, Baghdadi)	5	1	0.00267	0.000534	

Table 1. The number of harvested individuals from the regions of Guria, Samegrelo, Adjara and Imereti between 2020 and 2024. Source: Georgian Ministry of Environmental Protection of Georgia 2024.

Decree №	Date of Issue	Validity	Wolf (Planned)	Jackal (Planned)	Wolf (Harvested)	Jackal (Harvested)	Municipality / Region	Total Harvested
	12.10.202	13.10.202	5	20	5	20	Ozurgeti	Wolf - 24; Jackal - 63.
			5	20	5	14	Senaki	
			5	20	0	3	Batumi	
2-757			5	20	0	2	Martvili	
			5	20	3	0	Khobi	
			5	20	0	3	Kobuleti	
			5	20	5	20	Zestaponi	
			5	20	2	0	Tskaltubo	
			5	20	4	0	Tsalendzikha	
			5	20	0	1	Bagdadi	
N2-512 (Zestaponi municipality)	7/6/2023	10.09.202	10	0	0	0	Zestaponi	No Harvest
N-534 (Ozurgeti Municipality)	7/10/202 3	10.09.202	10	10	5	10	Ozurgeti	Wolf - 5; Jackal - 10.
N2-785 (all municipalitie s)	10/13/20 23	13.10.202 4	5	20	2	7	Abasha	Wolf - 28; Jackal - 48.
			5	20	6	20	Ozurgeti	
			5	20	5	12	Senaki	
			5	20	2	4	Martvili	
			5	20	7	3	Chkorotskhu	
			5	20	3	0	Lanchkhuti	

			5	20	0	2	Kobuleti	
			5	20	2	0	Tsalendzikha	
			5	20	1	0	Khobi	
N2-609 (Ozurgeti	7/1/2024	13.10.202	10	20	2	7	Ozurgeti	Wolf - 2; Jackal - 7.
municipality)		4						Jackai - 7.

Table 2. Harvested carnivores in the Georgian municipalities in 2023 - 2024. Source: Georgian Ministry of Environmental Protection of Georgia 2024.

Appendix II - Scientific Papers Used in the Literature Synthesis and Analyses

Wolf

- Ahmed, T., Khan, A., & Chandan, P. (2017). Dietary Spectrum of Two Sympatric Canid Species in Ladakh, India. *Proceedings of the Zoological Society*. doi:10.1007/s12595-017-0212-4
- Andersone, Žanete & Ozolins, Janis. (2004). Food habits of wolves Canis lupus in Latvia. *Acta Theriologica ACTA THERIOL.* 49. 357-367. 10.1007/BF03192534.
- Ansorge, H., Kluth, G. & Hahne, S. (2006). Feeding ecology of wolvesCanis lupus returning to Germany. *Acta Theriol* 51, 99–106. https://doi.org/10.1007/BF03192661
- Anwar, Muhammad & Nadeem, Muhammad & Shah, M. & Kayani, S.I & Mushtaq, A..
 (2012). A Note on the Diet of Indian Wolf (Canis lupus) in Baltistan, Pakistan. *Pakistan journal of zoology.* 44. 588-591.
- Barja, I. (2009). Prey and Prey-Age Preference by the Iberian Wolf Canis Lupus Signatus in a Multiple-Prey Ecosystem. *Wildlife Biology*. *15*. *147-154*. 10.2981/07-096.
- Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., & Apollonio, M. (2004). A comparative analysis of wolf (Canis lupus) diet in three different Italian ecosystems. *Mammalian Biology* 69(1), 1–10. doi:10.1078/1616-5047-112
- Capitani, C., Chynoweth, M., Kusak, J., Çoban, E., & Şekercioğlu, Ç. H. (2016). Wolf diet in an agricultural landscape of north-eastern Turkey. *Mammalia*, 80(3). doi:10.1515/mammalia-2014-0151
- Ćirović, Duško & Penezić, Aleksandra. (2020). Importance of slaughter waste in winter diet of wolves (Canis lupus) in Serbia.
- Ciucci, Paolo & Artoni, Luca & Crispino, Francesca & Tosoni, Elisabetta & Boitani, Luigi. (2018). Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. *European Journal of Wildlife Research*. 64. 10.1007/s. 10344-018-1166-1.
- Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., & Grottoli, L. (2019). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. *Global Ecology and Conservation*. 21. e00841. 10.1016/j.gecco.2019.e00841.
- Cuesta, L. & Barcena, F. & Palacios, F. & Reig, S.. (1991). The trophic ecology of the Iberian Wolf (Canis lupus signatus Cabrera, 1907). A new analysis of stomach's data. *Mammalia*. 55. 239-254. 10.1515/mamm.1991.55.2.239.
- Van Duyne, C., Ras, E., De Vos, A.E.W., De Boer, W.F., Henkens, R.J.H.G. And Usukhjargal, D. (2009), Wolf Predation Among Reintroduced Przewalski Horses in Hustai National Park, Mongolia. *The Journal of Wildlife Management*, 73: 836-843. https://doi.org/10.2193/2008-027
- Figueiredo AM, Valente AM, Barros T, Carvalho J, Silva DAM, Fonseca C, et al., 2020. What does the wolf eat? Assessing the diet of the endangered Iberian wolf (Canis lupus

signatus) in northeast Portugal., PLoS ONE 15(3): e0230433.

DOI: 10.1371/journal.pone.0230433

- Figueiredo AM, Valente AM, Barros T, Carvalho J, Silva DAM, et al. (2020). What does the wolf eat? Assessing the diet of the endangered Iberian wolf (Canis lupus signatus) in northeast Portugal. *PLOS ONE 15(3): e0230433*. https://doi.org/10.1371/journal.pone.0230433
- Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P. and Apollonio, M. (2005), Predation by wolves (Canis lupus) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology*, 266: 205-213. https://doi.org/10.1017/S0952836905006801
- Gade-Jørgensen, Inge & Stagegaard, Rie. (2000). Diet composition of wolves Canis lupus in east-central Finland. *Acta Theriologica*. 45. 537-547. 10.4098/AT.arch.00-52.
- Hamid, Abdul & Mahmood, Tariq & Fatima, Hira & Hennelly, Lauren & Akrim, Faraz
 & Waseem, Muhammad. (2019). Origin, ecology and human conflict of gray wolf (Canis lupus) in Suleman Range, South Waziristan, Pakistan. *Mammalia*. 83.
 10.1515/mammalia-2018-0167.
- Hosseini-Zavarei, F. & Farhadinia, Mohammad & Beheshti-Zavareh, M. & Abdoli, Asghar. (2013). Predation by grey wolf on wild ungulates and livestock in central Iran. *Journal of Zoology*. 290. 10.1111/jzo.12022.
- Hovens, J. P. M., & Tungalaktuja, K. (2005). Seasonal fluctuations of the wolf diet in the Hustai National Park (Mongolia). *Mammalian Biology* 70(4), 210–217. doi:10.1016/j.mambio.2004.12.003
- Imbert, C., Caniglia, R., Fabbri, E., Milanesi, P., Randi, E., Serafini, M., ... Meriggi, A. (2016). Why do wolves eat livestock? *Biological Conservation*, 195, 156–168. doi:10.1016/j.biocon.2016.01.003
- Khan, Muhammad & Mahmood, Tariq & Fatima, Hira & Akrim, Faraz & Andleeb, Shaista & Hamid, Abdul. (2019). Distribution, Diet Menu and Human Conflict of Grey Wolf Canis lupus in Mahoodand Valley, Swat District, Pakistan. *Pakistan Journal of Zoology*. 52. 10.17582/journal.pjz/2020.52.1.179.191.
- Lagos, L., & Bárcena, F. (2018). Spatial variability in wolf diet and prey selection in Galicia (NW Spain). Mammal Research, 63(2), 125–139. doi:10.1007/s13364-018-0352-6
- Lagos, L., Bárcena, F. (2015). EU Sanitary Regulation on Livestock Disposal: Implications for the Diet of Wolves. *Environmental Management 56*, 890–902. https://doi.org/10.1007/s00267-015-0571-4
- Lanszki, J; Márkus, M; Újváry, D; Szabó A; & Szemethy L. (2012). Diet of wolves Canis lupus returning to Hungary. *Acta Theriol*, *57*(2), *189*–*193*. doi:10.1007/s13364-011-0063-8
- Lino S., Rossa M., Fernandes J. M., Barros T, Lino A., Hipolito D., Ferreira E., Aliácar S. C., Cadete D., Fonseca C., Torres R. T., Rosalino L. M., Carvalho J. (2023). Dog in

- sheep's clothing: livestock depredation by free-ranging dogs may pose new challenges to wolf conservation. *European Journal of Wildlife Research 69:107*, doi:10.1007/s10344-023-01740-9
- Liu, Bingwan & Jiang, Zhigang. (2003). Diet composition of wolvesCanis lupus in the northeastern Qinghai-Tibet Plateau, China. *Acta Theriologica*. 48. 255-263. 10.1007/BF03194165.
- Llaneza, Luis & López-Bao, José Vicente. (2015). Indirect effects of changes in environmental and agricultural policies on the diet of wolves. *European Journal of Wildlife Research*. 61. 895-902. 10.1007/s10344-015-0966-9.
- Lyngdoh, Salvador & Habib, Bilal & Shrotriya, Shivam. (2019). Dietary spectrum in Himalayan wolves: comparative analysis of prey choice in conspecifics across highelevation rangelands of Asia. *Journal of Zoology*. 310. 10.1111/jzo.12724.
- Mattioli, Luca & Apollonio, Marco & Mazzarone, Vito & Centofanti, Ettore. (1995). Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta theriologica*. 40. 387-402. 10.4098/AT.arch.95-36.
- Maheshwari, A., & Sathyakumar, S. (2020). Patterns of Livestock Depredation and Large Carnivore Conservation Implications in the Indian Trans-Himalaya. *Journal of Arid Environments*, 182, 104241. doi:10.1016/j.jaridenv.2020.104241
- Mahmood, Tariq & Ismail, Shakeela & Akrim, Faraz & Farooq, Muhammad & Munawar, Nadeem & Khan, Muhammad. (2021). Diet Composition of Grey Wolf (Canis lupus) Varies Seasonally in Deosai National Park, Gilgit-Baltistan, Pakistan. *Pakistan J. Zool., Vol. 54, Iss. 5, pp. 2267-2275*. https://dx.doi.org/10.17582/journal.pjz/20210406040405
- Mengüllüoğlu D, İlaslan E, Emir H, Berger A. (2019). Diet and wild ungulate preferences of wolves in northwestern Anatolia during winter. *PeerJ.* 7:e7446. doi: 10.7717/peerj.7446. PMID: 31497386; PMCID: PMC6708370.
- Meriggi, A.. Brangi, A.. Matteucci, C. and Sacchi, O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. - *Ecography 19 287-295*.
- Meriggi, A.; Dagradi, V.; Dondina, O.; Perversi, M.; Milanesi, P.; Lombardini, M.; Raviglione, S.; Repossi, A. 2014. Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy. *Ethology Ecology & Evolution*, *1*–23. doi:10.1080/03949370.2014.986768
- Meriggi, A.; Brangi, A.; Schenone, L.; Signorelli, D.; Milanesi, P. (2011). Changes of wolf (Canis lupus) diet in Italy in relation to the increase of wild ungulate abundance.
 Ethology Ecology & Evolution, 23(3), 195–210. doi:10.1080/03949370.2011.577814
- Meriggi, A and Lovari, S. (1996). A Review of Wolf Predation in Southern Europe: Does the Wolf Prefer Wild Prey to Livestock?. *Journal of Applied Ecology*, 33(6), 1561–1571. doi:10.2307/2404794

- Merkle, J. A., Krausman, P. R., Stark, D. W., Oakleaf, J. K., & Ballard, W. B. (2009).
 Summer Diet Of The Mexican Gray Wolf (Canis Lupus Baileyi). *The Southwestern Naturalist*, 54(4), 480–485. http://www.jstor.org/stable/40588583
- Milanesi, P., Meriggi, A., & Merli, E. (2012). Selection of wild ungulates by wolves Canis lupus (L. 1758) in an area of the Northern Apennines (North Italy). Ethology Ecology & Evolution, 24(1), 81–96. https://doi.org/10.1080/03949370.2011.592220
- Morehouse, A.T. and Boyce, M.S. (2011), From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. Frontiers in Ecology and the Environment, 9: 440-445. https://doi.org/10.1890/100172
- Mohammadi A, Kaboli M, Sazatornil V, & Lopez-Bao JV. (2019). Anthropogenic food resources sustain wolves in conflict scenarios of Western Iran. *PLoS ONE 14(6):* e0218345. https://doi.org/10.1371/journal.pone.0218345
- Muhammad, R. K., Mahmood, T., Fatima, H., Akrim, F., Andleeb, S., & Hamid, A. (2020). Distribution, diet menu and human conflict of grey wolf canis lupus in mahoodand valley, swat district, pakistan. *Pakistan Journal of Zoology*, 52(1), 179.
- Mysłajek, R, W. Stachyra P., Figura, M., Nędzyńska-Stygar M.,,ski R., Korga M., Kwiatkowska, i., Stępniak, K, M., Tołkacz, k., and Nowak S.. (2022). Diet of the grey wolf Canis lupus in Roztocze and Solska Forest, south-east Poland," *Journal of Vertebrate Biology* 71(22040), 22040.1-12. https://doi.org/10.25225/jvb.22040
- Nores, C., Llaneza, L. and Álvarez, Á. (2008), Wild boar Sus scrofa mortality by hunting and wolf Canis lupus predation: an example in northern Spain. *Wildlife Biology, 14: 44-51.* https://doi.org/10.2981/0909-6396(2008)14[44:WBSSMB]2.0.CO;2
- Nowak, Sabina & Mysłajek, Robert & Jedrzejewska, Bogumila. (2005). Patterns of wolf Canis lupus predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). *Acta theriologica*. 50. 263–276. 10.1007/BF03194489.
- Nowak, S., Mysłajek, R. W., Kłosińska, A., & Gabryś, G. (2011). Diet and prey selection of wolves (Canis lupus) recolonising Western and Central Poland. *Mammalian Biology* 76(6), 709–715. doi:10.1016/j.mambio.2011.06.007
- Octenjak, D., Pađen, L., Šilić, V. et al. Wolf diet and prey selection in Croatia. Mamm Res 65, 647–654 (2020). https://doi.org/10.1007/s13364-020-00517-8
- Papageorgiou, N., Vlachos, C., Sfougaris A., & Tsachalidis, E. (1994). Status and diet of wolves in Greece. *Acta Theriologica*. *39*. 10.4098/AT.arch.94-48.
- Patalano, M., Lovari, S., Food habits and trophic niche overlap of the wolf Canis lupus, L. 1758 and the red Fox vulpes vulpes (L. 1758) in a Mediterranean mountain area. (1993). *Revue d'Ecologie, Terre et Vie, 1993, 48 (3), pp.279-294*.
- Petridou, Maria & Youlatos, Dionisios & Lazarou, Yorgos & Selinides, Kiriakos & Pylidis, C., Giannakopoulos, A., Kati, V., & Iliopoulos, Y. (2019). Wolf diet and livestock selection in central Greece. *Mammalia*. 83. 530-538. 10.1515/mammalia-2018-0021.

- Rigg, R., & Gorman, M. (2004). Spring-autumn diet of wolves (Canis lupus) in Slovakia and a review of wolf prey selection. *Oecologia 13, 30-41*
- Salvador, A., & Abad, P. L. (1987). Food habits of a wolf population (Canis lupus) in León province, Spain. *Mammalia*, 51(1). doi:10.1515/mamm.1987.51.1.45
- Shabbir, Sara & Anwar, Maqsood & Hussain, Iftikhar & Nawaz, Muhammad. (2013). Food habits and diet overlap of two sympatric carnivore species in Chitral, Pakistan. *Journal of Animal and Plant Sciences*. 23. 100-107.
- Shrestha, A., K. Thapa, S.A. Subba, M. Dhakal, B.P. Devkota, G.J. Thapa, S. Shrestha, S. Malla & K. Thapa (2019). Cats, canines, and coexistence: dietary differentiation between the sympatric Snow Leopard and Grey Wolf in the western landscape of Nepal Himalaya. *Journal of Threatened Taxa* 11(7): 13815–13821. https://doi.org/10.11609/jott.4217.11.7.13815-13821
- Shi, Y., Hoareau, Y., Reese, E.M. et al., (2021). Prey partitioning between sympatric wild carnivores revealed by DNA metabarcoding: a case study on wolf (Canis lupus) and coyote (Canis latrans) in northeastern Washington. *Conserv Genet 22, 293–305*. https://doi.org/10.1007/s10592-021-01337-2
- Sidorovich, V. E., Tikhomirova, L. L., & Jędrzejewska, B. (2003). Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. *Wildlife Biology*, *9*(1), 103–111. doi:10.2981/wlb.2003.032
- Sin T, Gazzola A, Chiriac S, Rışnoveanu G. (2019). Wolf diet and prey selection in the South- Eastern Carpathian Mountains, Romania. *PLoS ONE 14(11): e0225424*. https://doi.org/10.1371/journal.pone.0225424
- Śmietana, W., & Klimek, A. (1993). Diet of wolves in the Bieszczady Mountains, Poland. *Acta theriologica*. *38*. *245-251*. 10.4098/AT.arch.93-20.
- Shrotriya S, Reshamwala HS, Lyngdoh S, Jhala YV and Habib B. (2022). Feeding Patterns of Three Widespread Carnivores—The Wolf, Snow Leopard, and Red Fox—in the Trans-Himalayan Landscape of India. *Front. Ecol. Evol.* 10:815996. doi: 10.3389/fevo.2022.815996
- Tiralla, N., Holzapfel, M. & Ansorge, H. (2020). Feeding ecology of the wolf (Canis lupus) in a near-natural ecosystem in Mongolia. *Mammalian Biology*
- Torres, R.T., Silva, N., Brotas, G., Fonseca, C. (2015). To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (Canis lupus signatus) in a Human-Dominated Landscape in Central Portugal., *PLoS ONE 10(6): e0129379*. doi:10.1371/journal., pone.0129379
- Tourani, M., Moqanaki, E., Boitani, L., & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia*. 78. 117-121. 10.1515/mammalia-2012-0119.
- Trbojević, I., Penezić, A., Kusak, J., Stevanović, O., & Ćirović, D. (2020). Wolf diet and livestock depredation in North Bosnia and Herzegovina. *Mammalian Biology*. 100. 10.1007/s42991-020-00053-7.

- Van Duyne, C., Ras, E., de Vos, A. E. W., de Boer, W. F., Henkens, R. J. H. G., & Usukhjargal, D. (2009). Wolf Predation among Reintroduced Przewalski Horses in Hustai National Park, Mongolia. *The Journal of Wildlife Management*, 73(6), 836–843. http://www.jstor.org/stable/20616729
- Vos, J., (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal., *J. Zool. 251*, 457-462.
- Weber, J. M., & Hofer, B. (2010). Diet of wolves Canis lupus recolonizing Switzerland: A preliminary approach. *Revue Suisse de Zoologie*. 117. 235-241. 10.5962/bhl.part.117783.
- Wagner, C., Holzapfel, M., Kluth, G., Reinhardt, I., & Ansorge, H. (2012). Wolf (Canis lupus) feeding habits during the first eight years of its occurrence in Germany. *Mammalian Biology* 77(3), 196–203.
- Wang, J., Laguardia, A., Damerell, P.J. et al. Dietary overlap of snow leopard and other carnivores in the Pamirs of Northwestern China. Chin. Sci. Bull. 59, 3162–3168 (2014). https://doi.org/10.1007/s11434-014-0370-y
- Werhahn, G., Kusi, N., Li, X., Cheng, C., Lu, Z., Lázaro, M. Raquel & Sillero, C. & Macdonald, D. (2019). Himalayan wolf foraging ecology and the importance of wild prey. *Global Ecology and Conservation*. 20. e00780. 10.1016/j.gecco.2019.e00780.

Golden jackal

- Akrim, F., Mahmood, T., Nadeem, M.S., Dhendup, T. Fatima, H. & Andleeb, S. (2019).
 Diet composition and niche overlap of two sympatric carnivores: Asiatic jackal Canis aureus and Kashmir hill fox Vulpes vulpes griffithii, inhabiting Pir Lasura National Park, northeastern Himalayan region, *Pakistan. Wildlife Biology 2019(1): 1-9.* https://doi.org/10.2981/wlb.00440
- Bošković, I., Šperanda, M., Florijančić, T., Šprem, N., Ozimec, S., Degmečić, D. i Jelkić, D. (2013). Dietary habits of the golden jackal (Canis aureus L.) in the Eastern Croatia. *Agriculturae Conspectus Scientificus*, 78 (3): 245-248. Preuzeto s https://hrcak.srce.hr/106914
- Borkowski, J. & Zalewski, A. (2011). Diet Composition of Golden Jackals in Israel. *Annales Zoologici Fennici*. 48. 108-118. 10.5735/086.048.0203.
- Chourasia, P., Mondal, K., Sankar, K & Qureshi, Q. (2022). Food Habits of Golden Jackal (Canis aureus) and Striped Hyena (Hyaena hyaena) in Sariska Tiger Reserve, Western India.
- Ćirović, D., Penezić, A., Milenković, M., & Paunović, M. (2014). Winter diet composition of the golden jackal (Canis aureus L., 1758) in Serbia. *Mammalian Biology* 79(2), 132–137. doi:10.1016/j.mambio.2013.11.003
- Giannatos, G., Karypidou, A., Legakos, A., Polymeni, R., (2010). Golden jackal (Canis aureus L.) diet in Southern Greece. *Mamm. Biol.* 75, 227–232.

- Khan, K.A., J.A. Khan & N. Mohan. (2017). Winter food habits of the Golden Jackal Canis aureus (Mammalfa: Carnivora: Canidae) in Patna Bird Sanctuary, Uttar Pradesh, Indfa. *Journal of Threatened Taxa 9 10656–1066*; http://dof.org/10.11609/jott.3301.9.9.10656-10661
- Kirkova, Z., Evgeniy, R., Dimitrina, G. (2011). Studies on Feeding Habits and Parasitological Status of Red Fox, Golden Jackal, Wild Cat and Stone Marten in Sredna Gora, Bulgaria. *Journal of Life Sciences 5 264-270*.
- Lanszki, J., & Heltai, M. (2002). Feeding habits of golden jackal and red fox in south-western Hungary during winter and spring. *Mammalian Biology*, 67(3), 129–136. doi:10.1078/1616-5047-00020
- Lanszki, J., Giannatos, G., Dolev, A. et al., (2010). Late autumn trophic flexibility of the golden jackal Canis aureus. *Acta Theriol 55*, *361–370*. https://doi.org/10.1007/BF03193239
- Lanszki, J. & Hayward, M. & Nagyapáti, N. (2018). Feeding responses of the golden jackal after reduction of anthropogenic food subsidies. *PLOS ONE*. *13*. *e0208727*. 10.1371/journal.pone.0208727.
- Merkle, J. A., Krausman, P. R., Stark, D. W., Oakleaf, J. K., & Ballard, W. B. (2009). Summer Diet Of The Mexican Gray Wolf (Canis Lupus Baileyi). *The Southwestern Naturalist*, *54*(4), *480*–*485*. http://www.jstor.org/stable/40588583
- Mohammadi, A., Kaboli, M., Sazatornil, V., Lopez-Bao, J. V. (2019). Anthropogenic food resources sustain wolves in conflict scenarios of Western Iran. *PLoS ONE 14(6):* e0218345. https://doi.org/10.1371/journal.pone.0218345
- Mahmood, T. (2013). Diet composition of Asiatic jackal (Canis aureus) in Margallah Hills National Park, Islamabad, Pakistan. Journal of Animal and Plant Sciences. *The Journal of Animal & Plant Sciences*, 23(2): Page:444-456 ISSN: 1018-708
- Majumder, A., K. Sankar, Q. Qureshi, S. Basu (2011). Food habits and temporal activity patterns of the Golden Jackal Canis aureus and the Jungle Cat Felis chaus in Pench Tiger Reserve, Madhya Pradesh, India. *Journal of Threatened Taxa 3(11): 2221–2225*.
- Markov, G., Lanszki, J. (2012). Diet composition of the golden jackal, Canis aureus in an agricultural environment. *Folia Zoologica*, 61(1), 44–48. doi:10.25225/fozo.v61.i1.a7.2012
- Nadeem, M., Naz, R., Shah, S., Beg, Mirza, Kayani, A., Mushtaq, M., Mahmood, T. (2012). Season-and locality-related changes in the diet of Asiatic jackal (Canis aureus) in Potohar, Pakistan. *Turkish Journal of Zoology*. *36*. 798-805. 10.3906/zoo-1109-16.
- Penezić A., Ćirović D. (2015b). Diet of adult and juvenile golden jackals (canis aureus) during cubs' dependency stage. *Balkan Journal of Wildlife Research*. *2(1)*: 27-32. http://dx.doi.org/10.15679/bjwr.v2i1.27
- Raichev, E. G., Tsunoda, H., Newman, C., Masuda, R., Georgiev, D. M., Kaneko, Y. (2013). The Reliance of the Golden Jackal (Canis aureus) on Anthropogenic Foods in winter in Central Bulgaria. *Mammal Study*, 38(1): 19–27. doi:10.3106/041.038.0102

- Shabbir, S., Anwar, M., Hussain, I., Nawaz, M.A. (2013). Food habits and diet overlap of two sympatric carnivore species in chitral, Pakistan. *Journal of Animal and Plant Sciences*, 23: 100-106.
- Tourani, M., Moqanaki, E., Boitani, L., Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia*, 78: 117-121. 10.1515/mammalia-2012-0119.
- 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. *Journal of Zoology*, 303(1): 64-71. doi:10.1111/jzo.12464
- Vlasseva, A., Chassovnikarova, T., Mitkovska, V., Dimitrov, H. (2020). Compensatory Increase of the Reproductive Capacity of the Red Fox Vulpes vulpes (L., 1758) in Sympatric Coexistence with the Golden Jackal Canis aureus L., 1758. *Acta Zoologica Bulgarica*. Supplement. 217-222.

Stray dog

- Carrasco-Román, E., Medina, J.P., Salgado-Miranda, C., Soriano-Vargas, E., & Sánchez-Jasso, J.M. (2021). Contributions on the diet of free-ranging dogs (Canis lupus familiaris) in the Nevado de Toluca Flora and Fauna Protection Area, Estado de México, Mexico. Revista Mexicana de Biodiversidad.
- Lino S., Rossa M., Fernandes J. M., Barros T, Lino A., Hipolito D., Ferreira E., Aliácar S. C., Cadete D., Fonseca C., Torres R. T., Rosalino L. M., Carvalho J. (2023). Dog in sheep's clothing: livestock depredation by free-ranging dogs may pose new challenges to wolf conservation. *European Journal of Wildlife Research 69:107*, doi: 10.1007/s10344-023-01740-9
- Silva-Rodríguez, E.A., Ortega-Solís, G.R. & Jiménez, J.E. (2010). Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-domination landscape in southern Chile. *Austral Ecology*, 35(7): 765-777.
- Vanak, A.T, & Gompper M,T,. (2009). Dietary Niche Separation between Sympatric Free-Ranging Domestic Dogs and Indian Foxes in Central India, *Journal of Mammalogy*, 90(5): 1058–1065, DOI: 10.1644/09-MAMM-A-107.1

Appendix III – Habitat around Ponichala Natural Reserve

