Interactions between livestock guarding dogs and wildlife in the Carpathian Mountains, Romania

Bethany Rose Smith

August 2023

A thesis submitted in partial fulfilment of the requirements of Nottingham Trent University for the degree of Doctor of Philosophy

Copyright Statement

Abstract

Livestock guarding dogs (LGDs) are often suggested as a tool to help facilitate human-wildlife coexistence because they are considered effective at preventing livestock losses and reducing persecution of large carnivores. As LGDs have been observed chasing and killing wildlife, they could be perceived as predators or competitors in the environment, yet little is known about how the use of LGDs affects co-occurring wildlife. This research aimed to understand the ecological effects of using LGDs by 1) determining the wildlife species chased, killed, and/or consumed by LGDs, 2) quantifying LGD roaming behaviours by breed, sex, age, and reproductive status, and 3) quantifying spatial and temporal responses of wildlife to LGD presence.

A detailed overview of the potential and currently reported ecological effects of using LGDs was gathered via a literature review. Then, in 2021, LGD-wildlife interactions were investigated in the Carpathian Mountains, Romania. Thirteen sites were visited where shepherds were interviewed, 129 scats collected, and a total of twelve sheep and 40 LGDs GPS-tracked for an average of three weeks. Camera traps were deployed across 315 km^2 covering both pasture and forest. Wildlife remains in the scats were identified via traditional methods including microscopic hair analysis. Roaming behaviours were investigated from the GPS data by calculating pairwise distances between each sheep and LGD and the overlap in their daily home ranges, which were estimated using the Local Convex Hull (LoCoH) method. Habitat use by grey wolves, brown bears, red foxes, red deer, and wild boars was investigated from the camera trap data via detection rates, single- and two-species occupancy models, and activity patterns estimated by a nonparametric kernel density approach.

There were 56 records in the literature widely reporting, mostly anecdotally, LGDs interacting with wildlife. Similarly, all thirteen shepherds reported that their LGDs chased wildlife and seven reported that their LGDs had injured or killed wildlife. However, there were low occurrences of wildlife in LGD scats with only 9% containing wild vertebrate remains (mostly wild boar in scats collected at one site on one day). Some roaming occurred with LGDs being found up to 4 km away from sheep, but LGDs predominantly remained in close proximity to livestock. On average, LGDs were within 200 m of the sheep during the day and within 100 m at night whilst sheep were enclosed in the sheepfold. Differences in distances between LGDs and sheep, and overlap in daily home ranges, were not predicted by LGD breed, sex, age, or reproductive status. Only red deer showed potential spatial and temporal avoidance of LGDs with lower detection rates, lower occupancy, and a reduction in daytime activity in areas of more frequent LGD use. Grey wolves were potentially attracted to areas used by LGDs. However, it was not possible to disentangle the effects of LGDs alone and the effects of LGDs, sheep, and shepherds combined.

This is the first large-scale study assessing multiple elements of LGD behaviours and wildlife responses. Overall, there was little empirical evidence to suggest that LGDs have substantial detrimental effects on co-occurring wildlife in the Romanian Carpathian Mountains. These results help to establish that LGDs, both purebreds and mixed-breeds, are a suitable candidate tool for reducing the need for lethal control of wild predators and possibly helping to facilitate human-wildlife coexistence.

Contribution statement

I was responsible for the experimental design and analyses contained within this thesis with guidance from my supervisory team – Dr Antonio Uzal, Dr Richard Yarnell, and Dr Katherine Whitehouse-Tedd. The research was conducted in collaboration with Fauna & Flora who provided assistance with the field element of this research. Hence, supervisory guidance was also provided by Dr Iain Trewby from Fauna & Flora. Fieldwork was carried out by me in collaboration with several Fauna & Flora team members and with assistance from two master's students at Nottingham Trent University (NTU). Some fieldwork was conducted in my absence by members of the Fauna & Flora team, primarily checking camera traps over the winter months. Fieldwork was primarily conducted by me and:

Mircea Marginean (Fauna & Flora) – initial stakeholder engagement; shepherd interviews; GPS tracker deployment; scat collection; scat washing; camera trap deployment, checking, and collection.

Radu Popa (Fauna & Flora) – initial stakeholder engagement; GPS tracker deployment; scat collection; camera trap deployment, checking, and collection.

Mihaela Faur (Fauna & Flora) – initial stakeholder engagement; shepherd interviews; GPS tracker deployment; scat collection.

Alicia Morley (NTU) – collection of camera traps; camera trap image processing; scat washing.

Katherine Campbell (NTU) – GPS tracker deployment; scat collection; camera trap deployment and checking.

I was present at all but two shepherd interviews and with help from those above, I: deployed GPS trackers on sheep and dogs; deployed, checked, and collected camera traps then processed the majority of the resulting images; and collected and washed dog scats then identified the prey remains within (with the help of **Professor Dawn Scott**, NTU).

COVID-19 impact statement

This research was conducted from 2020 to 2023 during the COVID-19 pandemic. This impact statement aims to provide a brief overview of the substantial effects that the pandemic had on the research conducted for this thesis.

The study was originally designed to take place in South Africa with three field seasons conducted over two years. The aim of the project was to investigate the ecological effects of using livestock guarding dogs (LGDs) by quantifying LGD-wildlife interactions and comparing the presence of wildlife on farmland with and without LGDs. However, due to COVID-19 travel restrictions I was unable to start fieldwork in 2020 and instead focused on conducting the literature review that is presented in Chapter 2. When it eventuated that travel to South Africa in 2021 would not be permitted still, I established a collaboration with Fauna & Flora to work on LGDs in Romania instead.

The change in field site required me to adjust my objectives and previously planned methods. This was primarily due to the difference in how LGDs are used in the two countries with LGD use being traditional in Romania but more recently introduced in South Africa. Thus, not all farmers use LGDs in South Africa but almost all shepherds use LGDs in Romania. As such, it was not possible to compare wildlife activity in regions of livestock use with and without LGDs in Romania, as was initially planned in South Africa. Instead, wildlife presence and activity had to be assessed according to the distance from pastures in Romania.

After adjusting my work schedule for Romania, I had planned to conduct fieldwork from April 2021 onwards in order to capture the transhumance period whereby shephers graze their livestock on higher altitude pastures from May through October. However, legislative changes following the UK's withdrawl from the European Union and uncertainties relating to travel during the pandemic caused a further delay to both my arrival in Romania and the arrival of some of my research equipment. Consequently, I could not deploy any camera traps until July 2021 meaning that I missed collecting data on the presence of wildlife around pastures for the first two months (May and June) that LGDs were present.

Despite the challenges presented by the COVID-19 pandemic, I adapted my research to still collect sufficient data to produce a scientifically rigorous contribution to the understanding of LGDs in a country where their use is little studied.

Acknowledgments

It has been a privilege to carry out this PhD research and I thank NTU for funding my PhD with a scholarship and additional funds for purchasing research equipment and attending conferences. I have learned a great deal and developed as a research scientist, and as a person, throughout this process, which I will always be grateful for.

I owe a huge thank you to my three supervisors – Dr Antonio Uzal, Dr Richard Yarnell, and Dr Katherine Whitehouse-Tedd – for the opportunity to conduct this research in the first place. Richard, thank you for everything you have taught me about GPS tracking and camera trapping, and for your patience with certain elements of the project (am I allowed to say the forbidden word 'GoPro' here?). Kat, you have been amazing at guiding me through writing about sensitive topics and I will be forever grateful for the wonders you have worked on my late-night ramblings – thank you for sticking with me through the large time zone difference after you moved! Antonio, thank you so much for taking the reins from Kat as my Director of Studies and guiding me through the second half of my PhD journey. When I have struggled to stay focused you have gotten me back on track and I have appreciated knowing that you will always be there to help me when I ask. And, of course, thank you for giving me the opportunity to see my first brown bear in the wild! I would also like to thank Professor Dawn Scott at NTU for helping me get started with the microscopic hair identification, as well as Matt Binstead from the British Wildlife Centre for sending red deer, roe deer, and pine marten hair samples to me. For research equipment, I would like to thank Tractive for providing and servicing dog GPS trackers and I would like to extend a special thank you to Nora Rust and Amy Fisk from the customer care team at Tractive who went above and beyond to ensure I had working equipment and accurate data.

This project would not have been possible without the generous support of Fauna & Flora, the shepherds who participated in the study, and the game managers who permitted the study and helped with camera trap deployment – thank you! I am especially grateful to Dr Iain Trewby who saved my PhD by offering to host me in Romania when the COVID-19 pandemic meant I could no longer travel to South Africa. Thanks for also storing all of my samples in your freezer and allowing us to drop bags of dog scats at your door! To everyone in the Fauna & Flora team – Iain, Mihaela, Mircea, Radu, Razvan, Cosmin, and Anca – thank you for everything, it has been a pleasure to work with you all in such a beautiful country. In particular, I would like to thank Mihaela Faur for getting my project off the ground in Romania and co-ordinating fieldwork activities within the team. I would also like to thank Radu Popa for imparting reems of invaluable knowledge on livestock guarding dogs and Romanian history whilst helping in the field. Last but not least, thank you to Mircea

Marginean for his dedication to my PhD fieldwork as if it were his own. There are no words to express how grateful I am for your help, enthusiasm, and friendship through the lows (DHL shipping dramas, getting stuck in the snow, hiking through the heat to stolen cameras) and the highs (falling in the snow, sleeping in the car, the lingering handshake). Thank you for everything, except the ţuică. Thank you also to Katherine Campbell and Alicia Morley who helped with fieldwork activities whilst conducting their master's at NTU. You both contributed significantly to my PhD and to the fun times had in the field. Alicia, I have to say a huge thank you for being a trooper whilst washing all of the dog scats with me! Finally, for fieldwork-related thanks, I must say thank you to Amanda and Jon Williams who took me under their wing and welcomed me into their beautiful home in Romania. You are now my adopted parents and I look forward to my annual visits from here on.

That leads me on to thanking my parents (Helen and Steve), my grandparents (Val, Coop, Barbara, and Frank), and entire family, for their unconditional support, even when they have no idea what I am doing beyond 'in the mountains somewhere chasing dogs and looking for wolves'. I am extremely grateful as well to my partner who has stuck with me whilst I have been away conducting fieldwork for months on end. Hugh, thank you for always supporting my wildlife and career dreams no matter the emotional cost, and for feeding me / generally keeping me alive in these last few chaotic months of PhD thesis writing. I also could not have gotten through this process without my closest friends. Thank you in particular to Candice, Marisa, Faye, Tasha, Lanoue, Lizzie, Charlie and Sophie for listening to me drone on about my PhD and for visiting me in Romania. Thank you to the whole NTU PhD community, especially Lori, Helle, Jess, Kate, Aurelie and Anthony who have kept me sane, put me up in their homes, and offered invaluable scientific guidance. Thank you also to my bioacoustics research group for keeping me going and providing cool side projects to distract me! I owe an especially huge thank you to Dr Arik Kershenbaum for his continued mentorship and friendship since my undergraduate degree - I think I owe you a lifetime's supply of beer.

And finally, there were many dogs involved in my PhD, but I owe my greatest canine thanks to my own little fluffy puppy who started this PhD journey with me but sadly didn't make it to the end. Bodhi, you were the best little dog in the world, and I will miss you forever. Thank you for helping test my research equipment but most importantly, thank you for the pillow ruffles, meerkat poses, excuse for more walks during the lockdowns, and generally for the eleven years of your unconditional love.

"Dogs are not our whole life, but they make our lives whole."
Roger A. Caras

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Chapter 1: General introduction

With the increasing expansion of humans into rural areas, and in some cases the recovery and expansion of wildlife into human-dominated landscapes (Chapron *et al.* 2014), there is an ever-increasing risk of humans and wildlife encountering one another. As a result, conflicts over or about wildlife (human-wildlife conflicts) are escalating around the world (Penteriani *et al.* 2016; Gross *et al.* 2021; Bombieri *et al.* 2023). Though several definitions exist, human-wildlife conflict generally refers to negative interactions between people and wildlife that results in harm to both parties. Conflicts typically arise when wildlife pose a threat, whether real or perceived, to human life or livelihoods (Woodroffe *et al.* 2005a; Sillero-Zubiri *et al.* 2007; Torres *et al.* 2018). The risk to livelihoods typically stems from wildlife-inflicted damages such as crop-raiding and livestock predation, or from competition for natural resources, such as between people harvesting fish and wild piscivores (Peterson *et al.* 2010; Cook *et al.* 2022). The risk to human life involves the likes of physical attacks by predators, zoonoses, and wildlife collisions with vehicles; the latter clearly presenting a direct negative outcome for both the people and wildlife involved (Grilo *et al.* 2020; Moore *et al.* 2023). Thus, human-wildlife conflicts arise under a myriad of contexts and involve a huge variety of species from across the globe (Inskip and Zimmerman 2009; Torres *et al.* 2018), though conflicts are more widely understood in terrestrial than marine systems (Guerra 2019).

Whilst the cost to wildlife of human-wildlife conflict is often direct mortality from the interaction or subsequent persecution from humans, the costs to humans include financial, emotional, and opportunity costs (Dickman 2010; Barua *et al.* 2013). Financial costs are as named – economic costs such as a loss of income or a monetary expense incurred – whereas emotional and opportunity costs are more nuanced and less well understood (Manoa *et al.* 2021). Emotional costs include the sadness, stress, anxiety, and/or fear experienced by people due to the likes of livestock or pet loss, or when living in fear of attacks from large predatory wildlife (Barua *et al.* 2013; Stăncioiu *et al.* 2019). Opportunity costs refer to missed opportunities that arise as a result of human-wildlife conflicts, for example when people need to spend more time protecting their livestock or crops from wildlife at the expense of other activities (Barua *et al.* 2013). Though costs are felt globally, there is evidence of relatively greater costs and impacts associated with human-wildlife conflicts in developing economies (Braczkowski *et al.* 2023). To reduce costs incurred as a result of wildlife activities, humans have historically responded with lethal management of wildlife (Treves and Naughton-Treves 2005; Woodroffe *et al.* 2005b; Allen *et al.* 2023), though a suite of nonlethal management tools are constantly being developed and employed to help facilitate coexistence with wildlife (Sillero-Zubiri *et al.* 2007; Dickman 2010).

1.1 Lethal management of wildlife

Lethal management of wildlife typically takes one of three forms: population control – culling of a species to reduce or prevent conflicts; problem animal control – killing only the individual(s) responsible for conflicts (typically conducted at the government or institution level); or retaliatory killing – killing of a species in response to costs incurred, often in an indiscriminate way that does not target the individual animals responsible (typically conducted by members of an affected community rather than by government or institutions) (Dickman 2010). Whether lethal management of wildlife works at reducing conflicts is debated (Treves and Naughton-Treves 2005). In some cases, lethal removal is perceived as more effective, and cheaper, than non-lethal methods (Thorn *et al.* 2015; Drouilly *et al.* 2023) and its implementation, regardless of effectiveness, can help reverse disempowerment felt by local people living alongside wildlife and help increase overall tolerance towards the species in question (Majić *et al.* 2011; Hartel *et al.* 2019; Anderson 2021). Lethal management can also be particularly successful at reducing conflicts when damages are proportional to wildlife abundance and populations are sufficiently reduced (Herfindal *et al.* 2005; Bradley *et al.* 2015), or when specifically targeting particular 'problem animals' (Swan *et al.* 2017). Using lethal methods has also been theorised to help create a 'landscape of fear' that keeps wildlife away from particular areas, thus providing a long-term effect that is reinforced by the real risk of mortality imposed in the landscape from humans (Cromsigt *et al.* 2013; Meuret *et al.* 2021).

On the contrary, lethal management of wildlife is often expensive and not necessarily successful at reducing conflicts (McManus *et al.* 2015). In some areas, wildlife densities are not proportional to the damages caused (Fernández-Gil *et al.* 2016; Dalerum *et al.* 2020). In this case, reducing the numbers of the species involved in the conflict would not affect the level of damage or risk of recurrence of conflicts (Obbard *et al.* 2014; Santiago-Avila *et al.* 2018). Areas from which wildlife are removed can also simply be recolonised by neighbouring individuals leading to a continuation of, or even increase in, conflicts. For example, lethal management of cougars (*Puma concolor*) in the USA (Peebles *et al.* 2013) and grey wolves (*Canis lupus*) in Spain (Fernández-Gil *et al.* 2016) has been associated with an increase in livestock predation the following year, possibly through immigration and changes to the social structure of populations (Peebles *et al.* 2013; Borg *et al.* 2015). Similarly, compensatory demographic processes, such as increased reproduction, can even counter lethal management with increasing rather than decreasing populations (e.g. Minnie *et al.* 2016). New conflicts, or exacerbation of existing conflicts, can also arise if the killing of one species alters the behaviour or abundance of another, for example with mesopredator release (Prugh *et al.* 2009). If these mesopredators were also involved in human-wildlife conflicts, then the opposite of the desired effect might be observed. Lethal removal of animals can also shift the conflict elsewhere, meaning any local benefits are offset by detrimental effects for people living and working in the surrounding areas (Santiago-Avila *et al.* 2018).

Lethal wildlife management also has welfare implications (Nunny 2020) and other negative, or unintended, impacts on wildlife and ecosystems (Woodroffe *et al.* 2005b). First and foremost is that human persecution of wildlife can be substantial and is responsible for species population declines and even extinctions worldwide (Woodroffe *et al.* 2005b; Inskip and Zimmerman 2009). For example, large carnivores are often the taxa responsible for attacks on humans and livestock and have been heavily persecuted in response (Inskip and Zimmerman 2009; Ripple *et al.* 2014). Due to their low population densities, low reproductive rates, and the need for large home ranges, large carnivores are particularly vulnerable to persecution and many are now classified as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List (Ripple *et al.* 2014). Dramatic declines in large predator populations caused by lethal control has major implications for ecosystem functioning (Inskip and Zimmerman 2009; Colman *et al.* 2014; Thorn *et al.* 2015; Kuijper *et al.* 2016). Furthermore, it is not just target species that are killed as many non-target species can also be substantially impacted by indiscriminate forms of lethal control such as poisoning (Glen *et al.* 2007; Ogada 2014). Consequently, lethal management is now illegal, heavily criticised, and socially unacceptable in many regions (Treves *et al.* 2006; Allen *et al.* 2023). Though the killing of wildlife can serve many necessary ecological, economic, and social purposes (Linnell *et al.* 2017; Allen *et al.* 2023), it is critical to find effective, humane solutions that help facilitate human-wildlife coexistence (Sillero-Zubiri and Switzer 2001; Sillero-Zubiri *et al.* 2007).

1.2 Non-lethal management of wildlife

There are a plethora of non-lethal methods that aim to manage wildlife populations and mitigate conflicts without intentionally harming wildlife (Shivik 2004; Breitenmoser *et al.* 2005; Dickman 2010). First, modification of human behaviours can reduce conflicts, such as reducing risky behaviours, reducing attractants that draw wildlife into human-populated areas, and adopting protective measures such as improving livestock husbandry techniques (Breitenmoser *et al.* 2005; Carter and Linnell 2016; Penteriani *et al.* 2017). There are also many methods that rely on modifying the behaviour of wildlife, such as animal conditioning interventions (Snijders *et al.* 2019) and deterring animals from an area with the use of visual, auditory, or chemical repellents (Shivik 2006; Schakner and Blumstein 2013). Wildlife can also be deterred or excluded from areas with the use of human or animal guardians (Meadows and Knowlton 2000; Rigg 2001), or through physical barriers such as fencing and netting (Hayward and Kerley 2009). Instead of excluding wildlife from areas, they can also be attracted elsewhere with the use of diversionary and supplementary feeding

(Kubasiewicz *et al.* 2016), or, often only used in extreme cases, problem animals can be translocated to more suitable habitat (Bradley *et al.* 2005; Langridge *et al.* 2021). Finally, there are also non-lethal methods to reduce wildlife populations such as surgical sterilisation and the use of chemical contraceptives (Bromley and Gese 2001; Massei and Cowan 2014; Denicola and Denicola 2021).

Overall, there is little robust empirical evidence on the effectiveness of many non-lethal methods (Eklund *et al.* 2017; van Eeden *et al.* 2018b). Nonetheless, some methods certainly have been shown to be effective at reducing wildlife-inflicted damages (at least in the short-term) and more so than lethal management methods (Treves *et al.* 2016). For example, chemical and visual repellents involving chilli peppers and flashing lights reduce crop-raiding by elephants (Adams *et al.* 2021; Montgomery *et al.* 2022). However, results from testing the different methods are often mixed and depend on the context and target species. For example, one predator-deterrent method being trialled is the use of Foxlights® (Bexley North, Australia); different-coloured lights that flicker at random time-intervals to mimic a human with a torch. This system was found to be somewhat successful at deterring cougars though not Andean foxes (*Lycalopex culpaeus*) from farms in Chile (Ohrens *et al.* 2019), but appeared to be an attractant to red foxes (*Vulpes vulpes*) at a farm in Australia (Hall and Fleming 2021). Even when non-lethal methods are effective, habituation to these methods could mean they are not long-term solutions (Smith *et al.* 2000b; Musiani *et al.* 2003; Shivik 2006; Miller *et al.* 2016; Khorozyan and Waltert 2019). Furthermore, the implementation of non-lethal methods, if not employed at large scales across landscapes, can simply shift the conflict elsewhere rather than resolving the root issue (Osipova *et al.* 2018).

As with lethal management, there can be unintended consequences of non-lethal management. To take fencing as an example, a growing body of literature is acknowledging the social and ecological effects of using fences as they can exclude people and non-target wildlife from lands, trap and kill wildlife, fragment habitats, and act as a barrier to wildlife movements and gene flow (Hayward and Kerley 2009; Jakes *et al.* 2018; McInturff *et al.* 2020; Smith *et al.* 2020b). Such knock-on effects are not limited to fences as any alterations to wildlife populations and/or behaviours will induce some level of ecological knock-on effect. For example, in some cases diversionary feeding of ungulates concentrates wildlife in small areas leading to overgrazing and changes in soil and vegetation characteristics (Pascual-Rico *et al.* 2018) and has even been found to increase predation on ground-nesting birds in these areas due to attracting predators (Selva *et al.* 2014). Furthermore, although non-lethal management is often assumed to impose fewer welfare implications for animals, little research exists to evidence this and methods that seem humane, such as translocation of problem animals, could induce high levels of stress and mortality and the fates of translocated animals have rarely been monitored (Massei *et al.* 2010). As such, it is critical that all interventions to mitigate human-wildlife conflicts, whether lethal or non-lethal, are assessed through an objective scientific lens with both their effectiveness and efficiency at reducing conflicts, and direct and indirect ecological consequences and welfare implications taken into consideration.

1.3 A focus of on livestock guarding dogs

Livestock guarding dogs (LGDs) are specialised working dog breeds whose role it is to protect livestock from wild predators. Their use originated in Europe and Asia but has since been adopted around the world (Rigg 2001). In some countries, LGD use has been reintroduced where the practice was largely forgotten e.g. Mongolia (Lieb *et al.* 2021), but in others LGDs have been introduced as a new intervention tool, either by transporting LGD breeds such as the Maremma, Great Pyrenees, and Anatolian Shepherd to other countries (van Bommel and Johnson 2012; Marker *et al.* 2021; van Bommel and Johnson 2023) or using local domestic dog breeds in lieu of LGD breeds (Van Der Weyde *et al.* 2020; Horgan *et al.* 2021). Official pure breeds of LGD have been selectively bred over millennia for traits that make them effective protectors of livestock from wild predators (Rigg 2001). These traits are typically: trustworthiness (lack of predatory behaviour towards livestock), attentiveness (the tendency for the dog to stay with and watch the livestock), and protectiveness (the tendency for the dog to defend livestock from perceived threats) (Lorenz and Coppinger 1986). Generally, LGDs are raised with livestock from an early age so that they form a strong bond with them facilitating their protection of livestock as adults.

Protection of livestock is usually in the form of predator deterrence through protective displays (visual, auditory and perhaps olfactory deterrents), often without physical conflict (Allen *et al.* 2017b; van Bommel and Johnson 2017), though fights with target predators are observed (Landry *et al.* 2020; Smith *et al.* 2020a). Most commonly, LGDs are used to protect small ruminants such as goats and sheep (Rigg 2001; van Eeden *et al.* 2018b), but are also in more recent years used with cattle (VerCauteren *et al.* 2008; Gehring *et al.* 2011b; VerCauteren *et al.* 2012; Urbigkit 2019) and poultry (Roddick *et al.* 2022; McKellar *et al.* 2023). Whilst primarily used to protect livestock from predators, LGDs have also been suggested to play a role in helping deter non-target species, such as wild ungulates, thus reducing potential for disease transmissions between wildlife and livestock (VerCauteren *et al.* 2008). Furthermore, LGDs are being used in wildlife conservation projects. For example, the use of LGDs to protect little penguins (*Eudyptula minor*), Australasian gannets (*Morus serrator*) and Eastern barred bandicoots (*Perameles gunnii*) from wild predators is being trialled in Australia (van Bommel 2010; King *et al.* 2015; Parrott *et al.* 2017).

In contrast to many other methods, the effectiveness of LGDs as predator deterrents has been assessed around the world with studies frequently revealing a significant perceived or measured reduction in livestock losses after LGD placement on farms (Andelt 1992; Espuno *et al.* 2004; Marker *et al.* 2005a; Marker *et al.* 2005c; Gehring *et al.* 2010; van Bommel and Johnson 2012; Potgieter *et al.* 2013; Rust *et al.* 2013; Potgieter *et al.* 2016; Eklund *et al.* 2017; Kinka and Young 2019a), which can last for long time periods (Marker *et al.* 2021; van Bommel and Johnson 2023). The use of LGDs against not just terrestrial predators, but also avian predators such as black vultures in the USA, has also been perceived to be effective with regards to reducing livestock losses (Wahl *et al.* 2023). The ability of LGDs to prevent livestock predation and subsequently increase farmer-tolerance towards predators in some cases (González *et al.* 2012; Rust *et al.* 2013; Potgieter *et al.* 2016) has led to conservation organisations promoting the use of LGDs as a human-wildlife conflict mitigation measure. However, there are studies in which LGDs have not been associated with a reduction in livestock losses (Bruns *et al.* 2020; Davoli *et al.* 2022) and their effectiveness at deterring predators and protecting livestock has scarcely been quantified in a rigorous, controlled manner (Treves *et al.* 2016; van Eeden *et al.* 2018a; van Eeden *et al.* 2018b). There is also currently little to no quantitative evidence that their use benefits predator conservation due to the difficulty of conducting long-term studies on predator population dynamics (Smith *et al.* 2020a; Chapter 2).

Human-wildlife conflicts are socially complex and may not be solved simply by reducing wildlife-inflicted damages (Dickman 2010; Thorn *et al.* 2015; Zimmermann *et al.* 2021). Studies on whether LGDs improve human attitudes towards conflict species are currently rare, although one such study on this topic from the USA found that the use of LGDs has not been accompanied by more positive attitudes towards brown bears (*Ursus arctos*) or grey wolves amongst farmers (Kinka and Young 2019b). When LGDs are killed by predators whilst defending livestock, this could worsen human tolerance of predators and increase conflicts (Mertens and Schneider 2005; Bangs *et al.* 2005). Conflicts might also increase in other areas if LGDs push predators away towards unprotected livestock herds leading to an increase in livestock predation elsewhere. Thus, human-human conflicts could arise between those who do and do not use LGDs. Similarly, human-human conflicts could arise over the use of LGDs with neighbours complaining about LGDs barking (McKellar *et al.* 2023) or even killing LGDs that roam onto or near their land (Marker *et al.* 2005b; van Bommel and Johnson 2023). Conflicts also arise where LGDs are free-roaming in landscapes used by humans for recreational activities such as hiking and mountain biking as there are issues over LGDs harassing and even biting people (Mosley *et al.* 2020; Salvatori *et al.* 2020a). Thus, disentangling the role of LGDs in mitigating human-wildlife conflicts is more complex than measuring livestock losses alone.

Despite the uncertainty over the role of LGDs in mitigating human-wildlife conflicts, they are generally considered to be effective at protecting livestock when used correctly. However, of the predator-deterrent methods available, LGDs are particularly interesting because, unlike static, inanimate measures such as electric fencing and flashing lights, LGDs are living, biological control agents (Allen *et al.* 2019a). Thus, LGDs are quite unique in the non-lethal management toolbox and could have many unintended impacts on the environment they are used in. Primarily this is due to their nature as free-ranging domestic dogs. A growing body of research is starting to address the issue of domestic dogs acting as predators and trophic regulators (Ritchie et al. 2014), impacting wildlife through predation, fear of predation, competition, harassment, hybridisation and disease transmission (Young *et al.* 2011; Hughes and Macdonald 2013). The most recent review on the impacts of domestic dogs on wildlife suggested that dogs threaten at least 188 species worldwide (Doherty *et al.* 2017), and they have been shown to facilitate trophic cascades (Suraci *et al.* 2016). Despite this, the potential impacts of LGDs on wildlife have remained relatively understudied. There is some evidence that wildlife can coexist alongside LGDs (Spencer *et al.* 2020), but it is also possible that any reduction in depredation of livestock, or mitigation of human-wildlife conflicts involving large predators, occurs alongside other unintended ecological effects.

First, it has been suggested that LGDs could have significant welfare implications for the species they are intended to manage (Allen *et al.* 2019a). The authors of this paper argue that the welfare impacts of predation and fear of predation imposed by LGDs on wild species are similar, if not worse, than those caused by lethal control methods such as trapping and poisoning. In a response to this paper, others argue that LGDs “rarely engage in direct aggressive interactions with other species” (Johnson *et al.* 2019). However, there are very few empirical studies quantifying the interactions between LGDs and wildlife and whilst rare, there are a few studies and anecdotal reports of LGDs harassing, chasing, and killing wildlife (Timm and Schmidt 1989; Hansen and Bakken 1999; Gehring *et al.* 2010; Landry *et al.* 2020; Whitehouse-Tedd *et al.* 2020; Smith *et al.* 2020a). For example, in Namibia more black-backed jackals (*Lupulella mesomelas*) and caracals (*Caracal caracal*) were killed by LGDs and farmers combined after LGD placement than by farmers alone before LGD placement (Potgieter *et al.* 2016). Lethal interactions between LGDs and wildlife are not limited to target predator species either. A recent study reported almost as many lethal interactions between LGDs and wild herbivores in South Africa as LGDs and wild carnivores (Whitehouse-Tedd *et al.* 2020) and another in the USA reported that LGDs killed mesopredators including northern raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), red foxes, and skunks (Gehring *et al.* 2010). Thus, there are some potential conservation concerns over negative interactions between LGDs and wildlife.

If LGDs chase and kill wildlife, they could be perceived as predators in their environments with a myriad different ways in which their presence and behaviour could then influence the behaviour, physiology, and even populations of co-occurring wildlife (Say-Sallaz *et al.* 2019; Smith *et al.* 2020a; Chapter 2). For example, if seen as a predator, LGDs could induce fear responses in prey and competitor species, which might present as hormonal changes through stress, alterations to activity patterns and habitat use, or increased vigilance at the expense of foraging (Laundré *et al.* 2010; Say-Sallaz *et al.* 2019). The underlying ecological theory of LGD use is the disruption of optimal predator foraging by increasing the real and perceived risk to the individual of preying on livestock (Bagchi 2019; Haswell *et al.* 2019; Gaynor *et al.* 2020), thus some level of predator behaviour modification is expected. However, the extent and implications of such changes are currently not well-studied despite the potential for cascading ecological knock-on effects (Estes *et al.* 2011; Ripple *et al.* 2014; Suraci *et al.* 2016). Given the current trends in increasing human-wildlife conflicts globally, and the increasing advocacy of LGDs as a method for reducing conflicts over livestock predation, it is imperative that more quantitative studies are conducted on every facet of LGD use. For LGDs to be truly beneficial for conservation, the ecological consequences of using LGDs, starting with how they interact with wildlife and the outcomes of these interactions, must be evaluated and any undesirable outcomes mitigated.

1.4 Aims, objectives, and thesis structure

This thesis aims to help determine the ecological impact of using LGDs to protect livestock by quantifying and characterising their behaviours and interactions with co-occurring wildlife. To achieve this aim, the thesis has three objectives: 1) determine the wildlife species chased, killed, and/or consumed by LGDs, 2) quantify LGD roaming behaviours in relation to the sheep they guard by breed, sex, age, and reproductive status, and 3) quantify spatial and temporal responses of wildlife to LGD presence relative to other drivers of spatial and temporal patterns. These objectives are met by conducting a literature review and a field investigation of LGD behaviours in the Carpathian Mountains, Romania, in collaboration with Fauna & Flora. The structure of the thesis is as follows:

Chapter 2 reviews the current literature on the use of LGDs worldwide to provide a detailed overview of the potential and reported ecological effects of using LGDs (***Objective 1***). Both quantitative studies and anecdotal reports are included to build a fuller picture of known LGD behaviours and interactions with wildlife. The types of interactions and the species involved in these interactions are described and categorised as target species (typically responsible or perceived as responsible for livestock predation) or non-target species (not perceived as posing a predatory threat to livestock). The conservation status of the species involved in interactions with LGDs, or affected by LGDs, is also provided to establish whether the use of LGDs could be of conservation concern for threatened or endangered species.

Chapter 3 establishes the overarching context for the field study described in Chapters 4, 5 and 6 by providing an overview of shepherding practices in the Romanian Carpathian Mountains, and a description of the study area. This chapter also provides an overview of the shepherd recruitment process and a brief description of the methods used in Chapters 4-6. Finally, this chapter contains the results from interviewing participating shepherds, as they provide baseline informative data on shepherding practices and LGD-wildlife interactions to help with inference of results in Chapters 4-6.

Chapter 4 assesses the frequency of occurrence of wildlife in scats of LGDs. To do so, scats were collected off pastures, washed, and any remains of wildlife identified via traditional methods including microscopic identification of wildlife hairs. Scat analysis was undertaken to determine whether LGDs consume wildlife, either through predation or scavenging, and which, if any, species are consumed (***Objective 1***). Dietary information from scat analysis builds on the information provided by the shepherds in Chapter 3 to gain a more rigorous view of LGD diets and potential predation of wildlife.

Chapter 5 quantifies spatial relationships between LGDs and the sheep flocks they were guarding to determine whether LGDs remain near to sheep or roam away from them (***Objective 2***). The frequency, distance, and duration of LGDs roaming from sheep are established from tracking data obtained from fitting LGDs and sheep with GPS collars. These data were gathered from GPS collars rather than visual observations of the LGDs so as not to disturb their normal behaviours during the day and night (when they are not supervised by shepherds), and because it would not be possible in the densely forested areas surrounding pastures to observe or follow LGDs on excursions away from sheep.

Chapter 6 establishes if wildlife responds spatially or temporally to the presence of LGDs during the transhumance grazing season (approximately May through October) when sheep graze on higher altitude pastures (***Objective 3***). Camera traps were deployed across the study area at varying distances from pastures used by shepherds with their sheep and LGDs. The resulting detections of wildlife and LGDs are used to determine if the presence of LGDs affects the distribution of wildlife, how frequently wildlife use different habitats, and at what time they use different habitats. To determine the magnitude of spatial and temporal responses to LGDs relative to other drivers of habitat use and diel activity patterns, responses to LGDs are compared to responses to anthropogenic activity, habitat variables, and biotic variables such as the presence of apex predators.

Chapter 7 summarises and discusses the results from Chapters 2-6, including the implications of LGD-wildlife interactions for wildlife conservation and LGD management. Several avenues for future research stemming from the findings in this thesis are also suggested. Overall, the findings here provide much-needed evidence regarding the wider ecological impacts of using dogs to protect livestock, not just in Romania but across the world.

Chapter 2: The ecological effects of livestock guarding dogs (LGDs) on target and non-target wildlife

Published as: Smith, B. R., Yarnell, R. W., Uzal, A., and Whitehouse-Tedd, K. (2020). The ecological effects of livestock guarding dogs (LGDs) on target and non-target wildlife. *Journal of Vertebrate Biology 69*(3), 20103.1-17. https:/doi:10.25225/jvb.20103. See Appendix A.

2.1 Introduction

Livestock depredation by free-ranging predatory wildlife is one of the most widespread issues hampering human-wildlife coexistence (Thirgood *et al.* 2005; Torres *et al.* 2018). Livestock losses have substantial social and economic impacts (Moreira-Arce *et al.* 2018). Likewise, lethal predator control methods used on some farmlands are amongst the top causes of population declines for many threatened predator species (Inskip and Zimmerman 2009; Treves and Bruskotter 2014). Identifying and implementing livestock protection measures that can reduce livestock losses, increase farmer tolerance and promote associated positive (or neutral) behaviours towards predators are, therefore, key priorities for the conservation of these species and the sustainability of livestock farming (Torres *et al.* 2018).

Whilst commonly used to protect livestock, lethal predator control is often expensive and not always successful (McManus *et al.* 2015; Moreira-Arce *et al.* 2018; Bruns *et al.* 2020), unless targeting 'problem animals' (Swan *et al.* 2017). For some species, particularly mesopredators, the efforts of lethal control are sometimes offset by compensatory processes such as increased reproduction and immigration (Minnie *et al.* 2016), and can even result in an increase in livestock depredation (Nattrass *et al.* 2020). Several forms of lethal control, such as poisoning and some forms of trapping, are also indiscriminate (Ogada 2014). Furthermore, the use of lethal control is often controversial (Martínez-Espiñeira 2006). Alternatives to lethal control are non-lethal, or 'deterrent-based', methods of mitigating livestock depredation. These non-lethal methods typically involve reducing interactions between predators and livestock through protecting specific areas, improving husbandry techniques, and modifying predator behaviour through disruptive stimuli, such as scarecrows, noise, odour repellents and fladry (Eklund *et al.* 2017).

One method for modifying predator behaviour that is employed across the world is the use of livestock guarding dogs (LGDs; *Canis familiaris*) (Rigg 2001). Usually, LGDs are bonded to livestock from an early age then accompany the livestock as they roam, protecting them from predators by alerting farmers to the presence of a threat, or directly deterring predators with visual, olfactory, and auditory displays. The same breeds of dog have also recently been used in this way to protect threatened wildlife, including little penguins (*Eudyptula minor*), Australasian gannets (*Morus serrator*) and Eastern barred bandicoots (*Perameles gunnii*) from predation (van Bommel 2010; King *et al.* 2015; Parrott *et al.* 2017). Of the deterrent-based methods currently available, LGDs are often considered to be one of the most effective in the long term (Marker *et al.* 2005a; Scasta *et al.* 2017; Khorozyan and Waltert 2019), although effectiveness can be highly varied (Smith *et al.* 2000a; Bruns *et al.* 2020). Reductions in livestock losses while LGDs are in use, whether perceived or measured, can increase farmer tolerance of predators on their land resulting in a reduction of lethal control (González *et al.* 2012; Rust *et al.* 2013; Horgan 2015; Binge 2017). Thus, the use of LGDs is often considered beneficial for conservation and encouraged by conservation organisations to facilitate human-wildlife coexistence.

However, it is possible that benefits arising from the use of LGDs occur simultaneously with unintended ecological effects. The underlying ecological theory of LGD use is the disruption of optimal predator foraging by increasing the real and perceived risk to the individual of preying on livestock (Bagchi 2019; Haswell *et al.* 2019; Gaynor *et al.* 2020). As such, LGDs could be perceived as predators by both target and non-target species (van Bommel and Johnson 2016; Wilkinson *et al.* 2020). Through predation effects and competition, LGDs could, therefore, alter the perception of risk for co-occurring wildlife, which in turn could induce physiological and behavioural responses from affected species (Preisser *et al.* 2005; Say-Sallaz *et al.* 2019). As a form of free-ranging domestic dog, LGDs might also affect co-occurring species via disease transmission and hybridisation (Young *et al.* 2011; Hughes and Macdonald 2013; Ritchie *et al.* 2014). Overall, these effects could lead to changes in the survival, reproduction, health, and ultimately the population dynamics of the species involved (Preisser *et al.* 2005; Say-Sallaz *et al.* 2019). Furthermore, altering the behaviour or populations of some species could result in knock-on effects to other species, such as the prey and competitors of the directly affected species. Subsequently, whether or not LGD-mediated ecological effects are beneficial or detrimental will likely be species and context specific.

Following this, the use of LGDs as biological control agents has recently been challenged. For example, adverse effects on valuable non-target wildlife, such as some game species in southern Africa, are undesirable to farmers and likely influence whether they choose to use LGDs to protect their livestock (Potgieter *et al.* 2016). Furthermore, as LGDs have been reported to chase and kill target and non-target species (Urbigkit and Urbigkit 2010; Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020), some authors have raised welfare concerns over their use (Allen *et al.* 2019a; Allen *et al.* 2019b; Allen and Hampton 2020). In these studies, the authors argue that the welfare impacts imposed by LGDs on wildlife are potentially greater than traditional methods of lethal control. On the contrary, others have refuted these claims on the basis that LGDs rarely engage in direct aggressive interactions with wildlife and when they do, it is in defence of livestock, hence helping to reduce livestock losses and increase farmer tolerance of predators (Johnson *et al.* 2019; Whitehouse-Tedd *et al.* 2020). However, these claims require evidence that wildlife is not adversely affected by LGDs (Allen *et al.* 2019b). Few studies have actually quantified the frequency and outcome of LGD-wildlife interactions, hence the full extent of LGD impacts on wildlife are relatively unknown.

For LGDs to be truly beneficial for conservation, the ecological consequences of using LGDs must be evaluated, and any undesirable outcomes mitigated. In this review, an overview of the current scientific knowledge about LGD interactions with target and non-target species and how these species respond to these interactions is provided. Furthermore, the conservation status of each species known to interact with, or be affected by, LGDs is used to highlight interactions of conservation concern. Overall, this review identifies key knowledge gaps in the understanding of the ecological effects of LGDs, provides a platform for future research and urges relevant stakeholders to consider the unintended, as well as intended, consequences of using LGDs to protect livestock from free-ranging predators.

2.2 Methods

A literature search was conducted in July 2020 using Scopus (https://www.scopus.com) and Web of Science (WoS; https://www.webofknowledge. com). The following key-word Boolean combinations were used to search peer-reviewed articles from 1970 onwards: ALL “livestock guard* dog*” OR “livestock protect* dog*” OR “guard* dog*” OR “livestock dog*” OR “guard* animal*” OR “herd* dog*”). A simplified version of these search terms was used in Google Scholar (https:// scholar.google.co.uk) and the first 500 results were screened by reading the title and abstract. The Large Carnivore Initiative for Europe (LCIE) database was also searched (https://www.lcie.org/ Publications – accessed: 19/06/2020) along with the IUCN SSC Human-Wildlife Conflict Task Force (HWCTF) Digital Library (http://www.hwctf.org/resources/ document-library – accessed: 19/06/2020) under the themes “Livestock guarding dogs” and “Livestock guarding”, respectively. A backwards snowball search was then conducted by checking the reference lists of relevant publications (Wohlin 2014). Where it was clear that the results included in a report, thesis or book chapter were later published in a journal, only the peer-reviewed article was included to avoid duplication. Any non-English publications returned by the search were translated using online translation engines (e.g. Google Translate). However, it must be acknowledged that non-English reports and some grey literature have likely been overlooked.

Publications studying or discussing the use of LGDs for protecting animals, whether livestock or wildlife, anywhere in the world were included for full screening. Publications relating to the use of LGDs to protect agricultural crops were not included. This decision was taken as LGDs are not bonded to crops in the same way that they are bonded to animals; hence their defence mechanisms and any resulting ecological effects might not be comparable. The full text of these publications was then read, and publications were retained for analysis if they reported any of the following: 1) LGD-wildlife interactions (e.g. chasing and killing of wildlife by LGDs, disease transmission, hybridisation). 2) Behavioural or physiological responses by wildlife to LGD presence (e.g. changes in land use spatially and/ or temporally or altered stress levels). 3) LGD-mediated effects on the survival, reproduction, or population dynamics of wildlife. 4) Reductions in lethal predator control associated with LGD use.

Although following the structure by which free-ranging domestic dogs have been suggested to affect wildlife (predation, competition, disturbance, disease transmission and hybridisation (Young *et al.* 2011; Doherty *et al.* 2017), this ecological framework was altered to tailor it specifically to LGDs (Figure 2.1). Predation effects were split into two categories that encompass direct interactions (chasing and killing wildlife) and indirect interactions (visual, olfactory, and auditory cues). As LGDs are not typical predators, the ‘Chasing and killing wildlife’ category also accounts for incidences of LGDs chasing and killing wildlife in defence of livestock without consuming them. Furthermore, incidences where LGDs were associated with a reduction in lethal predator control by farmers were included as this could directly affect the survival, reproduction, and population dynamics of species and affects whether LGDs are considered a net benefit for predator conservation. No studies or reports of LGDs altering farmer tolerance of predators were included unless this was explicitly linked to changes in lethal control.

Each individual report of a species interacting with, responding to, or being affected by LGDs was extracted and classified according to the conceptual ecological framework (Figure 2.1). Dietary studies showing the consumption of wildlife by LGDs were classed as ‘Chasing and killing’ wildlife, though it is discussed how these results could be caused by scavenging in the next section. Next, each individual effect was categorised as present or absent for interactions, or as negative, neutral, or positive according to the outcome reported for the wildlife species, for responses and effects (Figure 2.1). Where the effect on a species was categorised as present, negative, or positive, the species was classed as having been affected by LGDs. For each species it was noted whether it was a target species (responsible for livestock depredation) or non-target species (not responsible for livestock depredation) in the study area. The IUCN Red List was then consulted to determine each species' conservation status (as relevant to the region of reported effect).

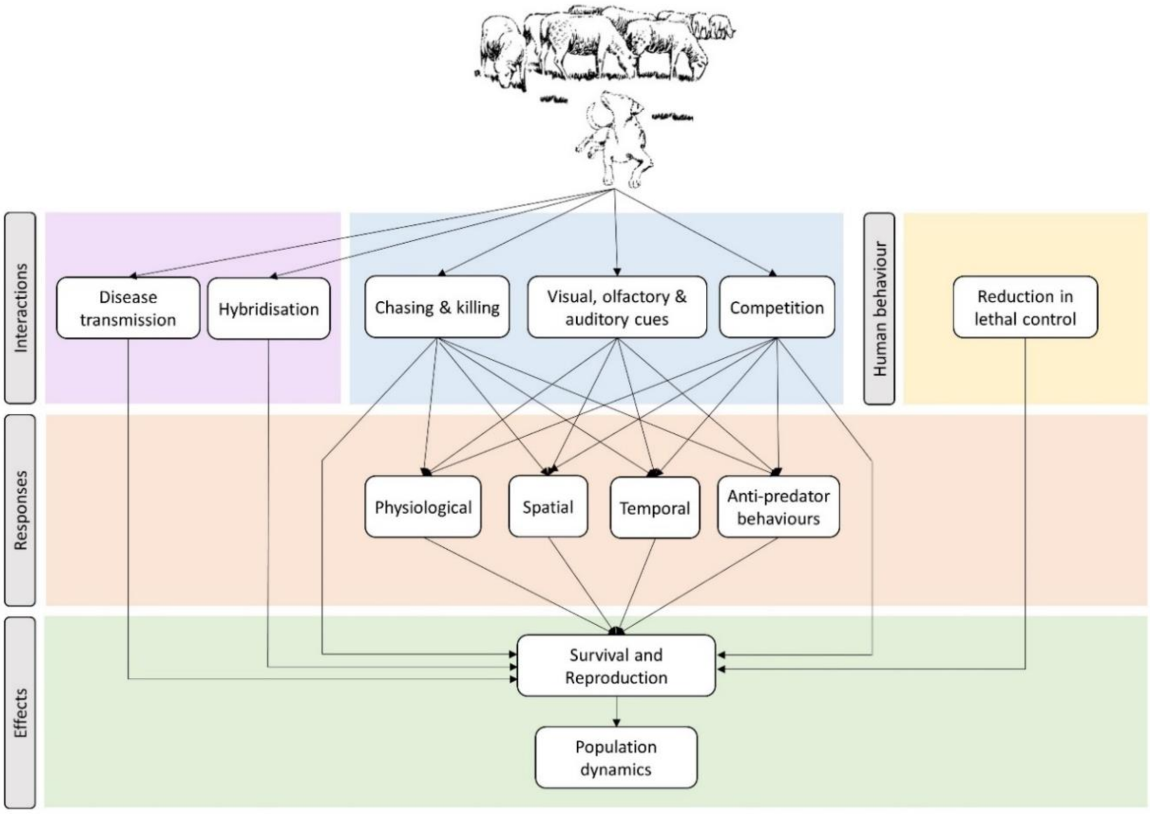

Figure 2.1. Conceptual ecological framework of the pathways by which livestock guarding dogs (LGDs) could affect wildlife. As a form of free-ranging domestic dog, LGDs could interact with wildlife and affect species via disease transmission and hybridisation (purple), or by acting as predators or competitors and altering risk perceptions of wildlife (blue). Similarly, LGDs are also thought to cause changes in human behaviour, predominantly a reduction in lethal control methods (yellow). Changing the level of risk for wildlife, via predation and competition effects, can induce physiological and behavioural responses in species (orange). Overall, all of these interactions, responses and changes in human behaviour could affect survival, reproduction and ultimately population dynamics of co-occurring wildlife (green). The direction of responses is not given in this figure, but all could be positive, neutral, or negative depending upon the context of the interaction and the species involved.

The following information was also extracted from each publication: country of study, total number of LGDs studied, number or percentage of LGDs involved in LGD-wildlife interactions, number of LGDs per farm or per livestock herd, and breed of LGDs studied. In publications that did not provide the percentage of LGDs that chased or killed wildlife, where possible it was calculated from the data reported. Instead of categorising these percentages as LGDs that chase or kill wildlife, the terms 'lethal' or 'non-lethal' interactions were used to match the terminology used in previous papers (Whitehouse-Tedd *et al.* 2020). Finally, the mean and standard error of the percentages of LGDs that were reported to have lethal and non-lethal interactions with target and non-target wildlife were calculated across all of the relevant studies.

2.3 Results and discussion

2.3.1 Publications summary

There were 145 publications in Scopus and WoS studying or discussing the use of LGDs to protect livestock or wildlife around the world. After applying the selection criteria, 27 publications were retained. A further 27 publications were sourced from the LCIE and HWCTF digital libraries, Google Scholar, and a backwards snowball search of relevant reference lists. Two more publications were included from a special issue after the initial search was conducted. In total, 56 publications were included that reported wildlife to interact with, respond to, or be affected by LGDs (Table B.1). These 56 publications consist of peer-reviewed journal articles (n = 34), magazine articles from Carnivore Damage Prevention News (n = 9), unpublished theses (n = 5), conference proceedings (n = 3), project reports (n = 3), and book chapters (n = 2). Together, these 56 publications studied LGD use in 18 countries, mainly in Europe and Asia (n = 25). The remaining publications studied LGDs in North America (n = 15), southern Africa (n = 10), Australasia (n = 4), and South America (n = 2). Although searching from 1970 onwards, the earliest publication date was 1980. Over half of the publications (n = 31) were published between 2010 and 2020 inclusive, suggesting a growing interest in the ecological effects of LGDs in the last decade.

The current literature is skewed towards reporting and studying incidences of LGDs chasing and killing wildlife, with 45 of the 56 publications reporting that LGDs chase, kill or consume wildlife (Figure 2.2). In comparison, there was only one study investigating how olfactory cues from LGDs affect wildlife, and two studies reporting on hybridisation between LGDs and wild canids. No studies have explicitly investigated the transmission of disease from LGDs to wildlife, or the occurrence and effects of competition between LGDs and wildlife. Despite many reports of LGDs chasing and killing wildlife, little attention has been paid to how these interactions might affect wildlife. There were no studies on physiological responses induced by LGDs and only 10 publications that studied behavioural responses. All 10 behavioural response publications reported on spatial responses; two also reported temporal responses and one reported an effect on anti-predator behaviours. A single study reported an effect on reproduction via reduced offspring survival. A reduction in lethal control by farmers following LGD introduction, such as a reduction in shooting, trapping, or poisoning of predators, was reported in six studies. Only one of these six studies explicitly monitored survival rates for species before and after LGD introduction. Overall, there were no studies monitoring LGD-induced changes at the population level, even as a result of reduced lethal control (Figure 2.2).

In addition, few studies have attempted to link ecological responses or effects to the underlying interaction mechanism. Only one study investigated how an olfactory cue affects spatial responses by a target predator, and another study investigated survival rates of predators as a result of mortality induced by both LGDs and human behaviour. The remaining responses and effects featuring in the publications simply reported changes relating to LGD presence (Figure 2.2).

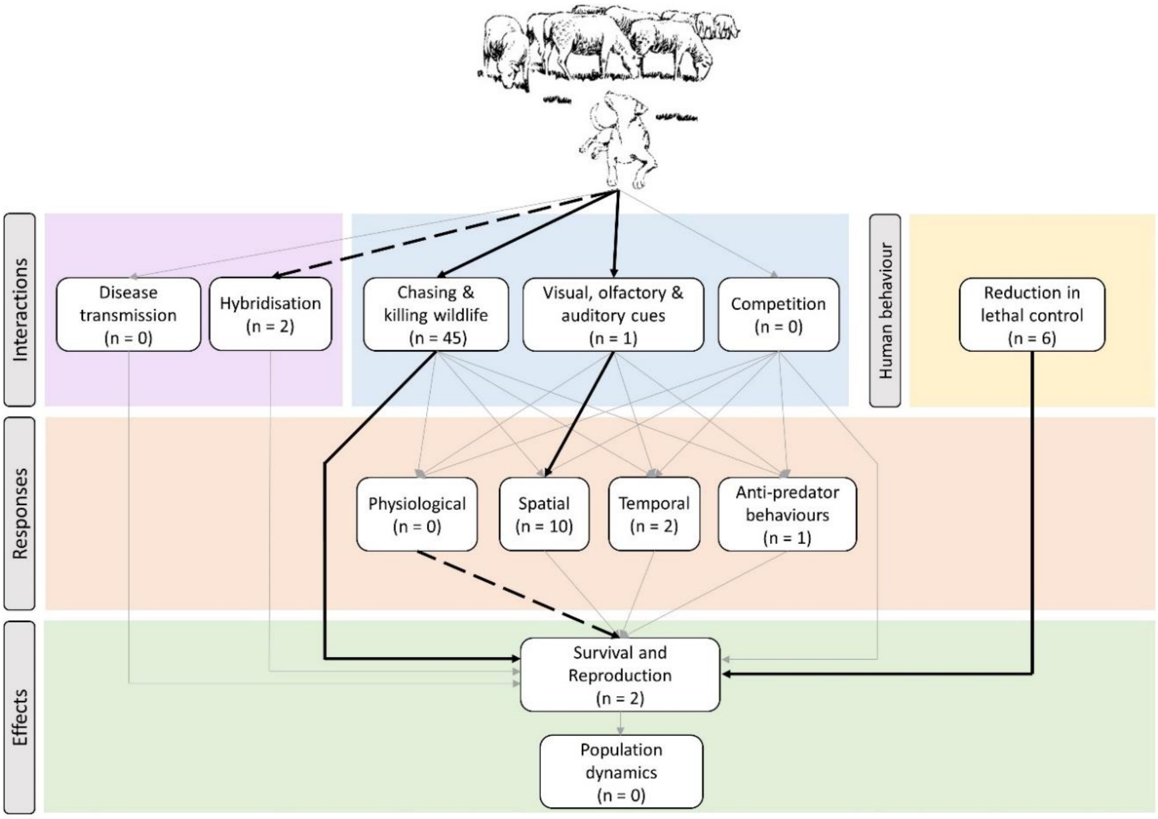

Figure 2.2. Representation of the 56 studies found investigating each of the pathways by which livestock guarding dogs (LGDs) could theoretically affect wildlife. The number of publications (n) reporting each interaction, response or effect is given in each associated box. These publication numbers are not mutually exclusive as publications could have reported multiple interactions, responses, or effects. Solid black arrows represent situations where a direct link from one stage of the framework to another was reported by at least one study. Dashed black arrows represent situations where an interaction, response or effect was hypothesised to occur or be linked to another stage of the framework by at least one study, but where evidence was limited. Grey arrows depict the underlying framework that has not yet been studied, and thus highlights key knowledge gaps in the understanding of the ecological effects of LGDs.

2.3.2 Interactions, responses, and effects

2.3.2.1 Chasing and killing wildlife

There were 43 publications reporting LGDs chasing and killing wildlife and two reporting the occurrence of wildlife remains in LGD scat. Over half of the 43 publications reporting LGDs chasing and killing wildlife provided observational or anecdotal accounts of these behaviours, with only 21 providing quantitative data. Two of these 21 publications provided information on the percentages of farmers or households that reported their LGDs to interact with wildlife, although both studied mixed-breed dogs as opposed to traditional breeds of LGDs (Black and Green 1985; Sepúlveda *et al.* 2014). Another two of the 21 publications gave an indication as to the frequency of LGD interactions with grey wolves (*Canis lupus*). The first reported that LGDs chased away wolves in more than 90% of encounters (Rigg *et al.* 2017). The second used infrared video observations to monitor LGD-wolf interactions on sheep pastures in France, finding that agonistic interactions accounted for 65.7% of the interactions and were significantly more frequent than any other type of interaction (Landry *et al.* 2020). The remaining 17 publications, consisting of peer-reviewed journal articles (n = 6), magazine articles from Carnivore Damage Prevention News (n = 5), student theses (n = 3), conference proceedings (n = 2), and project reports (n = 1), provided enough data to extract or calculate the percentages of LGDs involved in lethal and non-lethal interactions.

On average, a third of LGDs in each study were reported to have non-lethal interactions with wildlife, and this reduced to less than 10% of LGDs for lethal interactions (Table 2.1). The term ‘non-lethal’ is used to represent cases where LGDs were not known to directly kill the animals involved. Nevertheless, ‘non-lethal’ interactions can still be harmful to wildlife and both lethal and non-lethal LGD-wildlife interactions pose welfare concerns for the animals involved. Whilst these percentages help gauge how many LGDs directly interact with wildlife, only one study that provided the percentages of LGDs involved in interactions with wildlife used video cameras to monitor LGD behaviour (Landry *et al.* 2014). The remaining estimates originated from direct researcher observations and farmer reports, so are subject to human errors and biases. For example, LGDs might behave differently whilst being observed or accompanied by humans (Drouilly *et al.* 2020) and are often out of sight of farmers, meaning farmer reports may underestimate the occurrence of these behaviours (Whitehouse-Tedd *et al.* 2020). Furthermore, the percentage of LGDs involved does not provide insight into the frequency of the interactions per LGD over a defined time period.

Table 2.1. Summary of reported percentages of livestock guarding dogs (LGDs) having lethal and non-lethal interactions with target and non-target species. Target species are predators responsible for livestock depredation, non-target species are any other co-occurring species in the study area. Percentages of LGDs were extracted or calculated from 17 of the 43 publications that reported LGDs chasing, killing or directly interacting with wildlife.

LGD-wildlife interaction category	**Mean %**	**SE**	**Min %**	**Max %**
All species				
Non-lethal interactions	33.5	6.9	0.0	100.0
Lethal interactions	9.5	2.2	0.0	47.0
Target species				
Non-lethal interactions	25.6	13.7	1.0	89.0
Lethal interactions	9.2	3.3	0.0	47.0
Non-target species				
Non-lethal interactions	37.2	8.1	0.0	100.0
Lethal interactions	9.7	3.0	0.0	47.0

Adding to the uncertainty over the extent to which LGDs chase or kill wildlife is the high variability in the percentages of LGDs that engage in these behaviours (Table 2.1); some of which could be explained by factors related to the LGDs, such as the number and breed of LGDs used. The numbers of LGDs per farm were reported in 32 of the 56 publications. In 78% of these 32 publications, 1 or 2 LGDs per farm/livestock herd were used, but the numbers reached as high as 25 in France where up to 20 LGDs were reported to be involved in LGD-wolf interactions at any one time (Landry *et al.* 2020). There were not enough data to draw any conclusions from the number of LGDs used and the occurrence of LGDs chasing and killing wildlife, but using multiple LGDs per farm increases the chance that at least one of these dogs will engage in these behaviours. Similarly, some breeds may be more likely to exhibit behaviours such as chasing and killing wildlife (Green and Woodruff 1988; Sedefchev 2005). For example, one study reported that 23% of the studied Komondor LGDs had killed at least one predator, compared to none of the Great Pyrenees LGDs in the same study (Green and Woodruff 1980).

There are also human factors that likely influence whether LGDs chase or kill wildlife. First, studies have suggested that LGDs that are not treated or fed as well as others are more likely to chase and predate wildlife (Sepúlveda *et al.* 2014). Second, these behaviours can often be corrected with appropriate training, but their occurrence likely depends on human perceptions of desirable and undesirable behaviours (Whitehouse-Tedd *et al.* 2020). For example, sheep flocks in Turkey that were guarded by LGDs that actively chased wolves suffered lower rates of predation compared to those guarded by LGDs that did not chase wolves (Tuğ 2005). Thus, the chasing and killing of target, and even non-target species, may be desirable if it reduces agricultural damage so may be encouraged (Potgieter *et al.* 2013; Horgan 2015; Drouilly *et al.* 2020). As with any strategy working towards human-wildlife coexistence, the human dimensions of this research must be considered, and more empirical studies conducted to understand the drivers of LGD-wildlife interactions and how to mitigate undesirable interactions and outcomes.

Any negative ecological outcomes of LGD use must also be considered against potential positive effects. As has been hypothesised for red foxes (*Vulpes vulpes*) in Australia, wild predators might be more cautious around LGDs that chase and kill wildlife, thus increasing their vigilance at the expense of hunting (van Bommel and Johnson 2016). As such, LGDs could provide indirect protection to wild prey species (van Bommel and Johnson 2016). Gehring *et al.* (2010) counted more ground-nesting bird nests on pastures with LGDs, possibly due to the LGDs killing and suppressing mesopredators that would normally predate these nests. Similarly, the use of LGDs in the western USA has been suggested to reduce the impacts of predators on sage grouse (*Centrocercus urophasianus*), a species listed as Near Threatened on the IUCN Red List (VerCauteren *et al.* 2013). The chasing and killing of wildlife by LGDs might, therefore, be beneficial for some species. However, all of these effects have only been hypothesised and not statistically tested, thus highlighting the need to empirically determine the net ecological effect of LGD use.

In addition to the 43 publications reporting LGDs to chase and kill wildlife, there were two publications investigating LGD diet via morphological identification of prey remains in LGD scats. One revealed the consumption of ten wild mammal species by LGDs, as well as small quantities of invertebrates, reptiles and birds (Drouilly *et al.* 2020), and the other reported the rare occurrence of scrub hare (*Lepus saxatilis*), common duiker (*Sylvicapra grimmia*) and rodent remains in LGD scats (van Vliet 2011). However, it is not possible to confidently distinguish between remains in the scats that were actively hunted or scavenged by LGDs. Furthermore, although simple and inexpensive, morphological scat analysis has important shortcomings including uncertainty over identification of closely related species and variability in digestibility of species (Mumma *et al.* 2016). Methods that determine the ratios of consumed food originating from hunting versus scavenging, or use molecular techniques such as metabarcoding (Mumma *et al.* 2016; Gosselin *et al.* 2017), could further enhance the understanding of LGD diet and the ecological effects of LGDs.

2.3.2.2 Visual, olfactory, and auditory cues

Only one study investigated how indirect interactions such as visual, olfactory, or auditory cues of LGDs affect wildlife. This study recorded the spatial responses of captive dingoes (*Canis dingo*) to LGD urine, finding that LGD urine alone does not repel dingoes (van Bommel and Johnson 2017). Although many dingoes were tested (n = 28), the experiment took place in captivity so it is unclear whether this result would translate to the wild. As LGDs primarily bark to deter predators, and possibly scent-mark along territorial boundaries (Bidder *et al.* 2020), it is likely that co-occurring wildlife are exposed to these auditory and olfactory cues. Playback experiments of domestic dog vocalisations have been shown to dramatically reduce mesopredator foraging and increase vigilance, in turn benefitting the prey species of mesopredators (Suraci *et al.* 2016). The potential cascading ecological effects of indirect interactions between LGDs and wildlife likely have differing outcomes for species at different trophic levels and require much further investigation.

2.3.2.3 Disease transmission and hybridisation

There were no publications explicitly studying disease transmission from LGDs to wildlife. However, LGDs have been shown to carry intestinal diseases (Frey *et al.* 2010) and in one case were possibly responsible for the transmission of a parasitic tapeworm to domestic sheep in Denmark (Petersen *et al.* 2018). It is widely acknowledged that some diseases, notably rabies and canine distemper virus, can be transmitted between free-ranging domestic dogs and wildlife (Laurenson *et al.* 1998; Cleaveland *et al.* 2000; Knobel *et al.* 2014). As such, many LGDs are vaccinated against common diseases but vaccination rates can vary greatly. For example, in one report monitoring 129 LGDs in Italy, 87.5% farmers never vaccinated their dogs (Salvatori *et al.* 2017). Thus, the possibility of disease transmission from LGDs to wildlife should not be overlooked, especially in areas where vaccination rates are low.

On the contrary, LGDs might be beneficial in controlling the transmission of diseases between livestock and wildlife. Two of the included studies showed that LGDs deterred white-tailed deer (*Odocoileus virginianus*) from entering pastures and consuming cattle feed, in turn possibly reducing disease transmission from deer to cattle (VerCauteren *et al.* 2008; Gehring *et al.* 2010). Disease transmission at the wildlife-livestock interface is bi-directional (Cleaveland *et al.* 2001). Thus, deterrence of wildlife by LGDs could be beneficial for wildlife by also preventing the spread of disease from livestock to wildlife, as has been suggested for wild bighorn sheep (*Ovis canadensis*) in the USA (VerCauteren *et al.* 2013). More research is needed to elucidate the role that LGDs may play in regulating multi-directional disease transmission between LGDs, livestock, and wildlife.

Of the two publications reporting hybridisation between LGDs and wild canids, one simply stated that LGDs breed with grey wolves in Europe without any supporting detail (Linnell and Lescureux 2015). The second studied the genotypes of 102 grey wolves, 57 LGDs and 9 mongrel dogs from Georgia (Kopaliani *et al.* 2014). Recent wolf ancestry was found in more than 10% of the LGDs, and recent dog ancestry in 13% of the wolves. In addition, 2-3% of the sampled wolves and dogs were identified, with high probability, as first-generation hybrids. However, it was not differentiated whether these hybrids were a product of mongrel or LGD hybridisation with wolves. As such, although this study provides some suggestive evidence for LGD-wolf hybridisation, a dashed arrow from LGDs to hybridisation has been used in Figure 2.2 to represent the uncertainty. In general, hybridisation between domestic dogs and wild canids is of growing conservation concern internationally (Leonard *et al.* 2014). Future research on this topic should target regions where sterilisation of LGDs is less common, LGDs are wide-ranging or unaccompanied, and where there are small or fragmented populations of threatened canids (Gómez-Sánchez *et al.* 2018).

2.3.2.4 Physiological and behavioural responses

There were 10 publications investigating LGD-mediated behavioural effects on wildlife (Figure 2.2). Eight of these 10 studies provided quantitative data on behavioural responses through a variety of methods, including direct observations, camera traps, and GPS tracking. From the eight quantitative studies, there were 18 reports of spatial responses by both target and non-target species, 11 of which were negative (implied spatial avoidance), four neutral, and three positive.

Spatial avoidance by target predators could be deemed desirable by farmers if it prevents livestock depredation and was noted for coyotes (*Canis latrans*), grey wolves and bobcats (*Lynx rufus*) in the USA (Gehring *et al.* 2010; Bromen *et al.* 2019), and red foxes in Australia (van Bommel and Johnson 2016). Spatial avoidance by non-target wildlife could also be deemed desirable by farmers if it prevents agricultural damage. For example, spatial avoidance of LGDs by several large herbivores in Australia, including Eastern grey kangaroos (*Macropus giganteus*), is viewed as a positive outcome by some farmers due to these animals competing with livestock for feed and grazing opportunities (van Bommel and Johnson 2016). On the contrary, some game species, such as kudu in southern Africa, are highly valuable to farmers (Potgieter *et al.* 2016); their exclusion from farmland would likely be perceived as a negative outcome of LGD use. Generally, excluding wildlife from areas guarded by LGDs could restrict access to resources and fragment the available habitat for wildlife. Furthermore, spatial exclusion of target predators could exacerbate livestock depredation on neighbouring farms, thereby simply shifting the problem elsewhere (Gehring *et al.* 2010; Santiago-Avila *et al.* 2018).

To meet the expectations of facilitating human-wildlife coexistence, LGDs need to reduce agricultural damage, such as livestock losses, without excluding target species from agricultural land. The four neutral spatial responses were reported for three target species: dingoes in Australia that had overlapping territories with LGDs (Allen *et al.* 2017b) and did not avoid LGD urine (van

Bommel and Johnson 2017), and leopards (*Panthera pardus*) and black-jacked jackals (*Lupulella mesomelas*) that occupied LGD-guarded and unguarded farmland equally in South Africa (Spencer *et al.* 2020). Whilst neutral spatial responses could be indicative of coexistence, they need to occur at the same time as a reduction in livestock losses to prove the LGDs are effective. Spencer *et al*. (2020) reported that there were no livestock fatalities on the guarded farms during their study, thus suggesting LGD-mediated coexistence between farmers and predatory wildlife on South African farms. However, these relationships need further examination due to a small sample size of farms and more studies are needed that combine studying the ecological effects of LGDs with the effectiveness of LGDs at reducing livestock losses.

The three positive spatial associations with LGDs were reported for brown hyaena (*Hyaena brunnea*) in South Africa (Spencer *et al.* 2020), and northern raccoons (*Procyon lotor*) and ringtails (*Bassariscus astutus*) in the USA (Bromen *et al.* 2019). Positive spatial associations with LGDs might not be directly related to LGD presence, but to a perceived reduction in risk where LGDs have facilitated a reduction in lethal predator control. However, this hypothesis is untested and there remains the possibility that some species might be directly attracted to LGDs. For instance, LGDs might provide a refuge for some wildlife by deterring the competitors and predators of these species. Attraction to LGDs by target predators could be curiosity-driven, alternatively predators might be seeking out LGDs as prey or trespassing conspecifics (Bangs *et al.* 2005). Whether these spatial responses are considered as detrimental or beneficial is dependent on the context, the species, and the attitudes of the people involved. For example, although rarely reported, LGD fatalities do sometimes occur as a result of confrontations with predators whilst defending livestock and this can worsen tolerance of predators by LGD owners (Bangs *et al.* 2005; Mertens and Schneider 2005). Furthermore, exposing LGDs to harm in this way raises ethical considerations for their use (Allen and Hampton 2020).

In addition to spatial responses, five temporal responses were reported, all of which were negative or neutral. Negative temporal effects suggest a shift in activity to avoid LGDs and were reported for white-tailed deer that significantly reduced the time they spent in pastures guarded by LGDs (Gehring *et al.* 2010), and red foxes and Eastern grey kangaroos in Australia (van Bommel and Johnson 2016). This same study in Australia found that swamp wallabies (*Wallabia bicolor*) and sambar deer (*Rusa unicolor*) did not show a temporal response to LGD presence, suggesting again that behavioural responses are likely to be highly species-specific. In general, more studies on temporal responses by wildlife are needed to complement the studies on spatial responses as animals not responding spatially to LGDs might be compensating temporally (Sévêque *et al.* 2020). Similarly, animals might compensate with increased stress levels or by adjusting other anti-predator behaviours such as vigilance and grouping (Say-Sallaz *et al.* 2019). Yet, there were no studies on physiological responses and only one study reporting LGDs to affect the activity levels of a non-target species (Gingold *et al.* 2009). The complex behavioural, physiological and ecological impacts of the fear of predation are only just beginning to be understood (Say-Sallaz *et al.* 2019) and warrant much further investigation with regards to the use of LGDs.

2.3.2.5 Lethal control, survival, reproduction, and population dynamics

There is a paucity of studies investigating the ecological outcomes of LGD-wildlife interactions with regards to reproduction, survival, and overall population-level effects. Only one study investigated the reproductive output of a species, finding a lower survival rate of mountain gazelle (*Gazella gazella*) fawns when kept in enclosures with LGDs compared to without (Gingold *et al.* 2009). The authors suggest this reduction in offspring survival could be due to direct predation by LGDs or be physiologically-mediated, but they could not determine the exact cause (hence the dashed arrows in Figure 2.2). Despite the seemingly widespread occurrence of LGDs chasing and killing wildlife, only one study measured adult survival rates of wildlife before and after LGD introduction. This study found a net decrease in leopard and cheetah (*Acinonyx jubatus*) deaths, but a net increase in black-backed jackal and caracal (*Caracal caracal*) deaths due to combined killing from farmers and LGDs (Potgieter *et al.* 2016). The effects of LGDs are, therefore, dependent upon the abundance and type of species, and importantly, farmer behaviours towards specific predators.

Six publications reported changes in farmer behaviour in the form of a reduction in the use of lethal control, such as shooting, trapping, and poisoning, in association with LGD use. Two of these publications simply stated a decrease in the use of lethal control (Ribeiro and Petrucci-Fonseca 2005; Infante and Azorin 2017), whereas the other four provided more quantitative data on the percentages of farmers that employed lethal control methods before and after LGD introduction (González *et al.* 2012; Horgan 2015; Potgieter *et al.* 2016; Binge 2017). These studies found that as many as 88% of farmers reported that they no longer killed predators after using LGDs. However, all of the studies use farmer-reported data, which must be interpreted with caution. Furthermore, with the exception of Potgieter et al. (2016), none of these studies report on predator survival rates or the impact at the population level. Whilst actually measuring lethal control is extremely difficult, monitoring the effects on survival and populations of target predators is necessary to determine if LGDs are indeed beneficial for predator conservation.

2.3.3 Wildlife species

A total of 80 species were reported in the literature as being affected by LGDs (Table B.2). These species were predominantly mammals (n = 75), with the exception of five species of bird: western capercaillie (*Tetrao urogallus*), wild turkey (*Meleagris gallopavo*), helmeted guineafowl (*Numida meleagris*), ostrich (*Struthio camelus*), and little penguin. There were six publications that reported LGDs chasing, killing, or consuming birds, reptiles, or invertebrates, but the species were not named. Whilst LGDs likely affect many mammal species, future studies should ensure monitoring of a diverse range of taxa.

Although LGDs are used to deter target predators, 62 of the 80 affected species were non-target species ranging from small rodents and lagomorphs to non-target mesopredators and large ungulates. The proportion of non-target species involved was most often greater than target species for each interaction, response, or effect type with relevant data; exceptions to this were hybridisation, olfactory cues and survival (Figure 2.3). In addition, the percentage of LGDs involved in non-lethal interactions with wildlife were higher for non-target species, although the percentages of LGDs involved in lethal interactions with wildlife were similar for target and non-target species (Table 2.1).

Interacting more with non-target than target species could simply be caused by a typically higher species diversity and abundance of herbivores than predators. It could also be due to a lack of instinctive fear in non-target species in areas where LGDs have been only recently introduced. Regardless of the underlying cause, these results still highlight that LGDs interact with, and affect, many non-target species and, therefore, likely have unintended ecological effects. Interacting with non-target species could be deemed in defence of livestock if the animal is in close proximity to the herd, but a recent study from South Africa found that only 28% of cases of LGD-herbivore interactions were classed as defensive of livestock, compared to 100% of LGD-predator interactions (Whitehouse-Tedd *et al.* 2020). Future studies should focus on quantifying and characterising the interactions between LGDs and non-target species, as well as target species, in order to better understand the nature and outcome of LGD-wildlife interactions.

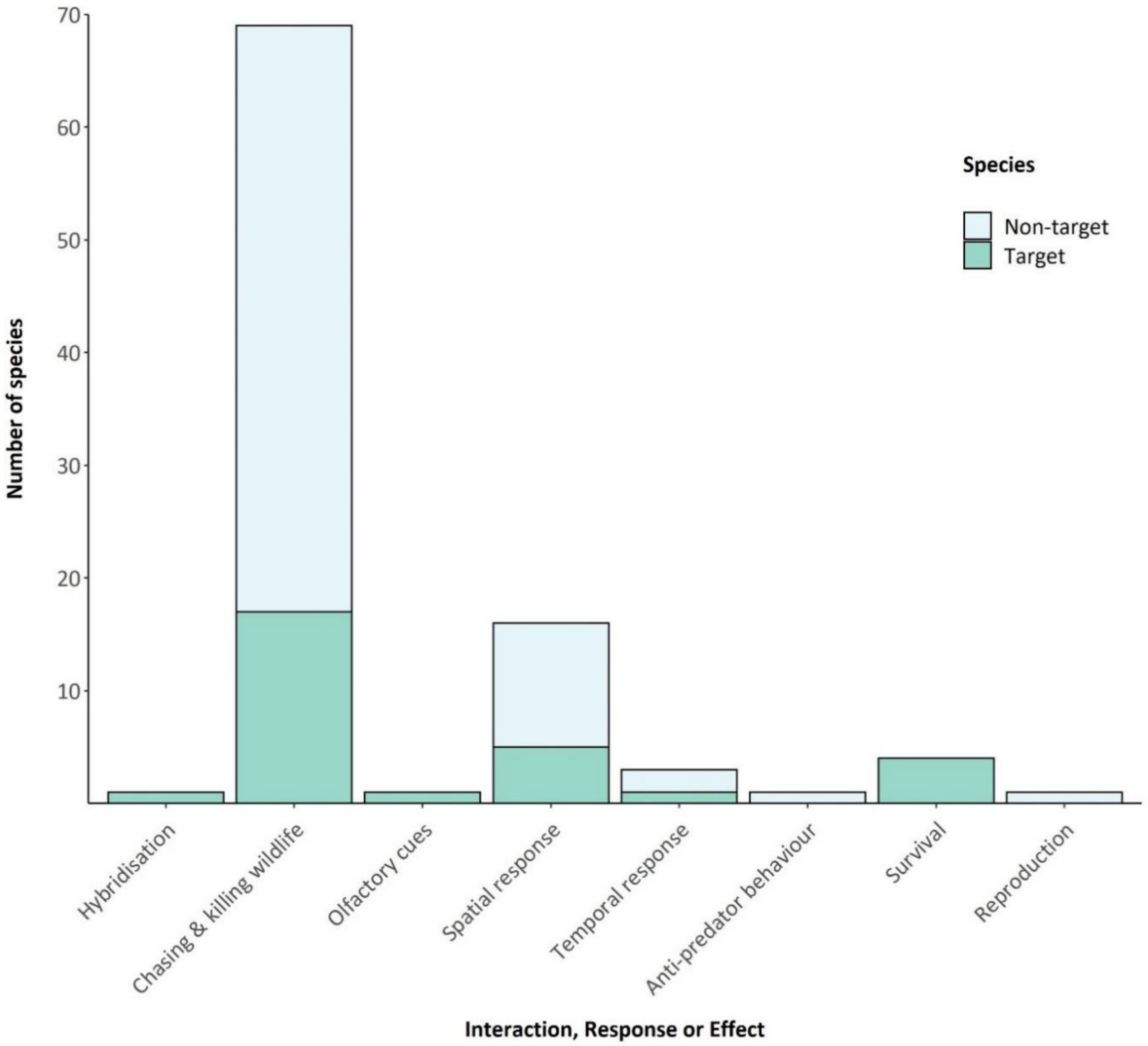

Figure 2.3. Number of named species reported to interact with, respond to, or be affected by livestock guarding dogs (LGDs) as determined from a literature search (1970-July 2020). Bars are stacked by the number of target species (responsible for livestock depredation) and non-target species.

Of the 80 named species in the publications, only one – the dingo – does not feature on the IUCN Red List. Although the conservation status of the dingo is debated, a recent study concluded that it does not meet the criteria for listing as a threatened species in Australia (Allen *et al.* 2017a), thus it has not been included here. Most of the listed species (n = 68) are classified as Least Concern, with the remaining species (n = 11) listed as Near Threatened (NT), Vulnerable (VU) or Endangered (EN) (Table 2.2). Although a substantial proportion of the species reported in the papers were of Least Concern, it is possible that observers are biased towards reporting LGD interactions with rare or threatened species. Thus, interactions with common species might be even more frequent and widespread than suggested by the literature. The 11 threatened species consist of 33% of the target species and 8% of the non-target species affected by LGDs. A greater proportion of threatened target than non-target species is to be expected as LGDs are often used as a conservation tool to protect threatened predators from lethal control. However, if these interactions have negative outcomes, for either target or non-target species, then they are of immediate conservation concern. Before LGDs can be considered beneficial for predator conservation, empirical studies need to assess if and how LGD-wildlife interactions affect both target and non-target species, especially those of conservation concern.

Table 2.2. Species found to interact with, respond to, or be affected by, livestock guarding dogs (LGDs) that are listed as Endangered (EN), Vulnerable (VU) or Near Threatened (NT) on the IUCN Red List. Species marked with an asterisk (*) were classed as target species in the study region. A description of the reported interactions and studied responses/effects are provided. The sambar deer is included here as a globally vulnerable species, though note that it was studied in Australia where it is a non-native species.

Species	**IUCN Red List Status**	**Interactions & Effects**
Mountain gazelle (*Gazella gazella*)	EN	Increase in anti-predator behaviour (running instead of resting), negative spatial response to LGD presence and reduced reproductive output via reduced offspring survival (Gingold *et al.* 2009)
Marine otter (*Lontra felina*)	EN	"Direct interactions" with LGDs (Sepúlveda *et al.* 2014)
European rabbit (*Oryctolagus cuniculus*)	EN	Chased and killed by LGDs (Ribeiro and Petrucci-Fonseca 2005; Ribeiro *et al.* 2017)
Cheetah (*Acinonyx jubatus)* *	VU	"Direct interactions" with LGDs (Whitehouse-Tedd *et al.* 2020) and killed by LGDs (Potgieter *et al.* 2016)
Wolverine (*Gulo gulo*) *	VU	Chased by LGDs (Hansen *et al.* 2002)
Kodkod (*Leopardus guigna*) *	VU	"Direct interactions" with LGDs (Sepúlveda *et al.* 2014)
Lion (*Panthera leo*) *	VU	"Direct interactions" with LGDs (Whitehouse-Tedd *et al.* 2020)
Leopard (*Panthera pardus*) *	VU	"Direct interactions" with LGDs (Whitehouse-Tedd *et al.* 2020), killed by LGDs (Marker *et al.* 2005c). Neutral spatial response to LGD presence (Spencer *et al.* 2020)
Sambar deer (*Rusa unicolor*)	VU	Negative spatial response to LGD presence, no temporal response to LGD presence (van Bommel and Johnson 2016)
Brown hyaena (*Hyaena brunnea*) *	NT	Killed by LGDs (Whitehouse-Tedd *et al.* 2020). Positive spatial response to LGD presence (Spencer *et al.* 2020)
Southern pudu (*Pudu puda*)	NT	"Direct interactions" with LGDs (Sepúlveda *et al.* 2014)

2.3.4 Future research

This review has highlighted an overall paucity of studies investigating whether interactions with LGDs induce behavioural or physiological responses by wildlife or affect wildlife populations. Before LGDs can be considered beneficial for conservation, their net effect on both target predator and non-target species populations must be empirically assessed. This is particularly important where species of conservation concern are involved in LGD-wildlife interactions.

For a comprehensive understanding of the ecological effects of LGDs, future studies should focus on: i) Quantifying and characterising LGD-wildlife interactions and their outcomes for both target and non-target species of a diverse range of taxa. As the direct outcome of lethal interactions are known, more research should investigate the outcomes of non-lethal interactions for affected wildlife. Assessment of factors influencing interaction parameters (e.g. breed, number, age, and sex of LGDs), as well as the effectiveness of corrective training, should also be investigated. Mitigation of any unintended ecological effects must follow accordingly. ii) Differentiating between scavenged and hunted prey items in LGD diet and complementing morphological scat analysis with molecular techniques. iii) Assessing the risk of hybridisation between LGDs and wild canids, and the role LGDs may play in multi-directional disease transmission between LGDs, livestock, wildlife, and humans. iv) Investigating how wildlife respond behaviourally and physiologically to direct and indirect LGD-wildlife interactions. v) Determining if and how LGDs affect the survival, reproduction, or population dynamics of co-occurring species, particularly target predators and non-target species that frequently interact with LGDs. vi) Combining studies on the ecological effects of LGDs with monitoring the effectiveness of LGDs at reducing livestock depredation.

2.3.5 Conclusion

Incidences of LGDs chasing and killing wildlife were widely reported in the literature. However, the frequency of these interactions and the outcome for the species involved has rarely been quantified. Although chasing and killing wildlife might be deemed desirable by farmers if it protects them from agricultural damage, LGD-induced behavioural and physiological responses by co-occurring species warrant concern from an ecological and conservation perspective. Some studies have begun to address spatial responses by wildlife to LGD presence, finding that whilst some species avoid, or are even attracted to LGDs, some show no spatial response at all. Similarly, the few studies reporting temporal responses by wildlife show mixed results for different species. In addition, through trophic knock-on effects, LGD-mediated effects on one species could benefit others. Therefore, the ecological effects of LGDs are likely to be context and species-specific, benefitting some species whilst adversely affecting others.

For LGDs to truly facilitate human-wildlife coexistence, their use needs to increase farmer tolerance and reduce lethal control of predators without adversely affecting these predators or other non-target species. This review found that LGDs affect a multitude of both target and non-target species, several of which are classified as Near Threatened, Vulnerable or Endangered on the IUCN Red List. By interacting with non-target as well as target species, LGDs likely incur unintended ecological costs. To date, there have been few quantitative studies examining the impacts of LGDs on wildlife, and no studies have explicitly monitored whether LGDs affect population sizes of co-occurring species. The wider ecological implications, whether detrimental or beneficial for wildlife, remain unclear. A more empirical and holistic approach needs to be taken to study the net ecological outcome of LGD use to ensure that any negative impacts on target or non-target species are mitigated and benefits maximised for both wildlife and farmers.

Chapter 3: Study context and overview

3.1 Background

The fieldwork component of this research was conducted in Romania where agriculture is one of the most important economic activities (Mertens and Promberger 2001). In 2020, an estimated 10.5 million sheep, 2 million cattle, and 1.5 million goats were raised almost exclusively for cheese production and live exports (https://www.statista.com/). Traditional short-distance transhumance grazing is still common in Romania, whereby shepherds graze their livestock near villages in the winter but escort them to higher altitude subalpine and alpine pastures during the summer months, typically from May until October, depending on the weather each year (Huband *et al.* 2010; Săgeată *et al.* 2023). During the day, flocks are moved around and grazed on pastures but are brought back to a central area known as the sheepfold, where they stay overnight, usually enclosed by wooden and/or electric fences. Shepherds tending the sheep stay with the sheep continuously and usually sleep next to the sheepfold in small shelters (Figure 3.1). Whilst some livestock owners tend to their livestock themselves or employ a shepherd to look after their livestock on their own private or rented land, other livestock owners and shepherds join together as shepherding associations for communal grazing.

Figure 3.1. Example of where a shepherd sleeps next to the sheep overnight. Photo by Bethany Smith.

When shepherds practice transhumance grazing, they move their livestock into prime large carnivore habitat for approximately five months of the year (May-October). Romania boasts large swathes of natural and semi-natural habitat (Rozylowicz *et al.* 2011), with largely unfragmented forests covering 6.9 million ha (~29% of the country area) (https://roifn.ro/site/). These forests are home to some of Europe's largest populations of large carnivores. Unlike in other countries where large carnivores were extirpated, Romania has maintained large carnivore populations, and populations have been increasing in recent years (Cazacu *et al.* 2014; Chapron *et al.* 2014). There are currently an estimated 6000 brown bears (*Ursus arctos*), which account for 35-40% of the entire European population, 2300-2700 grey wolves (*Canis lupus*), and 1200-1500 Eurasian lynx (*Lynx lynx*) (Kaczensky *et al.* 2013). All three large carnivores are designated as strictly protected species by the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, 1979), which has been applied in Romanian law since Romania joined the European Union (EU) in 2007. As a result, killing these animals is prohibited unless in exceptional circumstances for management purposes e.g. if a problem animal poses a serious threat to human life (Kaczensky *et al.* 2013; Popescu *et al.* 2019).

The combination of abundant large carnivores and livestock, and movement of these livestock into large carnivore habitat over the summer means that, inevitably, human-wildlife conflict occurs in Romania over livestock predation and crop-raiding, and even risk to human life from bear attacks (Bombieri *et al.* 2019; Pop *et al.* 2023). Although people coexist relatively peacefully with bears in Romania (Dorresteijn *et al.* 2014) there is concern that attacks on humans and damages to livestock, crops, and apiaries will increase with increasing large carnivore populations (Dorresteijn *et al.* 2016; Salvatori *et al.* 2020a; Pop *et al.* 2023). Annual surveys have been conducted by Fauna & Flora to collate data on attacks and damages by wildlife in the South-Western Carpathians. The latest available data from 2019 showed that 60.1% of reported attacks were by wolves, 39.5% by bears, and 0.4% by golden jackals (*Canis aureus*). Most of these attacks were on sheep (e.g. 97% of wolf attacks on sheep), but some were also on cattle, dogs, crops, and apiaries (per. comms.). A recent study looking at predictors of brown bear predation of livestock found that increasing abundance of bears was associated with increased predation of livestock (Pop *et al.* 2023). As such, all sheep flocks are accompanied by shepherds and livestock guarding dogs (LGDs) (Figure 3.2), which are considered to help lower predation of livestock on higher elevation pastures (Pop *et al.* 2023).

The native LGD breeds to Romania are the Carpathian, Mioritic, Bucovina, and Raven Shepherd Dogs (Ivaşcu and Biro 2020). Unlike other countries that experienced large carnivore reductions and lost traditional knowledge of livestock protection, such as the use of LGDs, Romania has experienced centuries of uninterrupted use of these dogs due to maintaining its large carnivore populations (Rigg

2001; Chapron *et al.* 2014; Yılmaz *et al.* 2015). However, although the use of LGDs remained, native breeds were replaced with the use of mixed-breed LGDs (Figure 3.2) as well as Kangal and Caucasian Shepherd LGDs – typically more aggressive breeds originating from Turkey and the Caucasus region, respectively (Ivaşcu and Biro 2020).

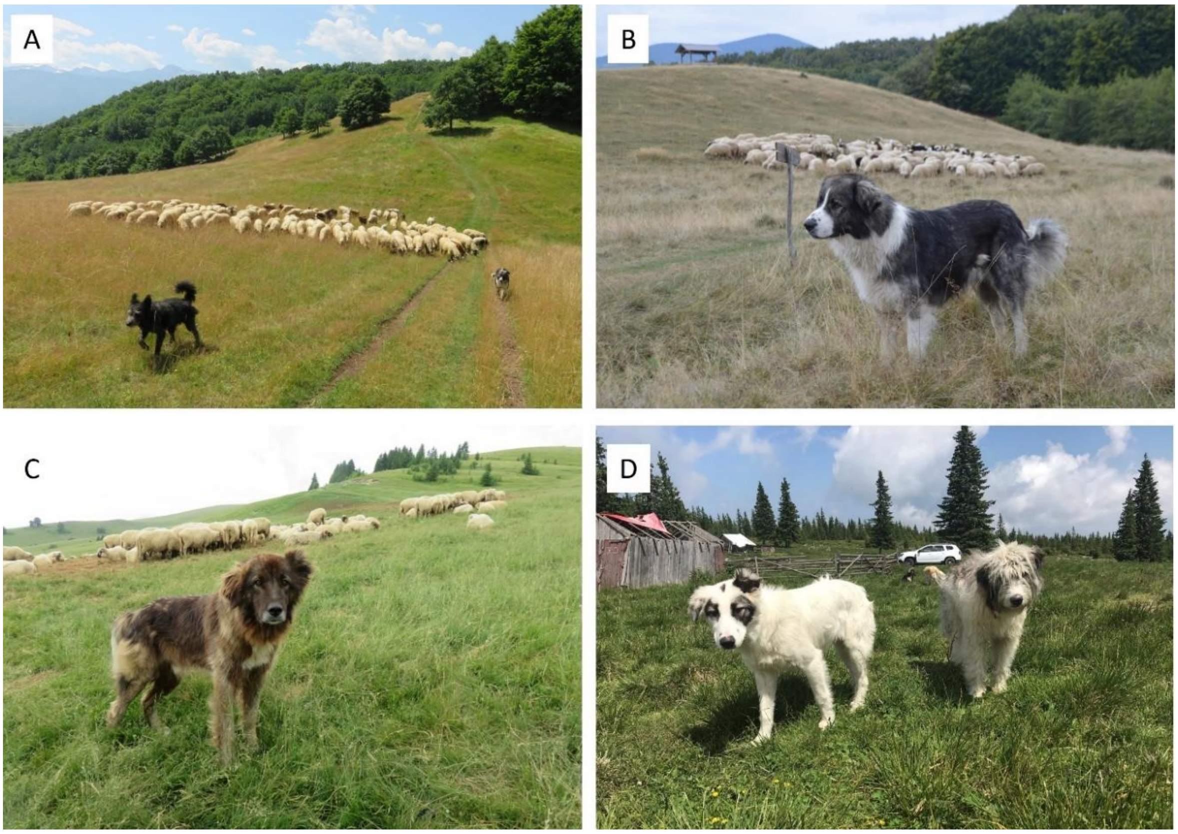

Figure 3.2. Examples of the different dogs in the study: A) small black herding dogs that all shepherds use to herd livestock, B) purebred Carpathian Shepherd livestock guarding dog, C-D) examples of mixed-breed livestock guarding dogs. Photos A and D by Bethany Smith, B and C by Mircea Marginean.

In recent years, the return of native purebred LGDs to Romania has been encouraged by several organisations, including Fauna & Flora. Established in 1903, Fauna & Flora is the world's oldest international wildlife conservation organisation, with many teams and projects spread across the globe. Since 1999, Fauna & Flora has been working in Romania, helping local organisations and communities to sustainably manage landscapes and live alongside large carnivores, with a focus on the Western and Southern Carpathian Mountains. After conducting baseline surveys in 2015 where farmers reported wolf attacks on sheep and wild boar raiding of crops as the main human-wildlife conflict issues in the area, a 'Facilitating Coexistence with Large Carnivores in the South-Western Carpathians' project was established whereby farmers were provided with damage prevention measures such as electric fences and LGDs.

As part of the Facilitating Coexistence with Large Carnivores project, 51 Carpathian Shepherd dogs have been distributed to 21 farmers since 2018. The donation of LGDs was made through loan agreements, with clauses in place to ensure shepherds are responsible for the husbandry and welfare of the dogs and Fauna & Flora retains the right to withdraw the dogs. Each recipient shepherd was trained on best practices for raising effective LGDs and correcting undesired behaviours such as chasing vehicles and wildlife. Regular visits are also paid to the LGDs by Fauna & Flora team members to check on their development and welfare and assess their effectiveness. Overall, shepherds report they are highly satisfied with their LGDs, which they have implicated in preventing bear, wolf and golden jackal attacks on livestock (per. comms.).

Only purebred Carpathian Shepherd dogs are donated by Fauna & Flora as they are considered to be more effective than mixed-breed LGDs - which are often not trained correctly as LGDs (Yılmaz *et al.* 2015) – and, therefore, are needed in lower numbers. In contrast to countries where it is typical to only use one or two LGDs per livestock flock (e.g. some areas of South Africa, Namibia, and the USA), it is common practice in Romania for many LGDs to be used (Rigg 2001). Ivaşcu and Biro (2020) reported average numbers of LGDs at each sheepfold of between five and eight, although others have suggested that only four to six Carpathian Shepherd LGDs are needed for sufficient protection (per. comms.). It is not clear exactly why different numbers of LGDs are used in different countries beyond maintaining traditional practices, but it is likely due to differing management regimes (e.g. free-ranging versus fenced livestock), different flocking behaviours of livestock (dispersed individuals versus herds), different property sizes or ranging distances, and differing levels and types of depredation risk (e.g. predator densities, different predator tactics, and landscape variables etc.). For example, in Romania in areas where shepherds perceive a higher density of bears and wolves, they will use a higher number of LGDs as they believe that using more LGDs offers better protection for their livestock; an effect that has been demonstrated in other studies from France and Iran (Landry *et al.* 2020; Soofi *et al.* 2022). Shepherds also state that using more LGDs prevents all of the LGDs being drawn away from the livestock by ‘decoy’ tactics employed by wolves (Ivaşcu and Biro 2020); a predator behaviour unlikely seen in southern Africa, for example, where predators are more solitary.

However, the large numbers of LGDs used is a source of contention in Romania, including concerns raised over LGDs hunting wildlife and posing a threat to human users of the landscape. For example, hunters contend that LGDs attack game species (e.g. deer and wild boar) (Ivaşcu and Rakosy 2017) and LGDs around the world as well as in Romania, are implicated in attacks on hikers and mountain bikers passing near to sheepfolds (Mosley *et al.* 2020; Salvatori *et al.* 2020a), thus potentially posing problems for developments such as eco-tourism. In response to these concerns, the Romanian government passed a national hunting law (407/2006) in 2015 limiting the number of LGDs that could be used to three dogs per flock of sheep in the mountains, two in the hills, and one on the plains (Ivaşcu and Rakosy 2017). However, the law was quickly rescinded after large-scale protests from shepherds claiming the measures attacked their rights and centuries of tradition. With LGDs being integral to traditional Romanian pastoralism enabling shepherds to raise livestock alongside large carnivores, but with such large numbers of LGDs used in Romania, it is critical to understand the behaviours of these dogs to not only mitigate human-wildlife conflicts, but also human-human conflicts.

3.2 Methods overview

3.2.1 Aims and objectives

The overarching aim of this thesis was to investigate how LGD behaviour and presence affect co-occurring wildlife. Working in collaboration with Fauna & Flora, an investigation of LGD-wildlife interactions was undertaken in the Romanian Carpathian Mountains to determine:

1. The frequency by which LGDs consume wildlife (whether through predation or scavenging).
2. How frequently and how far LGDs roam away from livestock, the extent of the area over which LGDs roam and could impact wildlife, and whether roaming behaviours are influenced by LGD breed, age, sex, or reproductive status.
3. The existence and characteristics of spatial and temporal responses to LGDs by target predators or non-target species such as herbivores and mesopredators not responsible for livestock losses.

3.2.2 Shepherd recruitment

An inventory of LGD users (shepherds) in the target study area who had previously been involved with Fauna & Flora projects, or were known to Fauna & Flora team members through their work with local communities, was examined and 16 shepherds invited to participate in the study. Shepherds were selected based on requiring a range of different LGD breeds to be included, such that shepherds using only purebred Carpathian Shepherd dogs (some provided by Fauna & Flora), only mixed-breed guarding dogs, or a mixture of the two LGD types were invited to participate. This sampling strategy aimed to ensure an overview of LGD behaviours was achieved, regardless of breed. Only shepherds predominantly grazing sheep were selected to prevent any variance in LGD behaviours arising as a result of guarding cattle (VerCauteren *et al.* 2012). Location was also used as a selection criterion, with invited shepherds’ summer sheepfolds being at least 1km from each other. Time and budget restrictions also dictated that most shepherd locations needed to be within Sibiu County closest to the researchers' base. Of the 16 shepherds invited to take part, one declined, and another was later removed due to one of their LGDs sustaining an injury in a bear attack, leaving 14 shepherds participating in the study.

3.2.3 Activities conducted

From the 14 participating shepherds, permission was sought for the following activities: interviews, collection of LGD scats off pastures for dietary analysis, and attachment of GPS collars on up to four LGDs and one sheep to track their movements. All activities were conducted between May and October 2021 (when shepherds are typically grazing their livestock on higher altitude pastures) and each method is explained in detail in the relevant chapters that follow. Although 14 shepherds were selected, the GPS tracking element of the study failed at site SB02, and so no further information was gathered at this location. Time and/or logistical constraints prevented the undertaking of all activities at each site, hence an overview of the activities conducted at each of the 13 sites is given in Table 3.1.

In addition to monitoring LGDs at sheepfolds, a camera trapping grid was established to monitor the spatial and temporal responses of wildlife to LGD presence from July 2021 until June 2022.

Table 3.1. Information on the sheep and dogs at each site along with the research activities undertaken and in which months. Activities: I – shepherd interview, S – scat collection, G – GPS tracking. LGD sexes: M – male, F – female. LGDs neutered: Y – yes, N – no.

Site	County	Elevation (m)	Months visited	Activities	# Sheep	# Herding dogs	# LGDs	LGD breeds (# of each)	LGD age range (years)	LGD sexes (M:F)	LGDs neutered (Y:N)	If/when LGDs last dewormed
AB01	Alba	1774	Aug	I, S, G	700	2	6	Mixed	0.5-13	2:4	0:6	Spring 2021
AB02	Alba	1776	Aug, Sep	I, G	800	1	2	Mixed	3	2:0	0:2	Unsure but always twice a year
HD01	Hunedoara	286	Sep, Oct	I, S, G	600	1	7	Carpathian	1-3	4:3	0:7	Unsure but always twice a year
HD02	Hunedoara	563	May, Jun	I, G	180	1	7	Carpathian (4) Mixed (3)	1-7	5:2	0:7	Unknown
HD03	Hunedoara	422	May, Jun	I, S, G	160	1	5	Carpathian (4) Mixed (1)	1.5-20	3:2	0:5	Spring 2021
HD04	Hunedoara	320	Sep, Oct	I, S, G	400	1	5	Carpathian (2) Mixed (3)	0.5-8	4:1	0:5	October 2021; always twice a year
SB01	Sibiu	1749	Jun, Jul	I, S, G	900	3	14	Mixed	0.5-10	11:3	3:11	Never
SB03	Sibiu	1215	Jul, Aug	I, S, G	300	1	5	Mixed	1-8	5:0	2:3	Never
SB04	Sibiu	1267	Jul, Aug	I, S, G	180	1	2	Mixed	3	1:1	0:2	Never
SB05	Sibiu	1219	Jun, Jul	I, S, G	500	1	6	Mixed	0.5-8	3:3	0:6	Never
SB06	Sibiu	1148	Jul	I, S, G	400	1	5	Mixed	3-13	5:0	4:1	Two years ago
SB07	Sibiu	1074	Aug	I, S, G	500	4	8	Carpathian (2) Mixed (6)	1-4	7:1	0:8	As puppies but not since
SB08	Sibiu	1496	Sep	I, S, G	400	1	10	Mixed	2-10	5:5	0:10	End of 2020; always once a year
						Total: 19	Total: 82					

3.2.4 Ethics statement

The activities conducted for this thesis were granted ethical approval from Nottingham Trent University under project code ARE192048R(21). At each shepherd location, written consent was received from the shepherd or livestock owner for all activities to be conducted. Participation was entirely voluntary, and no reward or payment was provided for participants. All personal and confidential data pertaining to each shepherd and their interview data are stored securely.

Throughout the study, every effort was taken to ensure the comfort and safety of the animals involved. At 200 g, the weight of the GPS tracking collar was less than 1% of the body weight of the study animals (approximately 32-45 kg for the average Carpathian Shepherd dog), thus conforming to the rule of thumb that animal-borne devices should be no more than 3-5% of an animal's body mass (Soulsbury *et al.* 2020).

For the camera trapping, 'no-glow' cameras were used to limit disturbance as wildlife have been known to react to standard infrared camera traps (Meek *et al.* 2014). The ethical implications of using camera traps with regards to human by-catch were also carefully considered and the basic principles as laid out in Sharma *et al*. (2020) followed. In brief, the objectives of the activity were presented in a clear document to share with local authorities, namely Game Management Units (GMUs), when requesting access to their managed lands and permission to set camera traps. For each participating GMU, written permission for the study was received and a representative of each GMU was present in the field on at least one occasion. From the outset, it was decided that any human photos would be blurred during the project duration before being deleted at the end of the project, and that each GMU would receive all of the photos captured in their areas with the exception of images containing humans where individuals could be identified. Each camera was also labelled with text in Romanian stating its purpose to monitor wildlife and providing a contact number for anyone seeking more information.

3.3 Study area

3.3.1 Shepherd locations

The 14 shepherds selected to take part in the study were based in three counties: eight located in Sibiu County, four in Hunedoara County, and two in Alba County (Figure 3.3). One site in Sibiu County (SB02) was later dropped from the study due to poor GPS signal. The elevations of the remaining 13 sheepfolds ranged from 286 m to 1776 m (Table 3.1). The sites at lower elevations were those in

Hunedoara County, where shepherds either did not take their livestock to higher altitude pastures (HD03) or had already migrated to slightly lower altitude pastures by the time their LGDs were monitored towards the end of the transhumance season in October (HD01 and HD04). The average elevation of the other sheepfolds in Alba and Sibiu counties was 1396 m (± 277 m SD).

3.3.2 Camera trapping study area

Most (92%) of Romanian land is split into 2153 game management units (GMUs). Each GMU manages populations of game animals and hunting activities in these areas independently from others (Cazacu *et al.* 2014). Due to having over half of the shepherd participants in Sibiu County, the aim was to establish a camera trapping grid overlapping some or all of these sites. Unfortunately, permissions to deploy camera traps were not granted by the corresponding GMUs in this area. As such, the camera trapping study area was established further south than most participants, overlapping with SB08 only, but also being close to SB01 (Figure 3.3).

The camera trapping area still fell within Sibiu County, covering a 315 km^2 region of the southern Carpathian Mountains, primarily the Cindrel Mountain range. The area was chosen due to the dense forest cover interspersed with high-altitude pastures used for grazing livestock in the summer months. All the roads in the camera trapping study area are unpaved forest roads, and in addition, there is a dense network of temporary tracks used for logging. During the summer months, human use of the area is characterised by the presence of shepherds grazing their livestock, humans foraging in the forests, and forestry personnel due to a high level of logging. Recreational activities, such as hiking, mountain biking, and riding ATVs are also common in the summer. Human presence is almost non-existent in the winter when snow makes the area inaccessible. The nearest human settlement was approximately 2.5 km (Euclidian distance) from a camera trap.

3.3.3 Study area environment

The climate in the southern Carpathians is temperate, experiencing warm summers and cold winters. Vegetation typically consists of three layers depending on the elevation. Alpine and subalpine vegetation (mainly sedges and grasses (*Carex ssp. Festuca ssp., Nardus stricta and Agrostis rupestris*)) are found at elevations >1800 m, coniferous forests (Norway spruce (*Picea abies*) and silver fir (*Abies alba*)) are found between 1200 m and 1800 m, and deciduous forests (mainly beech (*Fagus sylvatica*) are found <1200 m (Rozylowicz *et al.* 2011). The area is inhabited by an abundance of wildlife, including three of Europe's five large carnivores: brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*) (Rozylowicz *et al.* 2011; Cazacu *et al.* 2014;

Cristescu *et al.* 2019). Data on the numbers of large carnivores in the general study area were collected from the individual Game Management Units (Figure 3.4), though these numbers likely include double-counting and should be used as a rough guide rather than as absolute numbers (Popescu *et al.* 2016; Cristescu *et al.* 2019). Other large terrestrial mammals include: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), chamois (*Rupicapra rupicapra*), red fox (*Vulpes vulpes*), wildcat (*Felis sylvestris*), European badger (*Meles meles*), pine marten (*Martes martes*), beech marten (*Martes foina*), and European hare (*Lepus europaeus*). Some large birds, such as the ground-dwelling western capercaillie (*Tetrao urogallus*) are also common in the study area. Golden jackals (*Canis aureus*) have recently recolonised parts of Romania and are present in extremely low numbers in the study area (Farkas *et al.* 2017).

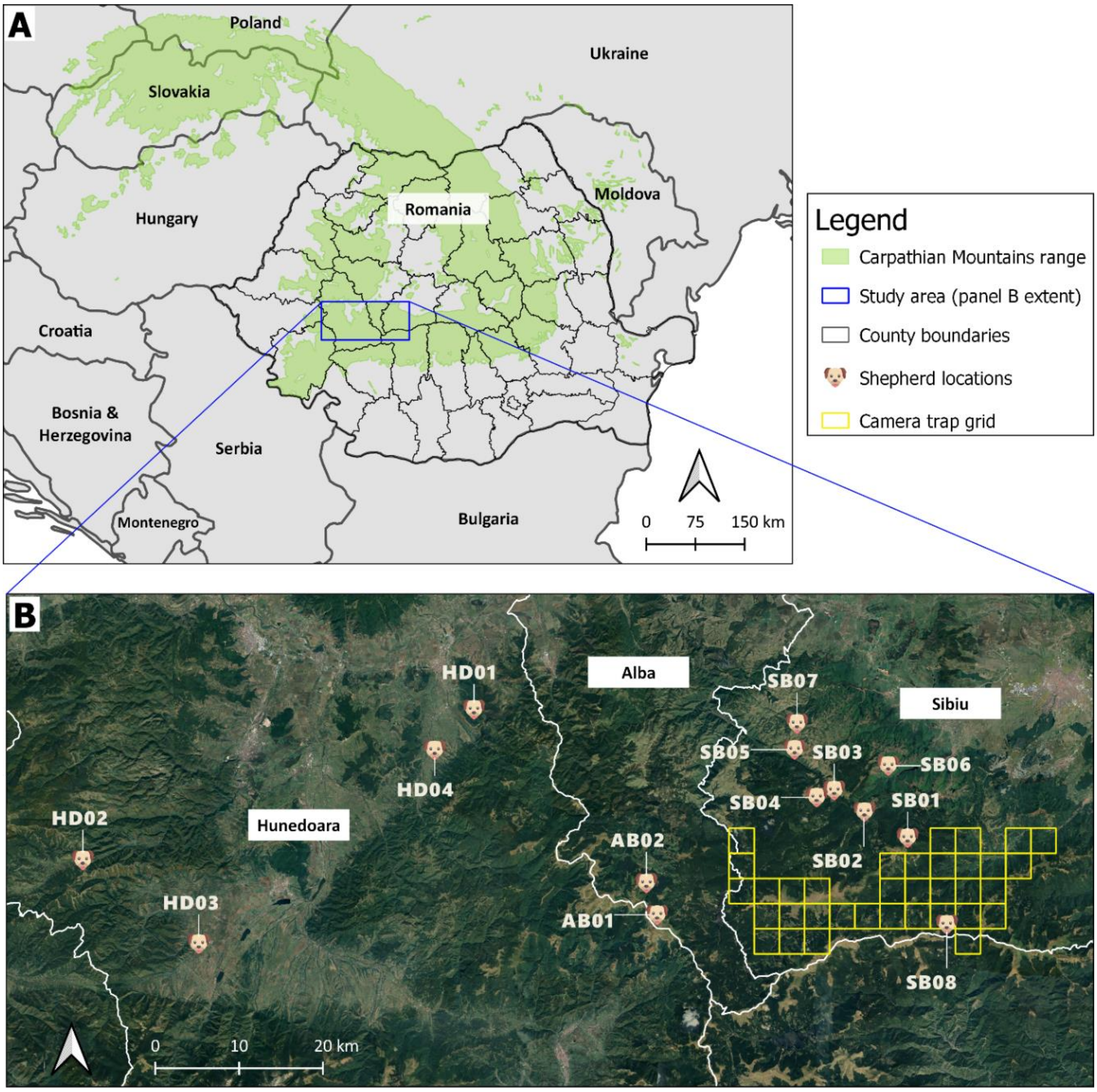

Figure 3.3. A) General study area in the southern Carpathian Mountains, Romania. B) Locations of each shepherd's sheepfold at the time of participation in the study (labelled with participant identifier) within each of the three counties: Hunedoara, Alba, and Sibiu. Location of the camera trap study area shown as the yellow grid. Maps produced in QGIS using Google Satellite imagery for Panel B.

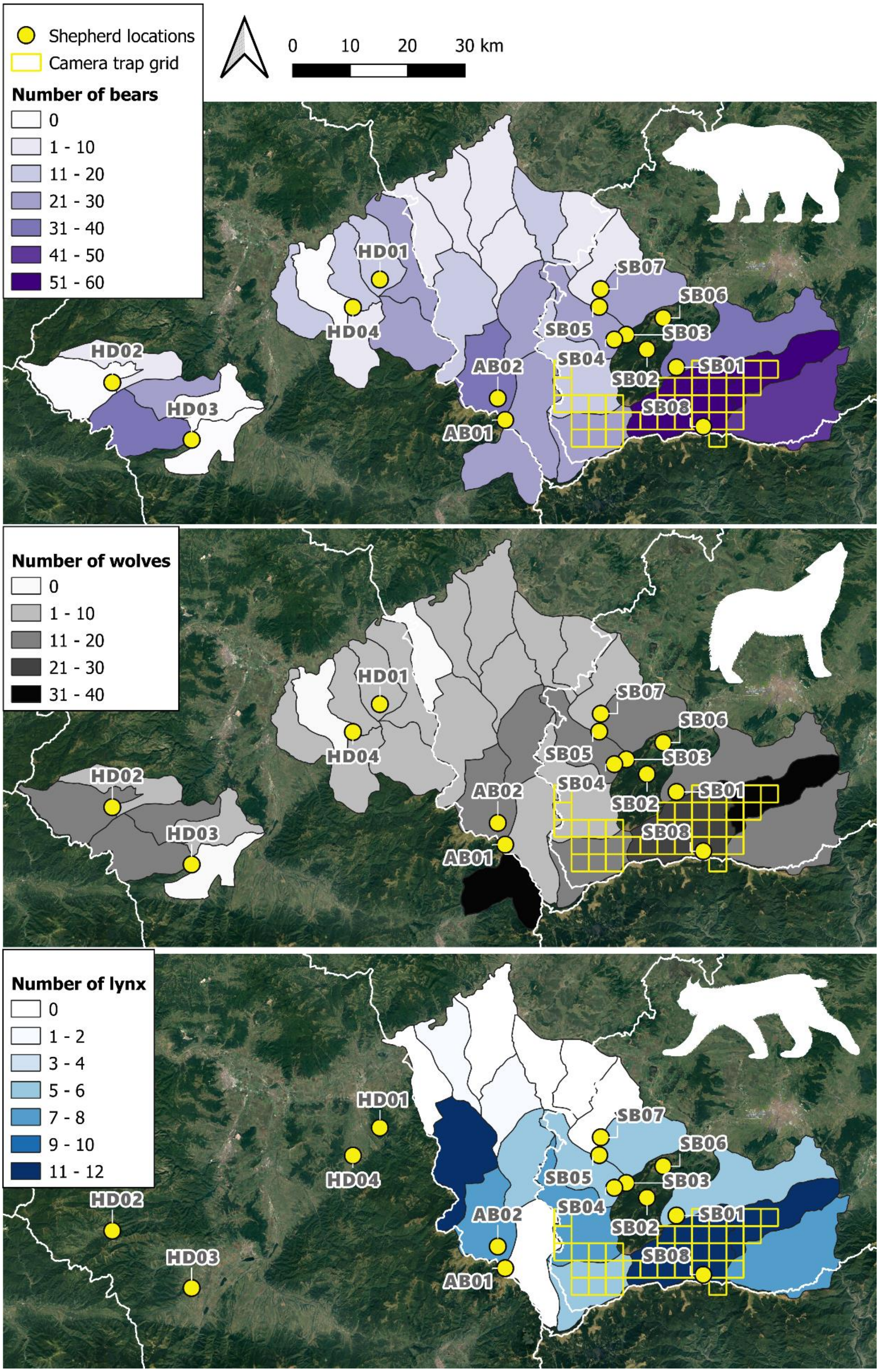

Figure 3.4. Number of large carnivores reported by each Game Management Unit (GMU) in 2021 (top to bottom: brown bears, grey wolves, Eurasian lynx). Locations of each shepherd participating in the study (yellow circles) and camera trapping study area (yellow grid lines) shown. Data from some of the GMUs were not available for use. Maps produced in QGIS using Google Satellite imagery.

3.4 Shepherding practices

3.4.1 Interview process

To ascertain the working practices of shepherds and management of LGDs included in this study, shepherds were asked a series of questions using a semi-structured interview process. Clarification and elaboration was sought with each shepherd, where necessary. Questions related to livestock numbers and husbandry practices, livestock losses to predators, LGD diets and LGD behaviours (Table 3.2). Shepherds were asked whether they had witnessed interactions between their LGDs and wildlife, and to describe the nature and outcome of these interactions. Shepherds were also asked to fill out a form giving the name of each of their herding or livestock guarding dogs, their breed, age, sex, whether neutered, and when they were last dewormed or vaccinated. Interviews were conducted at 13 out of 14 sites (SB02 was removed from the study due to a lack of GPS signal, impeding the tracking of LGDs). All interviews were conducted in Romanian and, with the exception of two, by a single Fauna & Flora team member who translated answers into English for the PhD researcher to transcribe in the field as no permission was granted for voice recordings. The interviews conducted at HD02 and HD03 were conducted by a different Fauna & Flora team member and transcribed in Romanian in the field. These were later translated to English by the same Fauna & Flora team member who conducted these two interviews. No back translation was performed.

Table 3.2. Questions that formed the basis of the semi-structured interview conducted with shepherds at each site.

Section A: livestock and livestock guarding dogs

1. How many shepherds are tending the flock?
2. How many sheep are in the flock?
3. Do you have any other livestock here and how many of each?
4. Are the sheep contained within a sheepfold every evening?
5. Where do the shepherd(s) sleep at night?
6. How many livestock guarding dogs do you have?
7. How many herding dogs do you have?
8. What, when, where and how much are LGDs fed?
9. Do the LGDs stay with the livestock overnight?
10. Are the LGDs enclosed in sheepfolds (or constrained somehow), or are they free to roam at night?
11. Please complete the separate form giving details of each of your dogs.

Section B: livestock-predator interactions

12. How often do you lose livestock to predators?
13. Which predators are responsible for these losses?
14. How often do predators approach the livestock? (Even if these approaches don’t result in losses of livestock)
15. How often are livestock counted?
16. What do you do if predators approach the livestock or are seen in the vicinity of livestock?
17. Do you use any of the following non-lethal livestock protection measures:
    Fencing (non-electric) / Fencing (electric) / Fladry / Auditory/visual deterrents / Other (provide description of other methods used)

Section C: LGD-wildlife interactions

18. Have you witnessed any of your LGDs interacting with predators? If so, how often and can you describe these interactions – what happens?
19. What are your LGDs’ responses to a predator approaching the livestock? (prompt if required - Do they bark at/chase/attack the predator?)
20. What were the outcomes of these interactions? (prompt if required – did the predator flee, was there physical contact, was the dog(s) or the predator injured or killed?)
21. Have you witnessed any of your LGDs interacting with other wildlife (species not posing a threat to livestock)? If so, how often and can you describe these interactions – what happens?
22. What were the nature of these interactions? (prompt if required – was the dog(s) chasing/hunting, was the dog(s) defending livestock?)
23. What were the outcomes of these interactions? (prompt if required – did the animal(s) flee, was there physical contact, was the dog(s) or the wild animal(s) injured or killed?)
24. If the dogs chase wildlife, do they undergo any additional training/reprimanding to correct these behaviours?

3.4.2 Interview responses

3.4.2.1 Section A: livestock and livestock guarding dogs

The number of sheep at each site guarded by LGDs ranged from 160 to 900 (Table 3.1). Five shepherds (sites HD01, HD02, HD04, SB03 and SB06) had only sheep with them at the sheepfold. The other shepherds had small numbers of other livestock in addition to sheep, these included cows, chickens, pigs, horses, donkeys, and goats, which usually stayed at the sheepfold. The livestock were predominantly accompanied by one to two shepherds during the day, although for some sites there were up to five people residing near the sheepfold if the shepherd's family stayed in the mountains too or when more people were needed to help with milking the sheep. All of the shepherds, except for at site HD03, slept beside the sheep in small wooden shelters (a common practice in Romania) so as to be easily alerted to threats to the livestock (Figure 3.1). The shepherd at site HD03 kept the sheep close to his permanent residence and so slept inside his house. None of the LGDs were enclosed overnight with the sheep or constrained in any way, meaning they were free to roam both during the day and night.

Eight shepherds used only mixed-breed guarding dogs, only one used purebred Carpathian Shepherd dogs alone, and four used a combination of mixed-breed guarding dogs and Carpathian Shepherd dogs (Figure 3.1; Figure 3.2). The number of LGDs ranged from 2 to 14 (mean: 7 ± 3.5 SD), which, when taking into account the number of sheep, equated to a range of 0.25-4 LGDs per 100 sheep (mean: 1.75 ± 1 SD) (Table 3.1). One shepherd owned an LGD which was reportedly 20 years old, but after removing this outlier, the age of the LGDs ranged from 6 months to 13 years old (mean: 3.5 ± 3 SD). Most shepherds used a mixture of male and female LGDs, though most used more males than females: 33-100% of LGDs at each site were male (mean: 71% ± 22% SD). At three sites (AB02, SB03 and SB06) all of the LGDs were male. Most (89%) LGDs were entire (unneutered). Those that were neutered were all male and from only three sites: SB01 (3 LGDs – 22% of LGDs at this site); SB03 (2 LGDs – 40% of LGDs at this site), and SB06 (4 LGDs – 80% of LGDs at this site). Typically, shepherds used one herding dog alongside the LGDs, although the highest number at one location was four herding dogs (Table 3.1). Herding dogs in Romania are small, black dogs that are not used to guard or defend the livestock but to herd and direct the sheep at the command of the shepherd (Figure 3.2). Information about the LGDs and herding dogs at each site is summarised in Table 3.1.

Provisioning of food to LGDs varied between shepherds, although most fed their dogs polenta (cornmeal and water) and whey (the protein-rich liquid remains after making cheese), as is common practice in Romania (Ivaşcu and Biro 2020). Other foods fed to LGDs included commercially prepared dog food, livestock remains including bones, and bread. All dogs were fed at the sheepfold either once during the day in the morning (n = 5) or twice a day in the morning and evening (n = 8). Information was not gathered on the quantities of food provided to LGDs at each feeding time, in part because this varied depending on the provisions available (i.e. how much whey was left after cheese-making), but primarily because shepherds were not expected to record or estimate feed quantities. Food provisioning information at each site is provided in Table 3.3.

Table 3.3. Type of food fed to livestock guarding dogs, frequency, and location.

Location ID	Food type	Frequency	Location
AB01	Polenta, whey, commercial dog food, livestock (incl. bones)	Morning & Evening	At the sheepfold
AB02	Polenta, sometimes meat, sometimes dog food	Morning & Evening	At the sheepfold
HD01	Polenta, bread, commercial dog food, sometimes but rarely bones (presumably livestock)	Morning & Evening	At the sheepfold
HD02	Polenta, whey	Morning & Evening	At the sheepfold or shepherd's residence
HD03	Dog food, bones, whey	Morning & Evening	At the sheepfold
HD04	Mostly commercial dog food, polenta, sometimes but rarely bones (presumably livestock)	Morning & Evening	At the sheepfold
SB01	Polenta	Morning	At the sheepfold
SB03	Polenta	Morning & Evening	At the sheepfold
SB04	Bread, whey, sometimes commercial dog food (specified biscuits)	Morning	At the sheepfold
SB05	Polenta, whey, livestock (specified sheep bones)	Morning	At the sheepfold
SB06	Polenta, whey, commercial dog food	Morning & Evening	At the sheepfold
SB07	Polenta, sometimes but rarely livestock (including bones)	Morning	At the sheepfold
SB08	Polenta, whey, sometimes commercial dog food, sometimes meat from the butchers	Morning	At the sheepfold

3.4.2.2 Section B: livestock-predator interactions

All shepherds reported attacks and frequent approaches by grey wolves and brown bears both prior to and during the study (Table 3.4). Concurrent with previous reports (e.g. Fauna & Flora per. comms.; Mertens and Promberger 2001), most of the shepherds (n = 11) reported wolves to be responsible for the most livestock losses. The other two shepherds (HD02 and HD03) did not specify which of the two predators they lost more livestock to. During informal conversations with shepherds, some revealed that they knew the species responsible for livestock losses either because they witnessed the attack or could tell from distinctive features on dead animals which predator was responsible, though this question was not specifically asked to all shepherds. Unlike in many other countries where livestock is left to roam alone, shepherds always accompany the sheep in Romania and most are milked regularly, usually daily. As such, shepherds reported that they knew their sheep individually and would notice if any were missing during milking and go searching for them until they were either found, or signs of an attack detected. The shepherds were, therefore, considered likely to recall with considerable accuracy when sheep had been lost to predators rather than other factors. Responses regarding the number of approaches made by large carnivores to the flocks and the numbers of livestock killed were highly varied and the qualitative, semi-structured nature of the interviews prohibited quantitative analysis. Details provided by each shepherd are summarised below (Table 3.4).

Reports of attacks occurring as frequently as 2-3 times a week and losses of up to 15 sheep per season (although on average this is approximately 5 sheep per season), were accompanied by shepherds using multiple protection measures. All shepherds except SB08 used non-electrified, typically wooden, fencing to enclose their sheep in the evenings. At SB08 the sheep were herded back to a central location but were not enclosed. On the day of the interview with SB08, Fauna & Flora team members installed an electric fence at the sheepfold, but the shepherd asked for this to have one open side. Including SB08, all but one shepherd (HD02) additionally used electric fencing that was deployed either permanently or on an as-needed basis in periods when attacks from large carnivores were more frequent. One shepherd (SB04) also used a motion-activated light as a visual deterrent. In the event of an attack, all shepherds reported that they would shout at the attacking predators and vocally encourage their LGDs to chase them away before also confronting the predators themselves. During night-time attacks, nine of the shepherds reported they would sometimes use flashlights and firecrackers to scare away bears and wolves.

Table 3.4. Shepherd-reported frequency of predator approaches to livestock and numbers of livestock lost.

Site	Frequency of predator approach to livestock	Comments on predator approaches	Number of livestock lost to predators	Predator species involved
AB01	4-5 times per season; maximum of 10 times.	Worse at lower altitude pastures.	2-3 sheep per year. At the time of interview (Sept 2021) had lost 1 lamb and had 4 attempted attacks that season.	Mainly wolves, sometimes bears. 3 of the 4 attacks that season from wolves, one from a bear.
AB02	Approximately 3 times per week.		6-10 sheep a year. During summer 2021, 6 sheep and 1 donkey depredated.	Mainly wolves, sometimes bears.
HD01	At least once per week.	Frequency of attacks dependent on weather – most attacks occur after it rains.	2 sheep depredated in summer 2021.	Mainly wolves, sometimes bears.
HD02	Up to 3 times per week.	Sometimes have periods of no approaches or attacks.	Not quantified – livestock losses not occurred that often in last 3 years.	Unknown (not asked).
HD03		No predators seen approaching the livestock for a while.	None in the last 4 years since switching from using mixed-breed LGDs to Carpathian Shepherd LGDs.	Unknown (not asked).
HD04	Once every 2 weeks.	Approaches could be more frequent at night as not seen by the shepherd.	4 sheep depredated on summer pasture in 2021. Usually no losses on lower altitude winter pastures.	Mainly wolves.
SB01	30-50 times over a 3-month summer period.		5-10 sheep per year (5-7 some years, 7-10 in worse years).	Mainly wolves.
SB03	2-3 times per week.		During the summer approximately 10 sheep a year.	Mainly wolves, sometimes bears.
SB04	Approx. 20 per year.		3-4 sheep per year. None lost during the night since electric fence installed.	Mainly wolves, sometimes bears.
SB05	>20 per year.		4-5 sheep in 2020. At the time of the interview (July 2021) 2 sheep depredated so far that season.	Mainly wolves.
SB06	60-70 times per season.		Approx. 10 sheep per season. At the time of	Mainly wolves.

			the interview (July 2021), 4 sheep depredated so far that season. Also reported a bear killed 5 sheep in July 2020.	
SB07	Usually once per week.		10-15 sheep per season.	Mainly wolves, sometimes bears.
SB08	2-3 times per week.		Approximately 5 sheep per year. At the time of the interview (September 2021), 2 sheep had been killed so far that season.	Mainly wolves, sometimes bears.

3.4.2.3 Section C: LGD-wildlife interactions

Given the relatively high frequency of predator attacks and the fact that all shepherds except one (HD03) experienced at least one attack per season in recent years, it was unsurprising that all shepherds reported they had witnessed their LGDs interacting with bears and/or wolves (Table 3.5). All of the shepherds said they encouraged their LGDs to chase away predators during attacks. Four of the shepherds said they had only ever seen their LGDs barking at and chasing away predators, but the other nine mentioned some physical contact during interactions. Some shepherds reported that physical contact, although it did occur, was rare. Physical interactions were described as the LGDs and predators fighting, with LGDs biting both bears and wolves. When asked what the outcomes of these interactions were, shepherds responded that the predators usually ran away. Some that reported their LGDs fighting with predators said they had witnessed their dogs injuring and killing predators (Table 3.5). Specifically, AB01 reported their LGDs had bitten and injured bears and wolves and said that although it was rare, the dogs had killed a wolf the year before in 2020; SB06 said the LGDs had chased a bear off a kill previously and again, though rare, had killed some wolves and more often injured them; and SB08 said they had witnessed the LGDs injuring bears and wolves. During the interview at HD04, the shepherd showed a video of the LGDs tearing at a wolf carcass, though stated they were not responsible for killing the wolf and had found it dead.

Shepherds also mentioned that they had experienced their LGDs being injured (AB01, AB02, HD01, SB01, and SB08) or even killed (AB01, AB02, and SB01) during fights with bears and wolves (Table 3.5). The shepherd at SB01 responded that LGDs are not ‘usually’, or hadn’t ‘recently’ been injured or killed, suggesting this had occurred in the past. A bear injured one LGD at site SB08 during the 2021 season, and the shepherd said this occurred frequently, and another LGD at site AB02 was injured by wolves whilst being monitored in this study. In addition, there was one shepherd who was shortlisted for recruitment to the study but chose not to participate after one of his LGDs sustained injuries from a bear during the study period.

When asked about LGD interactions with non-target species (i.e. animals other than large predators and not responsible for livestock losses), all 13 shepherds reported that their LGDs chased non-target species (Table 3.5). Although red foxes have the potential to predate smaller individuals such as lambs, foxes were not reported as responsible for livestock attacks in Fauna & Flora's annual surveys, so are included here as non-target wildlife. The general feedback was that the LGDs would bark at and chase any animals entering the pasture in defence of their territory as opposed to hunting. Some species were named by shepherds as being chased by LGDs: roe deer (n = 11), red fox (n = 11), wild boar (n = 7), European hare (n = 5), red deer (n = 2), and wildcat (n = 1) (Table 3.5). Rarer, though still present, was the occurrence of LGDs injuring and/or killing non-target wildlife, which was reported by six of the shepherds: AB01 said that sometimes foxes were killed by LGDs; HD02 said the LGDs sometimes killed foxes or small wild boars; HD03 said that two incidents of the LGDs chasing foxes resulted in the foxes being killed; HD04 initially said no physical contact between LGDs and non-target wildlife was witnessed but then said the LGDs had killed and then eaten foxes and wildcats; SB04 said sometimes the LGDs catch and injure foxes; and SB08 said sometimes the LGDs bite and injure animals they chase. The other seven shepherds (AB02, HD01, SB01, SB03, SB05, SB06, and SB07) stated they had never witnessed their LGDs injuring or killing non-target species, although HD01 said he had witnessed the LGDs eating animals they had found dead.

Following informal conversations with shepherds during fieldwork, a question regarding LGDs chasing, killing, or eating smaller animals was introduced later in the study period in response to feedback volunteered during initial interviews. When this question was posed to the shepherd at AB01, he responded that he had seen the LGDs searching for rodents on the pastures but not eating them, but that the LGDs probably ate rats and mice at the lower elevation pastures. Instances of this behaviour among the LGDs at the other shepherds are unknown. After noticing insect material in LGD scats (Chapter 4), shepherds at HD01 and HD04 were asked in conversation if their LGDs ate insects and they replied that they did as it was a good source of protein, although HD04 stated this occurred more as puppies for play than for food. Despite wild boar being of concern for injuring LGDs, none of the shepherds specifically mentioned that their LGDs had been injured in pursuit of non-target species, although no prompt was used to procure this information either.

The responses of shepherds to their LGDs chasing non-target species were mixed (Table 3.5). Five shepherds (sites HD01, HD04, SB04, SB05, and SB07) actively encouraged their LGDs to chase non-target wildlife saying they didn’t want other wildlife on the pasture. In particular, the shepherd at site SB07 said this was because other wildlife might bring disease and he knows the dogs will just run for 100-200 m before coming back as they won’t be able to catch any animals they chase. In contrast, two shepherds actively discouraged the chasing of wildlife. The shepherds at site AB01 said they liked roe deer and red deer and so called the LGDs back if they chased them as they didn’t want to see the animals killed. At site SB03, the shepherd reported calling the LGDs back if they chased wildlife, but only because he was scared the LGDs would run too far away. Four of the shepherds (sites AB02, SB01, SB06, and SB08) were more passive in their responses stating they didn’t encourage the chasing of non-target wildlife but just called the LGDs back or let the LGDs ‘do their thing’. At the remaining two shepherd sites (HD02 and HD03), the shepherds simply answered ‘Yes’ to the question of ‘If the dogs chase wildlife, do they undergo any additional training/reprimanding to correct these behaviours?’ suggesting they were not in favour of their LGDs chasing wildlife, but they were not probed for further detail.

3.4.2.4 Discussion and conclusion

The purpose of the interviews was to provide background information about the livestock, LGDs, and wildlife encounters at each site. As such, the interviews were not recorded verbatim in either Romanian or English and were instead translated informally in the field. Thus, it was not possible to conduct any qualitative analyses on the answers provided. It must also be acknowledged that some of the shepherds might not have been forthcoming with their responses due to a general lack of trust between shepherds and environmental organisations in Romania, or due to worrying there might be repercussions from their answers. It is also possible that having a non-Romanian speaking foreign interviewer could have heightened any feelings of distrust. However, every effort was made to build trust by spending time with the shepherds at their pastures and openly explaining the nature of the study in order to gather as accurate information as possible. The small sample size ($n = 13$) precluded any quantitative analyses of the data but it still provided valuable insight into the management of LGDs at each site. This information was useful for making inferences in later chapters, especially in relation to LGD diets with some LGDs known to chase and kill wildlife. Furthermore, the variation in provisioned food to LGDs and how shepherds respond to LGD-wildlife interactions provides a basis for future research investigating how management influences LGD behaviours.

Table 3.5. Summary of shepherd-reported LGD-wildlife interactions and shepherd responses to these interactions. Non-target species named by shepherds as being chased or killed/injured by LGDs are denoted in brackets by the initials of their scientific names: le – European hare (Lepus europeaus), vv – red fox (Vulpes vulpes), fs – wildcat (Felis silvestris), ss – wild boar (Sus scrofa), cc – roe deer (Capreolus capreolus), ce – red deer (Cervus elaphus). These LGD-wildlife interactions are described in more detail in the text.

Site	**LGDs chase target predators**	**LGDs injured a wolf at least once**	**LGDs injured a bear at least once**	**LGDs killed a wolf at least once**	**LGDs killed a bear at least once**	**LGD(s) previously injured by wolves or bears**	**LGD(s) previously killed by wolves or bears**	**LGDs chase non-target wildlife**	**LGDs kill (or injure) non-target wildlife**	**Shepherd response to LGDs chasing/ killing non-target wildlife**
AB01	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes (le, vv, cc, ce)	Yes, sometimes (vv)	Discourage
AB02	Yes	No	No	No	No	Yes	Yes	Yes (le, vv, cc, ce)	No	Passive
HD01	Yes	No	No	No	No	Yes	No	Yes (vv, ss, cc)	No	Encourage
HD02	Yes	No	No	No	No	No	No	Yes (vv, ss)	Yes, sometimes (vv, ss)	Unknown
HD03	Yes	No	No	No	No	No	No	Yes (vv, ss)	Yes, occasionally (vv)	Unknown
HD04	Yes	No	No	No	No	No	No	Yes (vv, fs, ss, cc)	Yes, occasionally (vv, fs)	Encourage
SB01	Yes	No	No	No	No	Yes	Yes	Yes (cc)	No	Passive
SB03	Yes	No	No	No	No	No	No	Yes (le, vv, cc)	No	Discourage
SB04	Yes	No	No	No	No	No	No	Yes (le, vv, cc)	Yes – injure only (vv)	Encourage
SB05	Yes	No	No	No	No	No	No	Yes (vv, ss, cc)	No	Encourage
SB06	Yes	Yes	No	Yes	No	No	No	Yes (le, ss, cc)	No	Passive
SB07	Yes	No	No	No	No	No	No	Yes (vv, cc)	No	Encourage
SB08	Yes	Yes	Yes	No	No	Yes	No	Yes (vv, ss, cc)	Yes – injure only (vv)	Passive

Chapter 4: Frequency of occurrence of wildlife remains in scats of livestock guarding dogs in Romania

4.1 Introduction

Livestock guarding dogs are used around the world to protect livestock from wild predators (Rigg 2001) and have been advocated for as a tool to facilitate human-wildlife coexistence by improving human tolerance of living alongside large predators (González *et al.* 2012; Rust *et al.* 2013; Potgieter *et al.* 2016; Van Der Weyde *et al.* 2020; Lieb *et al.* 2021). However, LGDs have been reported chasing and killing wildlife, including apex predators, mesopredators, and a variety of herbivores (Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020; Nayeri *et al.* 2022). Indeed, LGDs have been reported to chase and kill 80 different wild species, 78% of which were non-target species (animals deemed not to be a predation threat to livestock) (Smith *et al.* 2020a; Chapter 2), potentially acting as surrogate apex predators (van Bommel and Johnson 2016). With LGDs typically viewed as an alternative to lethal predator control methods, any evaluation of their ecological role must include an assessment of their dietary intake of wildlife.

To date, most information on LGD-wildlife interactions relies on farmer recollections, reports and anecdotes (Smith *et al.* 2020a; Chapter 2). Whilst these provide valuable information, reports may be biased or possibly underestimate LGD-wildlife interactions if LGDs are not being monitored continuously, e.g. during the night or whilst they are out of sight of humans (Whitehouse-Tedd *et al.* 2020). Many methods are available to determine if LGDs use wildlife as a food resource and how frequently they may do so. Methods including stomach content analysis, GPS cluster visitation of kill sites, metabarcoding of DNA found in faeces, and stable isotope analyses of animal tissues have been used in wildlife studies (e.g. Mumma *et al.* 2016; Jansen *et al.* 2019; Piontek *et al.* 2021; Canales-Cerro *et al.* 2022). However, these methods can be invasive and/or expensive; hence one of the simplest and most commonly employed methods to determine the diet of free-ranging animals is to identify undigested remains in faeces (Klare *et al.* 2011).

Scat analysis is a useful research technique for understanding predator-prey dynamics, competition between sympatric predators, and human-wildlife conflict issues such as livestock predation by large carnivores (Putman 1984; Meriggi and Lovarit 1996; Klare *et al.* 2011; Yarnell *et al.* 2013; Srivathsa *et al.* 2020). Several studies have previously examined the scats of free-ranging domestic dogs and documented wildlife from numerous taxa, including mammals, reptiles, birds, and even semi-aquatic marine mammals (e.g. Barnett and Rudd 1983; Campos *et al.* 2007; Krauze-Gryz and

Gryz 2014; Butler *et al.* 2018; Carrasco-Román *et al.* 2021). In some cases, the scats of other species have been analysed alongside those of dogs to assess dietary niche overlap and competition between dogs and co-occurring wild predators such as Ethiopian wolves (*Canis simensis*) (Atickem *et al.* 2010), dingoes (*Canis dingo*) (Newsome *et al.* 2014), and Indian foxes (*Vulpes bengalensis*) (Vanak and Gompper 2009a). However, few studies have quantified the wildlife component of LGD scats.

The few studies that have examined LGD diets are limited geographically to South Africa and to one breed of LGD, the Anatolian Shepherd dog (van Vliet 2011; Drouilly *et al.* 2020). In southern Africa where Anatolian Shepherd dogs have recently been introduced as LGDs, it is typical to use only one or two of these dogs per herd (Rigg 2001; Marker *et al.* 2005a; Potgieter *et al.* 2016). However, the number of LGDs used to guard each livestock herd varies significantly around the world and even the number of LGDs used per head of livestock varies within countries and is highly context-dependent (Rigg 2001). For example, a study in Greece found that the optimal ratio to protect livestock from wolves was three LGDs per 100 sheep/goats but six to eight LGDs per 100 cattle (Petridou *et al.* 2023). The number of LGDs used together could impact LGD behaviours, with successful hunting of wildlife previously documented to be more common when multiple dogs work together in packs (Silva-Rodríguez and Sieving 2011; Krauze-Gryz and Gryz 2014). In addition, different breeds of LGDs have different temperaments, with some breeds potentially being more aggressive and prone to behavioural problems (Green and Woodruff 1980; Green and Woodruff 1988; Sedefchev 2005; Ivaşcu and Biro 2020; Horgan *et al.* 2021). Other factors including the age and sex of LGDs, and whether they are accompanied by humans, can also influence LGD behaviours (Leijenaar *et al.* 2015; Drouilly *et al.* 2020; Marker *et al.* 2021). Thus, it is clear that more studies on LGD diets are required on different LGD breeds used under different management regimes and environmental conditions.

In Romania, it is common for shepherds to use multiple LGDs to protect their livestock from grey wolves (*Canis lupus*) and brown bears (*Ursus arctos*), with average numbers of between five and eight LGDs per livestock herd reported (Ivaşcu and Biro 2020; Chapter 3). The number of LGDs used per head of livestock varies greatly though; for example, in this study the shepherds used 0.25 to four LGDs per 100 sheep (Chapter 3). Shepherds use a range of native Romanian LGD breeds as well as mixed-breed LGDs (Ivaşcu and Biro 2020). Many Romanian shepherds still practice traditional transhumance grazing, moving their livestock and LGDs to high-altitude pastures during the summer months from May through October. Shepherds usually feed their LGDs a cereal-based diet comprising a mixture of polenta, wheat bran, corn, bread, and whey once or twice per day, with some shepherds also feeding dog biscuits and livestock remains including bones (Chapter 3). All shepherds in the study previously reported that their LGDs chased wildlife that entered the pasture. Some reported their LGDs occasionally killed wolves, red foxes (*Vulpes vulpes*), wild boar (*Sus scrofa*), and wildcat (*Felis sylvestris*). However, over half of the interviewed shepherds reported they had never witnessed their LGDs injuring or killing non-target species (Chapter 3).

To investigate these behaviours further, LGD scats from Carpathian Shepherd dogs and mixed-breed LGDs were collected from ten summer pastures in the southern Carpathian Mountains, and any wildlife remains within were identified. The study aimed to determine how frequently LGDs in Romania consume wildlife, and whether this behaviour is linked to factors such as the management of LGDs, and the number and breed of the LGDs at each site. It was hypothesised that there would be more wildlife remains in LGD scats from sites where 1) shepherds previously reported their LGDs to chase, kill or scavenge wildlife, 2) shepherds self-reported that they encouraged these behaviours, 3) mixed-breed LGDs were used either alone or in conjunction with Carpathian Shepherd dogs, and 4) higher numbers of LGDs were used. This study is one of few reporting LGD diets, and the first to quantify wildlife in the scats of LGDs from Romania or any similar landscape where transhumance grazing is practised with the aid of several LGDs per sheep flock, thus adding to the growing body of literature surrounding the impacts of LGDs on wildlife.

4.2 Methods

4.2.1 Study area and LGD selection

A description of the study area and process of selecting the sites and LGDs included in the study is provided in Chapter 3. Whilst 14 sites were included in the overall study, scats were only collected at ten of these sites. Between two and 14 LGDs were present at each of the ten sites, with scats collected potentially from 68 different LGDs. A summary of the LGD information at each of the ten sites where scats were collected is provided in Table 4.1.

Table 4.1. The number, breed(s), and ages of LGDs at each site where scats were collected. The type and timing of provisioned food is given, along with a summary of whether shepherds reported their LGDs to chase, injure, or kill predators or non-target species and if the shepherds discouraged, encouraged, or were passive in their response to these behaviours towards non-target wildlife (see Chapter 3 for more detail).

Site	**LGDs:**			**Provisioned food:**		**Shepherd reported that LGDs:**				**Shepherd response to LGDs chasing/ killing non-target wildlife**
	#	**Breeds (#)**	**Ages (years)**	**Type**	**When**	**Chase predators**	**Injure/kill predators**	**Chase non-target wildlife**	**Injure/kill non-target wildlife**	
AB01	6	Mixed	0.5-13	Polenta, whey, dog food, livestock (incl. bones)	AM; PM	Yes	Yes	Yes	Yes	Actively discouraged
HD01	7	Carpathian	1-3	Polenta, bread, dog food, livestock (incl. bones)	AM; PM	Yes	No	Yes	No	Actively encouraged
HD03	5	Carpathian (4) Mixed (1)	1.5-20	Dog food, livestock (incl. bones), whey	AM; PM	Yes	No	Yes	Yes	Unknown
HD04	5	Carpathian (2) Mixed (3)	0.5-8	Dog food, polenta, livestock (incl. bones)	AM; PM	Yes	No	Yes	Yes	Actively encouraged
SB01	14	Mixed	0.5-10	Polenta	AM	Yes	No	Yes	No	Passive
SB04	2	Mixed	3	Bread, whey, dog food	AM	Yes	No	Yes	Yes	Actively encouraged
SB05	6	Mixed	0.5-8	Polenta, whey, livestock (incl. bones)	AM	Yes	No	Yes	No	Actively encouraged
SB06	5	Mixed	3-13	Polenta, whey, dog food	AM; PM	Yes	Yes	Yes	No	Passive
SB07	8	Carpathian (2) Mixed (6)	1-4	Polenta, livestock (incl. bones)	AM	Yes	No	Yes	No	Actively encouraged
SB08	10	Mixed	2-10	Polenta, whey, dog food, meat from butchers (incl. bones)	AM	Yes	No	Yes	Yes	Passive

4.2.2 Scat collection

At each site, pastures were searched opportunistically for dog scats by two to four researchers for a minimum of 30 minutes. Sites were searched a varying number of times, with some searched on only one day and others up to a maximum of four days. The search was limited to the area around the sheepfold (where the sheep are enclosed during the night) on the assumption that LGD scats would be concentrated there. Searching the area around the sheepfold also increased the likelihood that scats were from domestic dogs and not from other species, such as wolves, as well as ensuring the scats were from the participant shepherd's LGDs rather than other nearby shepherds' LGDs or feral dogs. Scats were deemed to be from domestic dogs based on: morphological features – tubular with rounded ends (Laguardia *et al.* 2015); odour – confusion species such as wolf and fox scats have characteristic odours that aid in their identification (Llaneza *et al.* 2014; Werhahn *et al.* 2019); location – next to the sheepfolds so unlikely wildlife was able to defecate here without being chased away by LGDs (Chapter 3); and content – where scats clearly contained polenta or wheat bran remnants, commonly fed to LGDs in Romania (Ivaşcu and Biro 2020; Chapter 3). As well as using LGDs, shepherds in the study area also use much smaller herding dogs (Chapter 3). To ensure only LGD scats were collected, any small dog scats (those likely to originate from the herding dogs) were not collected. As such, although misidentification of scats is common in carnivore dietary studies and can bias results (Martínez-Gutiérrez *et al.* 2015; Morin *et al.* 2016), several steps were taken to ensure only LGD scats were collected here. As no molecular analyses were to be conducted on the scats, all scats were collected regardless of their freshness so long as they appeared intact. Once collected, scats were placed in plastic bags, labelled with the date and location, and stored in a freezer at -18°C until processing.

4.2.3 Scat processing

Each scat was removed from the plastic bag, photographed, and any notable features such as the shape, colour, and contents, were recorded. Any vegetation or insect material outside of the scat that was likely collected accidentally with the scats, was discarded. Initially, frozen scats were washed in a washing machine as this has been shown to be a reliable and fast method for separating prey remains from scats (Orr *et al.* 2003). Scats were placed into separate sections of a nylon stocking with up to 25 samples at a time then loaded into a washing machine and washed on a gentle cycle at 60°C without laundry detergent. Unfortunately, sharp bone fragments pierced the nylon stockings in the washing machine resulting in the loss of three samples. To prevent further losses, the rest of the samples were washed by hand. To do so, scats were left to thaw for at least 1 hour, placed in separate nylon fabric bags, and then washed individually in a sink to remove any faecal matter. During washing, a fine-pored sieve was positioned underneath the bag to catch any scat contents that got loose from the bag. Scats that were highly calcified were either soaked in hot water or gently crushed to finer dust before washing by hand. The washed contents of the scats were left to air dry on paper plates.

4.2.4 Scat contents identification

Dried scat contents were sorted into different categories: polenta/wheat bran (typical dog food), vegetation, bones, teeth, hairs, insects, other biological material (e.g. feathers, claws, tusks, horns), and non-food items (e.g. plastic, food wrappers). Hairs were grouped by morphological characteristics and then identified to the lowest taxonomic order possible by observing the macroscopic and microscopic characteristics of a subset of the hairs in each group. Hairs were identified microscopically by comparing the medulla and cuticle patterns to reference keys (Teerink 2003; De Marinis and Asprea 2006; Tóth 2017; Normandeau *et al.* 2018; Vaishnav *et al.* 2021) and a personal reference collection curated specifically for this study (Appendix C). Hairs were placed on microscope slides with coverslips and observed at 10-40x magnification using a compound microscope (GXM-L1500BHTG microscope, GX microscopes, GT Vision Ltd, UK) with a microscopy camera attached (GX Cam HiChrome Met Camera, GT Vision Ltd, UK). The cuticle pattern was studied by applying a thin layer of clear nail varnish to a microscope slide, pressing the hair into the varnish, removing the hair just before the varnish was dry, and then looking at the cuticle imprint under the microscope (e.g. Drouilly *et al.* 2020). Other recognisable biological contents, such as bones, teeth, claws, and hoof and horn materials were identified where possible. Vegetation, feathers, and insects were not identified beyond this broad classification.

The frequency of occurrence (FO) – the percentage of scats containing a particular food item or species – was then calculated. This metric is suited to dietary analysis where items occur relatively infrequently (Klare *et al.* 2011). The FO was defined as:

$$\mathrm{FO} = n/N*100$$

where n is the number of occurrences of each food item and N is the total number of scats.

A relative frequency of occurrence (RO) was also calculated for wildlife, defined as

$$\mathrm{RO} = n/T*100$$

where *T* is the total number of occurrences of all wildlife types in the samples (a summation of the individual *n* values for each wildlife category).

The frequency and relative frequency of occurrence of wildlife in the scats was compared qualitatively to LGD variables such as the number, breed, age, and sex of the dogs at each site and shepherd-reported behaviours at interview (Chapter 3; Table 4.1).

4.3 Results

Across the ten sites, 132 scats were collected, with the number of scats collected at each site varying substantially from three to 43. This was in part due to the difficulty of finding scats on some pastures (e.g. thicker or taller vegetation), but also due to visiting some locations more often than others throughout the study duration (Chapter 3), which meant that some scats were collected in just one day, others over four days. The three samples lost during the washing process were from sites HD03 (n = 1) and SB05 (n = 2). Thus, a total of 129 scats were analysed.

Scat contents were sorted into eight broad categories (Table 4.2). The non-wildlife material found comprised vegetation (FO = 97.7%), human-derived foods such as polenta, bran, and corn (FO = 41.9%), and non-food items (FO = 13.9%). Non-food items consisted of lengths of twine/string, pieces of both hard and soft plastic, material that seemed like paper food packaging, and a cigarette butt. Bones were found in 69% of the scats and comprised large, unidentifiable fragments except for two reptile skulls in one scat from site SB04. Unless accompanied by other identifiable remains such as wildlife hair or teeth, bone fragments were assumed to be livestock remains provisioned by shepherds as is common practice at the study sites (Chapter 3; Table 4.1). Livestock occurrence was not quantified any further in this study as the focus was on wildlife consumption by LGDs. Other biological material (FO = 16.3%) included claws (in one scat from site SB04), a feather (in a different scat from site SB04), eggshell fragments (in six scats from three sites – AB01, HD01, and SB05), and fragments of what seemed like tusks, horns and hooves (in 12 scats from six sites – AB01, HD01, HD04, SB01, SB05, and SB06). Shepherds were witnessed discaring egg shells on the ground, thus, due to a lack of accompanying feathers or bird bones, the eggshell fragments in the scats were assumed to be human-derived food as opposed to dogs raiding wild bird nests and consuming eggs. Teeth were found in five scats (FO = 3.9%) and identified as belonging to livestock (n = 3), wild boar (n = 1), and a member of the Carnivora family (n = 1). Hairs were found in all scats but one (FO = 99.2%) and identified as wildlife hairs in 11 of the scats.

Table 4.2. Frequency of occurrence (FO) of the eight different categories of ingested material (before further identification) and the sites they were found at.

Category	FO (%)	No. of sites (site IDs)
Hairs	99.2%	10 (All)
Vegetation	97.7%	10 (All)
Bones	69.0%	10 (All)
Polenta/bran/corn	41.9%	10 (All)
Insects	24.8%	7 (HD01, HD03, HD04, SB01, SB04, SB05, SB06)
Other biological items	16.3%	9 (AB01, HD01, HD04, SB01, SB04, SB05, SB06, SB07, SB08)
Non-food items	13.9%	7 (AB01, HD01, HD04, SB01, SB04, SB05, SB08)
Teeth	3.9%	3 (HD01, SB04, SB05)

Overall, materials from wildlife were found in 27.9% of the scats (n = 36). Two other scats potentially contained wildlife, but the hairs could not be identified conclusively due to degradation and a small sample size (only one or two hairs). Most of the wildlife remains found in the scats were from insects (n = 32, FO = 24.8%), with 75% of the scats (n = 24) containing wildlife comprising only insect fragments. The other eight scats containing insects also contained vertebrate remains. Four scats contained vertebrate remains only. Of the vertebrate remains, mammals were most commonly found (n = 11, FO = 8.5%) followed by reptiles (FO = 0.8%) and birds (FO = 0.8%), which were only found in one scat each at site SB04. Within the mammals category, two species could be identified from hairs – wild boar (n = 5, FO = 3.9%) and European hare (*Lepus europeaus*) (n = 1, FO = 0.8%) (Figure 4.1) – as well as two broader categories – Carnivora (n = 3, FO = 2.3%) and micromammals (n = 4, FO = 3.1%) (Table 4.3). These two broader categories were used to avoid misidentification at the species-level with micromammals comprising any small rodents and insectivores (those approximately <500g in body weight). Hairs grouped into the Carnivora category likely belonged to red fox and members of the mustelid family (e.g. Figure 4.2), and those in the micromammal category were identified as likely belonging to voles, mice, and shrews (e.g. Figure 4.3 and Figure 4.4). In total, there were 47 occurrences of wildlife in the 36 scats containing wildlife remains, leading to relative occurrence (RO) frequencies for each category as follows: insects – 68.1%, wild boar – 10.6%, micromammals – 8.5%, Carnivora – 6.4%, European hare – 2.1%, reptiles – 2.1%, and birds – 2.1% (Table 4.3).

Table 4.3. Frequency of occurrence (FO) and relative frequency of occurrence (RO) of wildlife remains found in scats with the sites where they were found.

Wildlife	**n**	**FO (%)**	**Wildlife RO (%)**	**No. of sites (site IDs)**
Insects	32	24.8	68.1	7 (HD01, HD03, HD04, SB01, SB04, SB05, SB06)
Mammals				
Wild boar	5	3.9	10.6	1 (HD01)
Micromammals	4	3.1	8.5	3 (HD01, HD04, SB04)
Carnivora	3	2.3	6.4	2 (SB04, SB06)
European hare	1	0.8	2.1	1 (HD03)
Reptiles	1	0.8	2.1	1 (SB04)
Birds	1	0.8	2.1	1 (SB04)

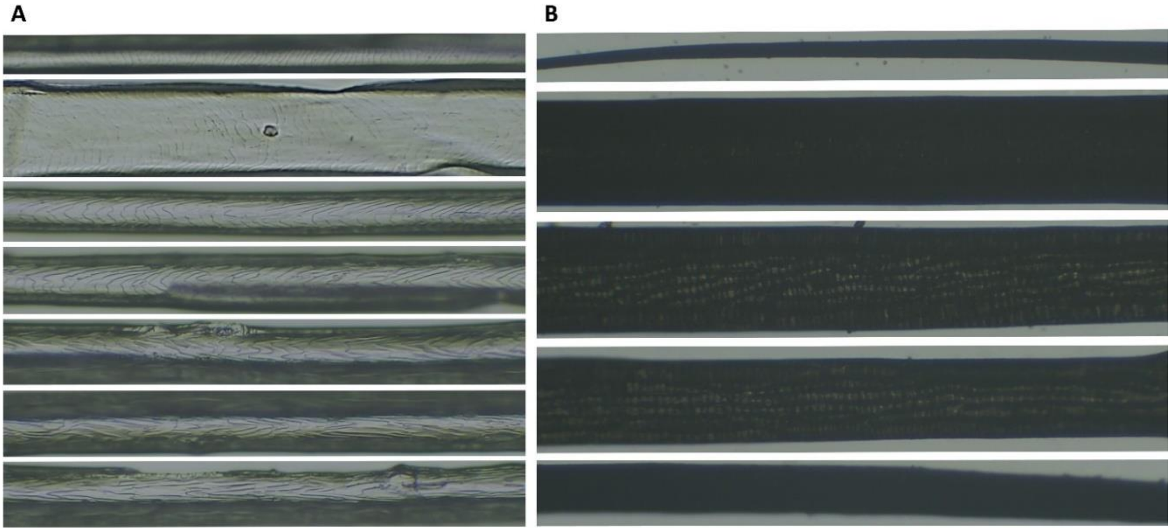

Figure 4.1. Cuticle (A) and medulla (B) patterns of a hair from an LGD scat collected at site HD03. The hair was identified as Lagomorpha; the only species known to be present in the study area is the European hare (Lepus europeaus). Hairs run from left to right from the apical region at the top to the basal region at the bottom. Images taken on a light microscope at 40x magnification.

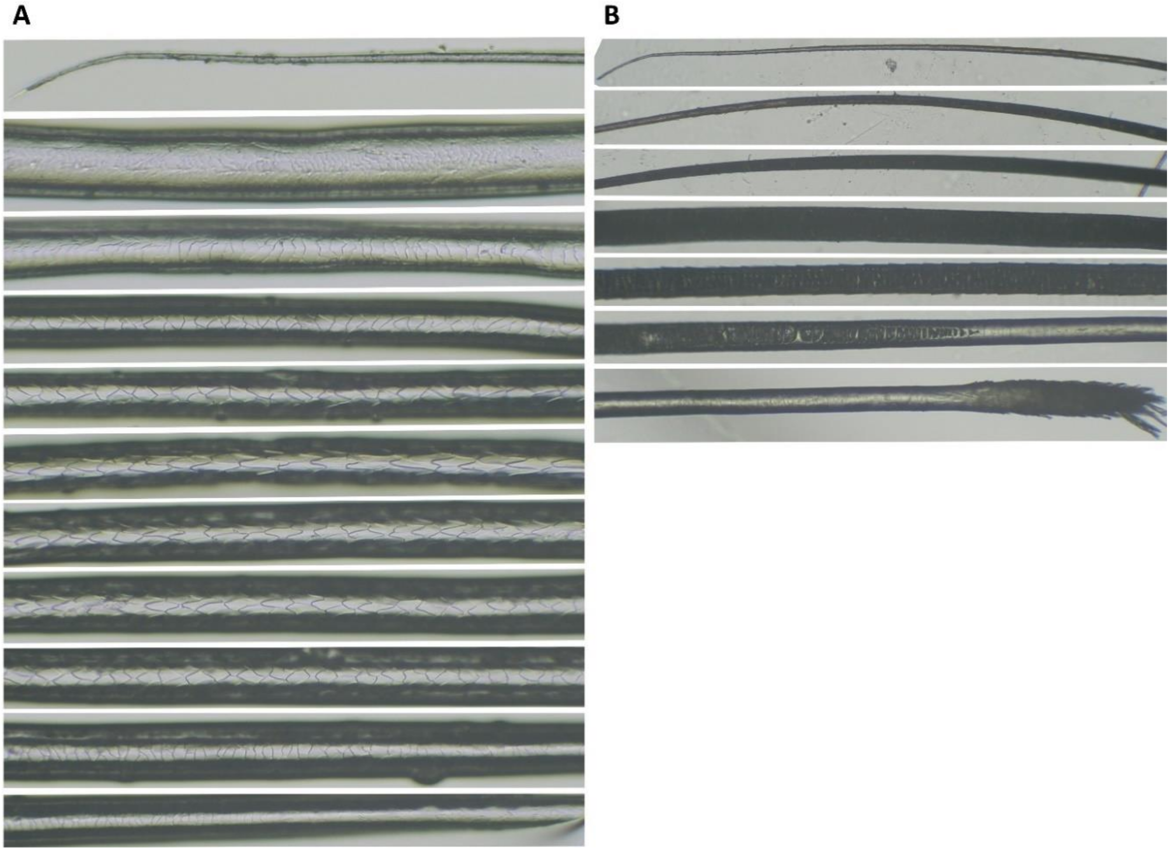

Figure 4.2. Cuticle (A) and medulla (B) patterns of a hair from an LGD scat collected at site SB04. The hair was identified as belonging to the order Carnivora, and almost certainly as one of the Mustelidae family. Hairs run from the apical region (top) to the basal region and bulb (bottom). Images taken on a light microscope at 10x magnification.

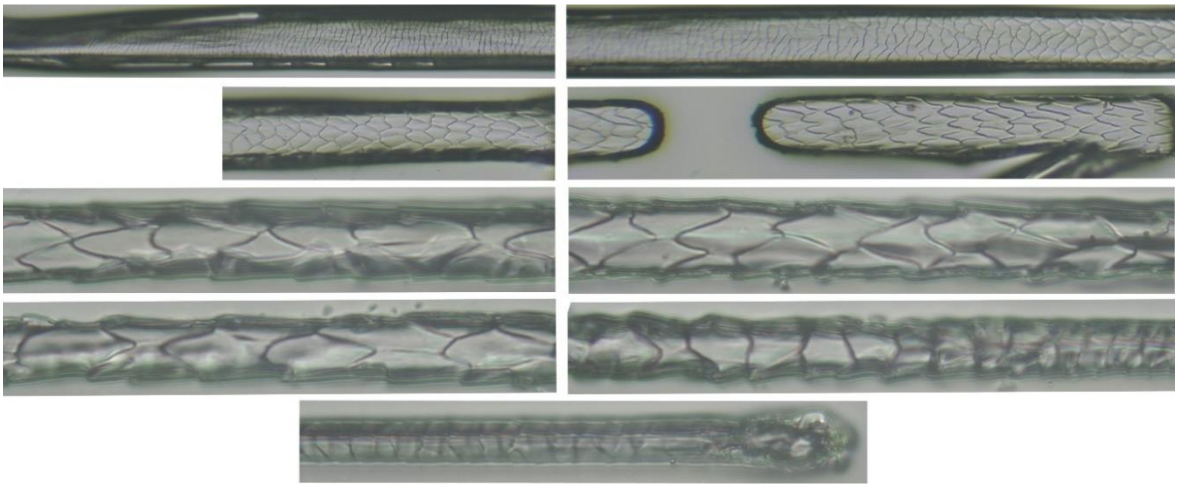

Figure 4.3. Cuticle patterns of hairs from an LGD scat collected at site SB04. The hairs were identified as micromammal, most likely a mouse species. Hairs run from left to right, bottom to top running from the apical to the basal region. Images taken on a light microscope at 10x and 40x magnification.

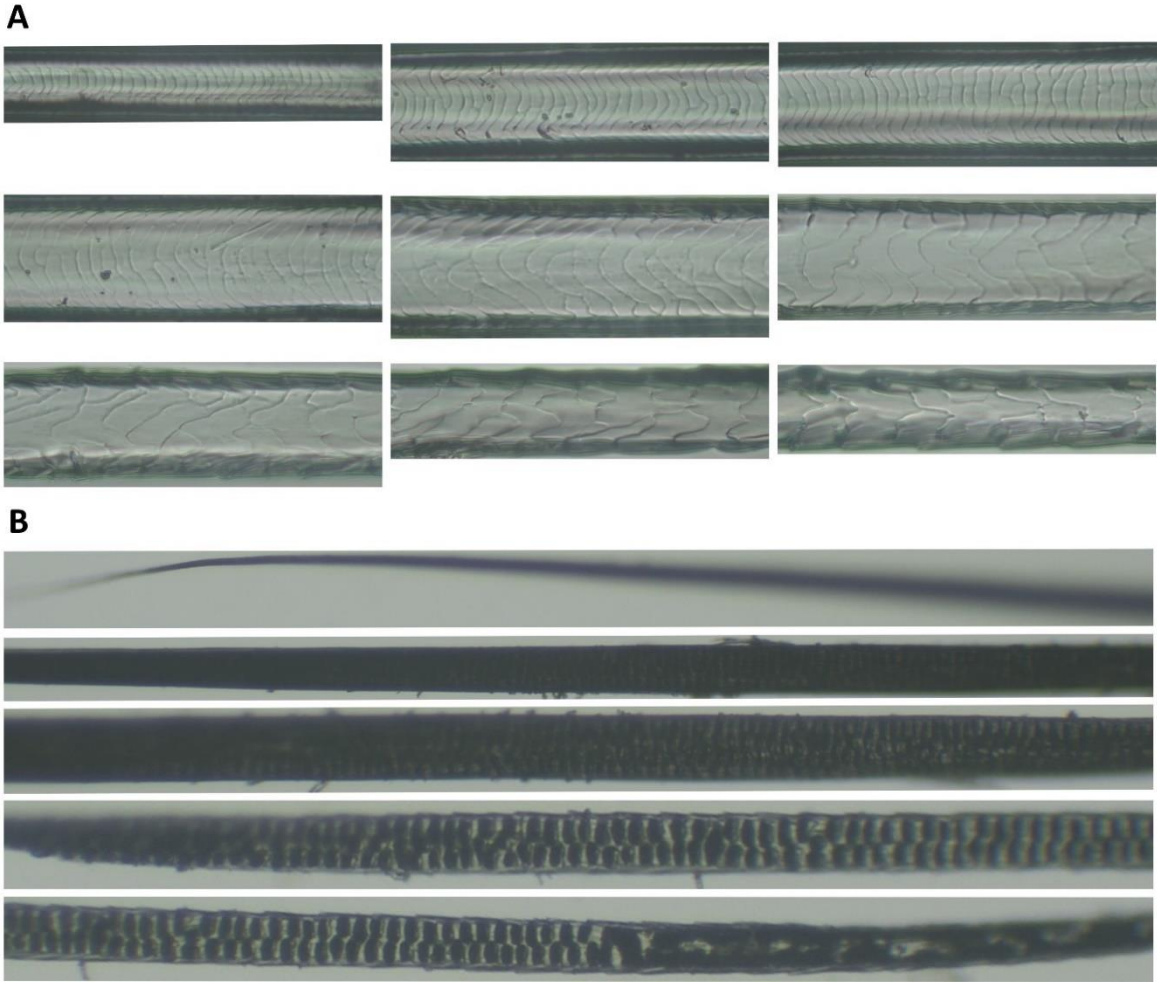

Figure 4.4. Cuticle (A) and medulla (B) patterns of a hair from an LGD scat collected at site HD01. The hair was identified as micromammal, most likely a vole species. Hairs run from left to right, bottom to top running from the apical to the basal region. Images taken on a light microscope at 40x magnification (A) and 10x magnification (B).

At three of the ten sites, none of the scats contained wildlife (AB01, SB07, SB08), and at two sites there were only insects (SB01, SB05) (Table 4.4). Therefore, vertebrate wildlife remains were found at half of the sites (n = 5), with site SB04 providing the greatest diversity comprising insects, reptiles, birds, Carnivora (likely a mustelid) and micromammals. Seven of the ten scats collected at this location in just one day contained wildlife, and this location was the only place where a scat contained more than one vertebrate wildlife type. Wild boar remains were only found in scats from site HD01 on one sampling day in October. A full breakdown of the wildlife remains in scats at each location over the different sampling days is provided in Table 4.4.

Table 4.4. Wildlife remains in the scats of LGDs per location and per wildlife grouping. The percentage of scats containing each wildlife group from each location is presented, along with the number of sampling days that each was found in. Instances where wildlife was found are highlighted with bold, blue text.

Site	**Total scats**	**Sampling days**	**All wildlife**		**Insects**		**Reptiles**		**Birds**		**Wild boar**		**Carnivora**		**European hare**		**Micromammals**	
			% scats	**# days**	**% scats**	**# days**	**% scats**	**# days**	**% scats**	**# days**	**% scats**	**# days**	**% scats**	**# days**	**% scats**	**# days**	**% scats**	**# days**
AB01	19	2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2
HD01	7	2	**85.7**	**2/2**	**57.1**	**2/2**	0	0/2	0	0/2	**71.4**	**1/2**	0	0/2	0	0/2	**14.3**	**1/2**
HD03	2	1	**100.0**	**1/1**	**100.0**	**1/1**	0	0/1	0	0/1	0	0/1	0	0/1	**50.0**	**1/1**	0	0/1
HD04	14	1	**14.3**	**1/1**	**7.1**	**1/1**	0	0/1	0	0/1	0	0/1	0	0/1	0	0/1	**7.1**	**1/1**
SB01	12	4	**8.3**	**1/4**	**8.3**	**1/4**	0	0/4	0	0/4	0	0/4	0	0/4	0	0/4	0	0/4
SB04	10	1	**70.0**	**1/1**	**70.0**	**1/1**	**10.0**	**1/1**	**10.0**	**1/1**	0	0/1	**20.0**	**1/1**	0	0/1	**20.0**	**1/1**
SB05	41	4	**39.0**	**4/4**	**39.0**	**4/4**	0	0/4	0	0/4	0	0/4	0	0/4	0	0/4	0	0/4
SB06	14	2	**14.3**	**1/2**	**7.1**	**1/2**	0	0/2	0	0/2	0	0/2	**7.1**	**1/2**	0	0/1	0	0/2
SB07	4	2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2	0	0/2
SB08	6	1	0	0/1	0	0/1	0	0/1	0	0/1	0	0/1	0	0/1	0	0/1	0	0/1

Although no statistical analyses were conducted due to small and irregular sample sizes across sites, the number, breed, sex, or age of the LGDs at each site do not seem associated with the occurrences of wildlife remains in the scats; scats containing wildlife remains originated from packs of LGDs comprised of two, five and seven dogs, purebred Carpathian Shepherd dogs and mixed-breed dogs, males and females, and dogs ranging in age from six months old to 13 years old (Table 4.1; Table 4.3). No link between the shepherd-reported LGD behaviours and the occurrence of wildlife in the scats was apparent, though the occurrence of wildlife remains in the scats largely aligned with self-reported shepherd responses to their LGDs chasing wildlife (Table 4.1; Table 4.3). Wildlife remains were found in scats from sites HD01, HD04, SB04 and SB06 where shepherds either all encouraged or did not actively discourage the chasing of wildlife, while no wildlife remains were found in any of the 19 scats collected at AB01 where chasing of wildlife was actively discouraged. The exceptions were sites SB07 and SB08 where no wildlife was found, despite LGDs being encouraged to chase wildlife (Table 4.1; Table 4.3).

4.4 Discussion

This study provides the first assessment of the frequency of occurrence (FO) of wildlife remains in the scats of Romanian LGDs used as part of a transhumance grazing system. The findings show that wildlife consumption by LGDs over the summer months in the Romanian Carpathian Mountains does occur but at seemingly low frequencies.

Overall, wildlife remains were found in less than a third of the scats and largely consisted of insect fragments. Vertebrate remains were found in less than 10% of the scats at only half of the sites with two of the sites contributing a considerable proportion of these vertebrate occurrences. The most common mammalian category found was wild boar, occurring in only 4% of the scats, all collected from the same site on the same day. Thus, the wild boar remains likely originated from only one individual wild boar being consumed. It was not possible in this study to attribute scats to individual LGDs, hence all of the scats containing wild boar could have originated from a single LGD. From a total of 68 LGDs across the ten sites, the scats containing wildlife could have originated from 10-34% of the LGDs, calculated as a minimum of seven LGDs (if all scats containing wildlife from each site originated from the same LGD) up to a maximum of 23 LGDs (if each scat containing wildlife was produced by a different LGD, whilst accounting for the maximum number of LGDs per site). Similarly, the scats containing vertebrate remains could have originated from between five and 12 LGDs (7-18% of the total LGDs); lower percentages than those from a recent study in Romania that found vertebrate wildlife remains in the stomach contents of 29% of the feral dogs examined (Dănilă *et al.* 2023).

The low FOs of wildlife in LGDs scats found in this study are similar to those from another recent study on LGD diets in South Africa (Drouilly *et al.* 2020). Successful hunting of wildlife has been found to be more common where multiple dogs work together in packs (Butler *et al.* 2004; Silva-Rodríguez and Sieving 2011; Krauze-Gryz and Gryz 2014), hence it was expected that the FOs of wildlife in this study would be higher than those found in the study from South Africa due to greater numbers of LGDs used together in Romania. However, the comparable results from both studies suggest that this is not the case. Furthermore, it has been suggested that LGDs might act as surrogate top predators by creating a landscape of fear leading to avoidance of LGD-inhabited areas by wildlife (van Bommel and Johnson 2016). If LGDs were acting as top predators, it might also be expected that far more of their scats would contain wildlife remains. For example, one study found that over 95% of grey wolf scats in the Carpathian Mountains contained at least one wildlife food type, with wild ungulates being found in over 80% of the scats (Sin et al. 2019). Such high FOs of wildlife would not be expected for animals that have access to human-provisioned food, but the low FOs of wildlife found in both this study and that in South Africa suggests that LGDs are not acting as surrogate top predators, at least in regard to exerting predation pressure on prey.

However, it is possible that scat analysis underestimates how frequently LGDs kill wildlife if carcasses are not consumed, as seen with domestic cats (Cecchetti *et al.* 2021; Piontek *et al.* 2021). In this study, only one shepherd explicitly said he had witnessed his LGDs consuming wildlife that the LGDs had killed (Chapter 3). This behaviour could be typical of domestic dogs as they have an instinctive prey drive to chase animals without necessarily wanting to eat them. For example, Martinez *et al.* (2013) found that over half of the free-ranging dogs in their study were reported not to consume their wildlife kills, and Home *et al.* (2017) found that only 36% of killed wildlife were then consumed by free-ranging dogs in India. These numbers could be greater for LGDs as they are tasked with the protection of livestock, so they might instinctively kill wildlife in defence of livestock with no desire to consume the carcass. This behaviour has in fact been reported for LGDs in Botswana (Potgieter *et al.* 2013), therefore highlighting the risk of scat analysis underestimating the frequency of LGD-related wildlife mortality.

In contrast, scat analysis could overestimate predation as it is not possible to distinguish between hunted and scavenged remains in scats. Whilst being interviewed, one shepherd (site HD01) stated he had witnessed his LGDs eating wildlife carcasses that the dogs had found rather than killed (Chapter 3) and previous studies have documented domestic dogs as effective scavengers (Butler and du Toit 2002; Selva *et al.* 2005; Martinez *et al.* 2013; Newsome *et al.* 2014; Butler *et al.* 2018). Shepherds did report that their LGDs chased and killed wild boars (Chapter 3) and this behaviour has been reported in other countries too (Rigg 2004; Caporioni *et al.* 2005; Nayeri *et al.* 2022), but there were also likely to have been wild boar carcasses in the study area due to hunting and recent outbreaks of African swine fever (Boklund *et al.* 2020; Sauter-Louis *et al.* 2021). Thus, any remains in the scats could equally have been predated or scavenged.

While it is not possible to determine whether wildlife in the scats in this study were predated or scavenged, both have important ecological and social impacts. Predation can directly affect prey population numbers, as well as induce morphological, physiological or behavioural adaptations in prey animals (Say-Sallaz et al. 2019), which can lead to cascading effects in ecosystems (Ripple *et al.* 2014; Suraci *et al.* 2016). Predation of wildlife by LGDs could also exacerbate human-human conflicts, as is the case in Romania where tensions arise between game managers and shepherds due to the former claiming that LGDs predate game species (Ivaşcu and Rakosy 2017; Chapter 3). Where dogs act as kleptoparasites feeding on the kills of other predators, or scavenge wildlife carcasses, they compete with other scavengers for food resources and potentially alter scavenger community structures that have important ecological roles (Beasley *et al.* 2015; Landry *et al.* 2020). Scavenging of wildlife carcasses by LGDs could also be a public health concern with the increased potential for disease transmission between wildlife and dogs, which are then in close proximity to livestock and humans (Costanzi *et al.* 2021). It is, therefore, important to quantify predation and scavenging by LGDs, which could be attempted with extensive observations of LGDs in the field, camera traps positioned at known carcasses near agricultural pastures, or with the attachment of animal-borne video cameras to LGDs.

Regardless of whether the vertebrate remains in the scats were from hunting or scavenging, their occurrence was still at low levels with all FOs below 4%. In comparison, insect remains were found in 25% of the scats; a much higher frequency than reported in other studies analysing dog scats (e.g. Drouilly *et al.* 2020 - 2.3% FO; Carrasco-Román *et al.* 2021 - 1.5% FO). The LGDs in this study were observed consuming grass and vegetation so could have consumed insects passively in this process. Furthermore, although insects on the outsides of the scats were removed before the washing process, it is possible that some coprophagous insects remained inside the scats and were not actually consumed by the LGDs. However, much of the insect material appeared to be Orthoptera in origin, some of the scats contained large quantities of insect material, and two of the shepherds interviewed said their LGDs ate insects as it is a source of protein and also as a form of play for their younger LGDs (Chapter 3); all of which suggests that most insect remains were not of coprophagous origin. The insect material found in the scats in this study was not rigorously quantified or identified to any lower taxonomic grouping, but with a quarter of scats containing insects, future studies should investigate the amount of insect biomass consumed on agricultural pastures by LGDs and whether there are any potential ecological knock-on effects or impacts on threatened invertebrate species.

Whilst the results of this study suggest low levels of wildlife consumption by LGDs, it must be acknowledged that the sample size was limited. In addition, morphological scat analysis has important shortcomings, including uncertainty over species-level identification and the possibility of overlooking smaller items such as micromammal hairs (Klare *et al.* 2011; Gosselin *et al.* 2017). It is, therefore, possible that some micromammal hairs were missed in the analysed scats. Faecal DNA metabarcoding (high-throughput sequencing to amplify and identify DNA assemblages in scats) can overcome some of these problems by providing information on species' DNA within scats, which can sometimes provide better estimates of dietary composition (Shores *et al.* 2015; Gosselin *et al.* 2017; Oja *et al.* 2017). Another alternative is stable isotope analysis, which has previously been used to assess domestic dog diets by analysing the stable carbon and nitrogen composition of whiskers (e.g. Kernaléguen *et al.* 2012; Mutirwara *et al.* 2018; McDonald *et al.* 2020; Wilson-Aggarwal *et al.* 2021; Canales-Cerro *et al.* 2022). Stable isotope analysis on LGD whiskers would provide dietary information for individual dogs, thus enabling more detailed comparisons between different ages, sexes, and breeds of dogs than is possible for scats collected opportunistically off pastures.

The ability to assign specific diets to individual LGDs would greatly improve understanding of the extent of LGD impacts on wildlife and potential mitigation options. In this study, most of the vertebrate remains were found at only a subset of the sites, suggesting that consumption of wildlife could be limited to specific groups of LGDs. Although the number, breed, sex, or age of LGDs at each site did not seem to play a substantive role, a considerable proportion of the wildlife remains in the scats originated from site SB04 where the LGDs were primarily fed bread (Chapter 3). Dogs provided with a nutritionally-inadequate diet might need to hunt to meet their energetic and nutritional requirements and thus be associated with increased wildlife predation (Silva-Rodríguez and Sieving 2011; Vanak *et al.* 2013; Sepúlveda *et al.* 2014; Merz *et al.* 2022), but this remains to be rigorously tested. However, if the consumption of wildlife by LGDs is linked to their provisioned diet, then this could be altered to hopefully reduce predation and scavenging. Furthermore, the occurrence of wildlife in the scats largely aligned with self-reported shepherd behaviours, similar to the study on LGD diets in South Africa that found that the occurrence of birds, reptiles, and wild mammals in LGD scats were higher when accompanied by a human (although not significantly so) (Drouilly *et al.* 2020). Thus, it is possible that LGD behaviours towards different species are driven by human attitudes towards wildlife and that efforts to change shepherd behaviours could help with mitigating undesirable LGD behaviours such as chasing and killing wildlife. Likewise, correctional training could be provided to LGDs exhibiting undesirable behaviours (Whitehouse-Tedd *et al.* 2020) or the use of physical deterrents, such as collar covers that have been shown to reduce wildlife predation by domestic cats (Cecchetti *et al.* 2021), could be explored. For example, some LGDs in Romania are fitted with 'dangle sticks'. These are sticks that hang from their collars and hit their front legs when they run to prevent them from chasing livestock and wildlife. None of the shepherds in this study used dangle sticks on their LGDs, and the welfare implications for the LGDs has been questioned, but their existence highlights that there are deterrents and other options to be investigated further.

4.5 Conclusion

This study has demonstrated that consumption of wildlife by LGDs in the Romanian Carpathian Mountains does occur, but at low frequencies. The occurrence of wildlife in the LGD scats was minimal and largely attributed to only two specific groups of LGDs. Wildlife remains in the scats were predominantly from insects, with few occurrences of mammals and even fewer occurrences of birds and reptiles. In this study, it was not possible to differentiate between predated and scavenged material in scats. Although hunting of wildlife by LGDs would have the greater impact on wildlife populations through consumptive effects, scavenging also has important ecological and social implications through competition with predators and scavengers, and potentially exacerbating existing human-human conflict between shepherds and game managers. However, given the low occurrence of wildlife in the scats, it is unlikely that LGDs are negatively impacting co-occurring wildlife populations through consumptive effects of predation or scavenging. Future studies assessing the relationship between wildlife consumption and LGD breed, age, and sex, shepherd behaviours, and human-provisioned diet, will help to determine which LGDs are most prone to wildlife predation and/or scavenging and aid in informing appropriate, targeted mitigation measures to ensure LGD use offers a net benefit to both human livelihoods and wildlife conservation.

Chapter 5: Spatial associations between livestock guarding dogs and sheep in the Carpathian Mountains, Romania

5.1 Introduction

Livestock guarding dogs (LGDs) are working domestic dogs (*Canis familiaris*) that are used to protect livestock, typically small ruminants, from wild predators (Rigg 2001). These dogs are considered effective in helping to reduce livestock losses and facilitate coexistence with predators (González *et al.* 2012; Rust *et al.* 2013; Van Der Weyde *et al.* 2020; Lieb *et al.* 2021). The use of LGDs originated in Europe and Asia, but now many different breeds are used worldwide (Rigg 2001). Whilst distinctive in morphology, all LGD breeds share similar character traits, typically: trustworthiness (lack of predatory behaviour towards livestock), attentiveness (the tendency for the dog to stay with and watch the livestock), and protectiveness (the tendency for the dog to defend livestock from perceived threats) (Lorenz and Coppinger 1986). These three traits rely on a strong bond between LGDs and livestock and dictate that LGDs should remain in close proximity to livestock to be effective guardians (Gehring *et al.* 2011a).

However, livestock owners sometimes report behavioural problems with LGDs (van Bommel and Johnson 2023), including that their LGDs do not always remain with the livestock (e.g. Marker *et al.* 2005b; Gehring *et al.* 2011; Potgieter *et al.* 2013). Some level of roaming away from livestock could be beneficial in that LGDs could be patrolling the wider area searching for threats (Landry *et al.* 2020), they could be establishing territories to discourage predators from travelling into areas where livestock are grazed (van Bommel and Johnson 2014a; van Bommel and Johnson 2014b), or they could be actively chasing predators away from livestock (Sedefchev 2005). However, LGDs cannot directly protect the livestock from a predator attack if they are not physically with them when the attack occurs. Indeed, a study on Anatolian Shepherd LGDs in Namibia suggested that the LGDs that stayed closer to the livestock were perceived as the most effective by their owners (Aslam *et al.* 2022).

Beyond impacts on livestock guarding effectiveness, LGDs roaming away from livestock could present ecological and social issues. Recently, the effects of LGDs on wildlife have been highlighted (Allen *et al.* 2019a; Smith *et al.* 2020a; Whitehouse-Tedd *et al.* 2020; Chapter 2), hence instances of LGDs leaving the livestock could be due to LGDs chasing and even predating wildlife. These excursions also increase the area over which any ecological effects of LGDs might occur. Such ecological effects include displacing wildlife (van Bommel and Johnson 2016; Kinka *et al.* 2021; Ugarte *et al.* 2021), spreading diseases to wildlife (Knobel *et al.* 2014), and hybridising with other wild canids (Kopaliani *et al.* 2014; Linnell and Lescureux 2015). If LGDs are leaving the sheep, this also means they are no longer under human supervision (if a human usually attends the livestock), and could pose a traffic hazard or nuisance to people participating in recreational activities such as hiking and mountain biking (Mosley *et al.* 2020; Salvatori *et al.* 2020a). In some cases, LGDs roaming away from the livestock onto neighbouring properties or land results in those LGDs being killed (Marker *et al.* 2005b; van Bommel and Johnson 2023), which could cause or aggravate existing human-human conflicts. As such, understanding where LGDs spend their time in relation to the livestock they are guarding is crucial for assessing LGD effectiveness and their potential impacts on the wider environment from an ecological and social perspective.

Information on LGD behaviours can be obtained from traditional observational studies (e.g. Lapeyronie and Moret 2003; Landry *et al.* 2020; Aslam *et al.* 2022), but these are labour-intensive, can affect the behaviour of the focal animals, and usually cannot be conducted over a 24-hour monitoring period. In addition, if LGDs roam away from the livestock it can be difficult or impossible to follow them through dense vegetation and at high speeds, thus LGDs would not be visible to the observer at all times. Fortunately, developments of GPS and other sensors into miniaturised tracking devices have dramatically improved the ability to capture location and activity data and, therefore, study animal movement (Kays *et al.* 2015).

Several studies have previously used GPS tracking methods to monitor the movements and behaviours of free-ranging domestic dogs (Foley and Sillero-Zubiri 2020; Warembourg *et al.* 2021; Schüttler *et al.* 2022; Ladd *et al.* 2023), and of LGDs specifically. Tracking of LGD movements has been conducted primarily with a focus on measuring the proximity of LGDs to livestock as an indirect measure of their effectiveness at guarding livestock (e.g. Zingaro *et al.* 2018; Young *et al.* 2019), though some studies have used movement data to investigate LGD-wildlife interactions and how LGDs respond to the presence of predators (e.g. van Bommel and Johnson 2014a; Allen *et al.* 2017; Bromen *et al.* 2019). Most of the previous studies on LGD movements were conducted in the USA and Australia, where breeds such as the Maremma and Great Pyrenees have been introduced as a novel method for protecting livestock. Only two studies have focused on LGD breeds in their native habitats: Akbash LGDs in Turkey (Akyazi *et al.* 2018), and Maremma and Great Pyrenees LGDs in Italy (Zingaro *et al.* 2018).

This study focuses on the movement behaviours of native LGD breeds in Romania, where transhumance grazing and the use of LGDs are long-standing traditional practices (Chapter 3). The objective was to determine the frequency and extent of LGDs roaming away from livestock and whether this was affected by LGD breed, sex, or age, whether the LGDs were neutered, or whether the sheep were enclosed or freely grazing. To conduct this study, sheep and a mixture of Carpathian Shepherd dogs and mixed-breed LGDs were fitted with GPS collars and the distance between LGDs and sheep at simultaneous time points was used to determine how far LGDs were from sheep, how frequently they were far away from the sheep, and for how long. Greater distances between LGDs and sheep could be caused by the LGDs roaming away from the sheep or by the LGDs not following the sheep onto the pasture. These two behaviours were distinguished by examining daily overlaps in space use between LGDs and sheep.

As shepherds in the study had previously reported that their LGDs chase, kill, and scavenge wildlife carcasses (Chapter 3), and wildlife remains were found in LGD scats collected from the same sites, although at very low frequencies (Chapter 4), it was expected that some instances of LGDs roaming away from the sheep would be observed. From previous studies investigating LGD behaviours, it was also hypothesised that: 1) sexually intact LGDs and male LGDs would roam further in search of mating opportunities (Timm and Schmidt 1989; Green and Woodruff 1990); 2) older dogs would remain closer to livestock as they bond with livestock and become more attentive over time (van Bommel and Johnson 2014b; Zingaro *et al.* 2018); and 3) different breeds would generally have different temperaments and effectiveness of livestock protection (Andelt 1999), with mixed-breed dogs roaming further and more frequently than purebred Carpathian Shepherd dogs. This study is the first to monitor the fine scale movement of LGDs in the Carpathian Mountains where shepherds practice transhumance grazing, thus contributing to a wider understanding of LGD behaviours under different environmental contexts, potential environmental impacts, and conflicts over LGD roaming behaviours.

5.2 Methods

5.2.1 Study area

This study was conducted at 14 sites in the southern Carpathian Mountains, Romania (Chapter 3).

5.2.2 Ethical approval

The GPS tracking of LGDs and livestock received ethical approval from Nottingham Trent University under project code ARE192048R(21), see Chapter 3 for details.

5.2.3 GPS tracker deployment

Between 27 May and the 12 October 2021, 14 sites were visited where one sheep from the flock and up to four of the associated LGDs were fitted with Tractive® XL GPS Pet Trackers (Tractive GmbH, Austria) fixed to nylon dog collars (Figure 5.1). At sites where more than four LGDs were guarding the sheep flock, an attempt was made at randomly selecting a mixture of breeds, sexes, and ages of LGDs. However, this was not always possible, as some of the LGDs could not be safely handled. As in Zingaro *et al.* (2018), it was assumed that the location of the one tracked sheep would represent the movement of the entire flock as the shepherds stated that their sheep stayed closely associated with each other naturally and by use of herding dogs. In total, 14 sheep and 47 LGDs were fitted with GPS tracking collars over the 14 sites (Table 5.1).

Figure 5.1. Carpathian Shepherd dog fitted with a GPS tracking collar at site HD01.

Due to the difficulty and effort involved in reaching each site, visits were limited to three occasions: one to deploy the GPS collars, one to switch the batteries, and one to collect the GPS collars. In the event of a malfunctioning GPS tracker, an additional visit was made to swap devices. The aim was to gather approximately four weeks of data from each animal, but this was constrained by the battery life of the devices at different sites and how much data could be captured from two tracking periods (i.e. two full batteries). The GPS devices required cellular reception to transmit and subsequently store the location information on the Tractive® server. Where the cellular reception was poor or intermittent, the batteries depleted faster due to the devices constantly searching for a signal; hence not all animals were tracked for the same length of time (Table 5.1).

The GPS tracking devices were duty cycling so were factory-programmed to record one fix every 2-3 minutes when the animal was moving and one fix every 60 minutes when the animal was resting. The average accuracy of each device for each recording period was provided by request to Tractive® customer services (Table 5.1).

5.2.4 Pre-processing of GPS data

5.2.4.1 Data cleaning

Processing of GPS data must be executed prior to data analysis to discard duplicates and outliers (Joo *et al.* 2020; Gupte *et al.* 2022), thus any duplicated time values per individual were removed and outliers identified. Outliers are often identified by lower horizontal dilution of precision (HDOP) values and fewer satellites being used to provide the location (Gupte *et al.* 2022). However, these two attributes were not provided with the data downloaded from the devices used in this study. Another method is removing biologically implausible speeds; often achieved by removing the top 5% or 10% of speeds (Gupte *et al.* 2022). However, this value is arbitrary and it was clear that this method would remove plausible locations: the 95th percentile of speeds from the LGD data was 0.81 ms^{-1}, a pace that has been classed as 'walking' in another study of a shepherd dog breed (Maes *et al.* 2008) and similar to the average walking speed of sheep at 0.75 ms^{-1} (Young *et al.* 2019). Even the 99th percentile was only 1.4 ms^{-1}, a pace similar to trotting (Maes *et al.* 2008). Although the top speed of the LGDs in the study is unknown, a study on Kangal LGDs in Turkey found they travelled at speeds of up to 8.9 ms^{-1} (Akyazi *et al.* 2018), thus the percentile values were not appropriately high enough to use as a threshold for removing biologically implausible locations based on dog speeds. Instead, each animal's tracking data (both the locations and trajectories) were inspected manually by the researcher in QGIS. The researcher looked at the data for each site at 10 minute intervals searching for 'spikes' in the data where GPS fixes seemingly jumped from one location to another and then back to the initial location with no intermediate fixes (Gupte *et al.* 2022). Considering the distance and time between consecutive fixes in these spikes, and knowledge of the study species' behaviours, the researcher made an informed decision for each spike as to whether to remove or keep it. Although this was subjective, it was a more conservative approach that would not remove as much true data as using arbitrary threshold values to filter the data.

The presence of the researchers with the shepherd meant that some LGDs did not join the sheep straight after having the GPS collars fitted. Researchers were usually present for no more than one hour, thus the first hour of data for all animals was removed. Only temporally overlapping data between LGDs and their associated sheep were included in analyses. For example, if the sheep GPS tracker ran out of battery before an LGD's GPS tracker, any data for the LGD beyond the time at which the sheep GPS tracker turned off were discarded.

5.2.4.2 Sheepfold use

Sheep were enclosed in a sheepfold each evening but roamed the pastures with the shepherd during the day (Chapter 3). To determine whether LGD movements differ when the sheep are enclosed, the analyses needed to be split temporally into two periods: when sheep were inside the sheepfold versus when the sheep were grazing on the pastures. These two periods largely align with night and day hours, respectively, but not perfectly. Thus, it was necessary to manually classify the GPS locations to within each time period by visualising the GPS data at an hourly rate at each site. As the location of each sheepfold was known, the researcher could note the time of the first sheep GPS fix back at the sheepfold in the evening and the time of the first GPS fix outside of the sheepfold in the morning when sheep were taken out to graze on the pastures. Any GPS fixes occurring between these two times were categorised as occurring when sheep were inside the sheepfold, and any GPS fixes occurring outside of these two times were categorised as occurring when the sheep were grazing on the pasture.

5.2.4.3 Data regularisation

Due to the duty-cycling nature of the GPS tracking devices (locations every 2-3 minutes when moving, but every 60 minutes whilst resting) and losses of GPS signal, the raw data were collected at irregular time intervals. Temporally irregular data can be difficult to analyse, thus, the cleaned raw data were used to predict the most likely movement path of each individual with locations at regularly spaced intervals. This was achieved using the R function '*crawlWrap*' provided in the '*momentuHMM*' package (McClintock and Michelot 2017; McClintock and Michelot 2018), which fits continuous-time correlated random walk models to the data using the Kalman filter (Johnson *et al.* 2008; Johnson and London 2018). Although the resulting data were predicted rather than observed locations, this method allowed the data to be used without arbitrarily subsampling or aggregating locations to fit regularly spaced intervals (Gupte *et al.* 2022). To decide an appropriate regular time interval to use, all time intervals between successive locations were calculated and the frequency of intervals plotted as a histogram (Figure 5.2). Peaks in frequency occurred at approximately 2.5-, 5-, 7.5-, and 10-minute intervals (Figure 5.2) so a regular interval of 5 minutes was chosen for the predicted locations to average the temporal spacing. As 60 minutes was the longest programmable time interval possible, any intervals between consecutive points of greater than 60 minutes were assumed to be caused by a signal loss rather than stationary behaviour. If the animal was moving during this time, this would result in inaccurate straight-line movement being predicted between the two points. As such, any predicted points between time intervals greater than 65 minutes (60 minutes of stationary time plus a 5-minute leeway to acquire a GPS signal) in the raw data were removed from the regularised dataset. Observed and predicted locations were visualised at 6-hour intervals with no obvious outliers apparent to raise concerns about the accuracy of predicted locations (see Figure 5.3 for example). However, assigning time thresholds for when the sheep were in the sheepfold versus on the pasture based on the raw data meant that some predicted locations could be located outside of the sheepfold during the time at which sheep were classed as being in the sheepfold. To prevent these points from influencing comparisons between when the sheep were in and out of the sheepfold, these were manually removed. Whilst doing so, any erroneous points outside of the sheepfold during the time when sheep were deemed to be in the sheepfold were manually relocated to be within the sheepfold.

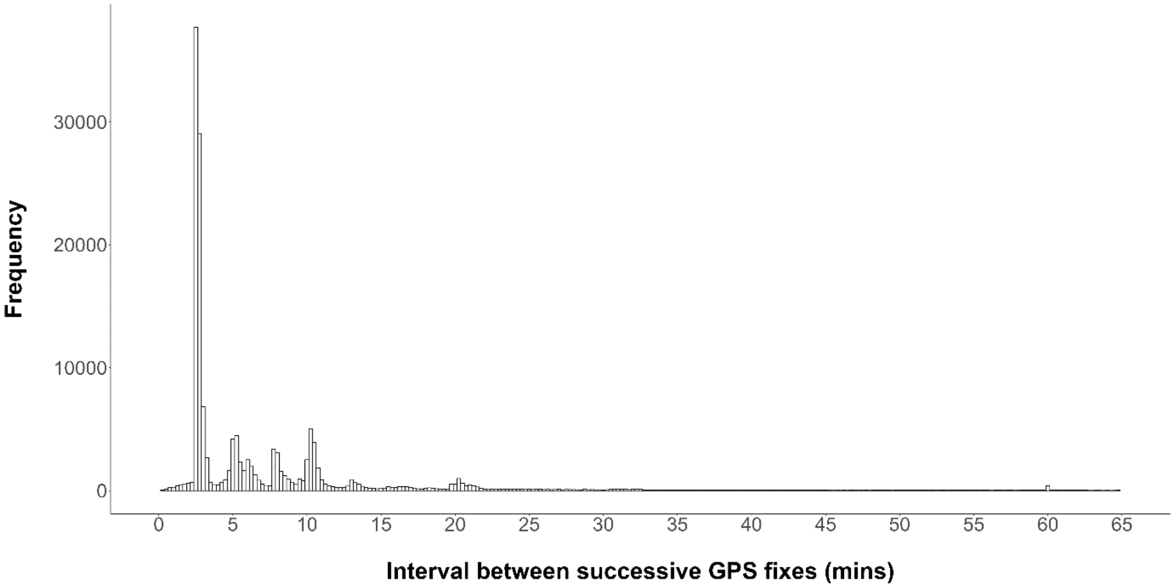

Figure 5.2. Histogram of time intervals between successive GPS fixes showing peaks at approximately 2.5, 5, 7.5 and 10 minutes.

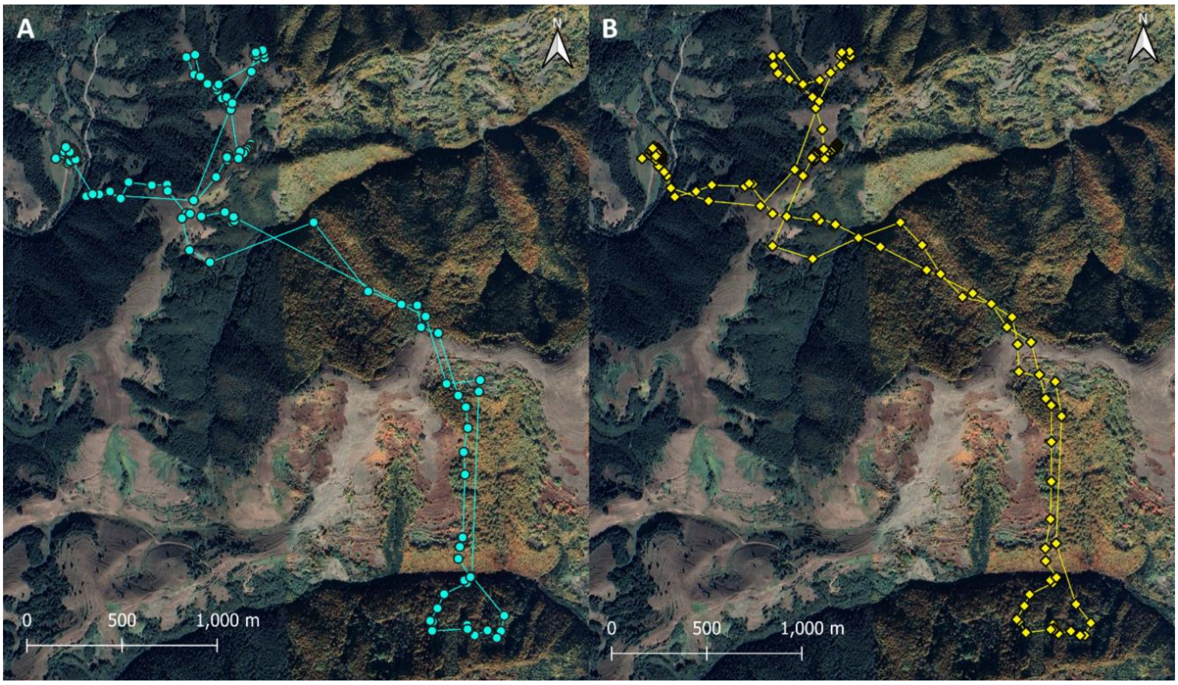

Figure 5.3. Location data for the LGD named Dina at site HD02 during the day on 03/06/2021. A) Observed locations – raw, cleaned data provided by the GPS tracker but at irregular temporal spacing. B) Predicted locations at a regular 5-minute interval. Maps produced in QGIS using Google Satellite imagery.

5.2.5 LGD-sheep distances

For each simultaneous location of the sheep and an LGD in the regularised, predicted data, the Euclidean (straight-line) distance between the two was measured, producing a set of time series distances between every LGD and the tracked sheep (where the tracked sheep is representative of the sheep flock's location).

5.2.5.1 Sheepfold effect

It seemed likely that the LGDs would exhibit different behaviours based on whether the sheep were moving and grazing on the pastures versus stationary and restrained within the sheepfolds and that any further analyses would need to be split between these two periods each day. To test this assumption, a linear mixed effects model was fitted to the data with LGD-sheep distance as the response variable and whether sheep were in or out of the sheepfold as a categorical explanatory variable (In/Out - referred to as 'sheepfold'). To account for repeated measures at hierarchical levels, the site and individual LGD were included as nested random effects. To account for likely differences between sites and individual LGDs, site- and individual-level random effects on intercept and slope were included. Models were fitted using the R package '*lme4*' (Bates *et al.* 2015). After first fitting the model with the original distance values, it was clear that the residuals were not normally distributed, hence the response variable was log-transformed. To determine if the sheepfold explanatory variable significantly altered the model fit, the full model fitted to the log-transformed data was compared, using an ANOVA test, to a null model omitting the explanatory sheepfold variable but keeping the nested random effects.

Null model formula:

lmer(log(distance) ~ 1 + (1|site/ID))

Full model formula:

lmer(log(distance) ~ sheepfold + (sheepfold|site/ID))

Including whether sheep were in the sheepfold or not significantly improved the model fit in comparison to the null model (χ^2 (5, N = 165,626) = 34,536, $p < .001$). Compared to when the sheep were in the sheepfold (model intercept: beta = 3.90, 95% CI: 3.56 – 4.20), LGD-sheep distances were significantly greater when the sheep were out of the sheepfold (beta = 0.77, 95% CI: 0.45 – 1.10). After back-transforming the model outputs, LGDs were on average 57 m further from their sheep when the sheep were out of the sheepfold compared to when they were enclosed in the sheepfold. The model's total explanatory power was substantial (conditional R2 = 0.33), and the part related to the fixed effects alone (marginal R2) was 0.12. Thus, for the rest of the analyses, the data were split between whether the sheep were in the sheepfold or not, hereafter referred to as 'sheepfold state'.

5.2.5.2 Analyses of LGD-sheep distances

LGD-sheep distances were assessed on a daily scale by calculating the median, mean, minimum, and maximum distances per day per sheepfold state for each LGD. Due to the skewed nature of the data it is likely that the median provides a better representation of the central tendency of the data, but both the mean and median are provided for transparency. These four summary metrics were then summarised further per LGD by calculating the mean and ranges of the daily median, mean, minimum, and maximum distances and then also summarised for all LGDs by calculating the mean and standard deviation of all of the daily mean values.

To ensure the data each day represented the LGD's movement, any day by sheepfold state time periods containing too few data points were removed. It was considered that for a given day and sheepfold state there were too few data points when the data did not cover at least half of the average time sheep spent either in the sheepfold or out of the sheepfold each day for each site. For example, if the average time spent in the sheepfold at one site was 10 hours, then any ‘day by sheepfold state = in’ tracking periods of either less than 5 hours from start to finish or comprising fewer than 60 locations (locations every 5 minutes means 60 locations needed to cover 5 hours, even if spread unevenly across the 5 hours) were discarded. This process resulted in 10% of day by sheepfold state time periods being removed.

There is currently no established rule for how far away LGDs can be from their sheep before they can be classified as ‘too far’ away, and this will vary depending on the habitat characteristics at different locations. Instead of using such a binary response, distances were grouped into five distance ranges, which covered the spread of the data: ≤100 m, 101-250 m, 251-500 m, 501-1000 m, and >1000 m. For each LGD, the percentages of LGD-sheep distances within each distance category during each sheepfold state were calculated. Maximum LGD-sheep distances per day by sheepfold state time period were also assigned to one of these five distance groupings, and percentages were calculated to give the percentage of days that each LGD was at different distances from the sheep.

Though the percentage of days that the LGDs spent at greater distances from the sheep helps to determine the frequency of this behaviour, a day where an LGD’s maximum LGD-sheep distance was >1000 m could be due to one quick excursion from the sheep, or it could be due to the LGD spending the entire day >1000 m from the sheep. Thus, the percentage of the total number of locations per LGD within each distance category was calculated to determine how long LGDs spent at these different distances each day. Furthermore, the length of time spent at each distance category was approximated by equating each location to 5 minutes due to the regular sampling interval. However, due to gaps in the data from loss of cellular reception or malfunctioning GPS trackers, these time values are only indicative of whether an LGD spent a long time with, or away from, the sheep, rather than summing to the entire day length.

5.2.6 Daily area of use

It is not possible from the LGD-sheep distances alone to determine the underlying behaviours leading to greater distances between LGDs and sheep. Particularly with LGDs, there are two commonly reported behavioural problems - roaming away from the sheep and not following the sheep onto the pasture - either of which could result in large LGD-sheep distances but for quite different reasons. Thus, to infer how different LGD-sheep distances arise, the area of land used by each LGD and associated sheep was examined.

There are many methods available to estimate animal space use, most of which lead to the estimation of what is known as the animal's home range*:* the area repeatedly used by an animal for its everyday behaviours (Silva *et al.* 2022). However, the home range excludes excursions away from the core of the range, and it is these excursions that are of interest with regard to the roaming behaviours of LGDs. One simple measure to consider all of the data is to use minimum convex polygons (MCPs), which assign the area contained within a polygon around the outermost locations as the area of use. However, knowing that the sheep and LGDs often used narrow movement corridors between pastures and that the LGDs might carry out narrow excursions from the sheep, MCPs would have greatly overestimated the size of the areas used (Harris *et al.* 1990; Huck *et al.* 2008). Instead, the local convex hull (LoCoH) method was deemed more appropriate for the data. This method takes into account the nearest neighbours of each GPS location, drawing smaller local convex polygons (i.e. hulls) around these neighbouring points and then joining the hulls to create one larger area, or utilisation distribution (UD) (Getz *et al.* 2004; Getz *et al.* 2007). In comparisons between home range estimation methods, LoCoH has been shown to produce smaller area estimates and be more appropriate in cases where animal movements are geographically constrained (e.g. for European badgers (*Meles meles*) (Huck *et al.* 2008), African buffalo (*Syncerus caffer*) (Getz *et al.* 2007), and grey wolves (*Canis lupus*) inhabiting coastal environments (Roffler *et al.* 2023).

The LoCoH method can also be further refined to the Time Local Convex Hull (T-LoCoH) method by incorporating the time of locations into the nearest neighbours selection, such that locations close in space but not in time are not classified as nearest neighbours (Lyons *et al.* 2013). However, model parameters for T-LoCoH, specifically '*s*', which is a measure of how nearest neighbours should be selected based on a balance between time and space, need to be selected manually. Due to the need to compute thousands of areas of use (an area for each LGD and each sheep, each day by sheepfold state) the LoCoH method was used instead with fixed parameters to improve efficiency and reduce subjectivity in the selection of parameters for more robust comparisons between areas of use. Thus, areas of use were calculated using the '*tlocoh*' package in R but setting the '*s*' parameter to 0 so as not to factor in the time of locations. Nearest neighbours are assigned by one of three methods: *r* – by a radius of fixed distance (*r*) around each root point; *k* – by selecting a fixed number (*k*) of nearest neighbours; or *a* – an adaptive method in which all points within a variable sphere around a root point are used to construct the local hulls such that the sum of the distances between nearby points and the root point is less than or equal to *a* (Getz *et al.* 2007). Where possible, it is advised to use the *a* method as it is adaptable to the data, thus nearest neighbours were selected according to *a* where *a* was set, as a rule of thumb, to the maximum distance between any two points in the data (Getz *et al.* 2007). Models failed to compute using this rule for selecting *a* for approximately 7% of the total day by sheepfold states. These data were modelled manually, reducing the value of *a* until reasonable home range estimates could be generated.

Pairwise areas of use were calculated for each LGD and the sheep at each site, such that only simultaneous locations between each pair of data were used. As such, differing numbers of locations for the sheep could be used for each LGD-sheep comparison at the same site if there were fewer locations for one of the LGDs, for example. As with the LGD-sheep distance calculations, data were split by day per sheepfold state and any time periods with too few locations removed. Once the local hulls were estimated and merged for each time period, the 100% isopleth was extracted and designated as the daily area of use per sheepfold state (studies often use the 95% isopleth to avoid incorporating outliers, but this would have removed excursions by the LGDs away from the sheep). No consideration of the density of locations (the utilisation distribution) was considered as the objective was to determine the extent of the daily area of use and not to find areas of frequent use. The daily areas of use were then compared in a pairwise manner for each LGD and sheep each day per sheepfold state. The area of intersection (where the two areas overlapped) was calculated, along with the proportion covered by the intersecting area of each LGD and sheep area of use. The proportion of the total area of the sheep and LGD areas of use made up of the intersecting area was also calculated as an overall metric of similarity between the two areas. Finally, the size of the LGD area of use was compared to the size of the sheep area of use.

The proportions of each LGD and sheep area of use that intersected were compared to determine whether differences in space use were likely due to LGDs roaming from sheep, or not following the sheep (Figure 5.4). High proportions of the overlapping dog and sheep area would suggest they are using the same areas - the LGDs are staying with the sheep. A large proportion of the sheep area overlapping with only a low proportion of the LGD area suggests that LGDs have covered where the sheep are but have also gone somewhere else - they are exhibiting roaming behaviour. On the contrary, a large proportion of the LGD area overlapping with only a small proportion of sheep area suggests the sheep have gone somewhere that the LGDs have not - the LGDs have not followed the sheep but have also not roamed far away as most of their area is also covered by the sheep area. Low proportions of both sheep and LGD areas overlapping suggest very different uses of space. However, this latter scenario could arise from either the LGDs roaming in the opposite direction to the sheep or staying somewhere away from the sheep without necessarily roaming very far (for example, staying at the sheepfold and not accompanying the sheep onto the pastures).

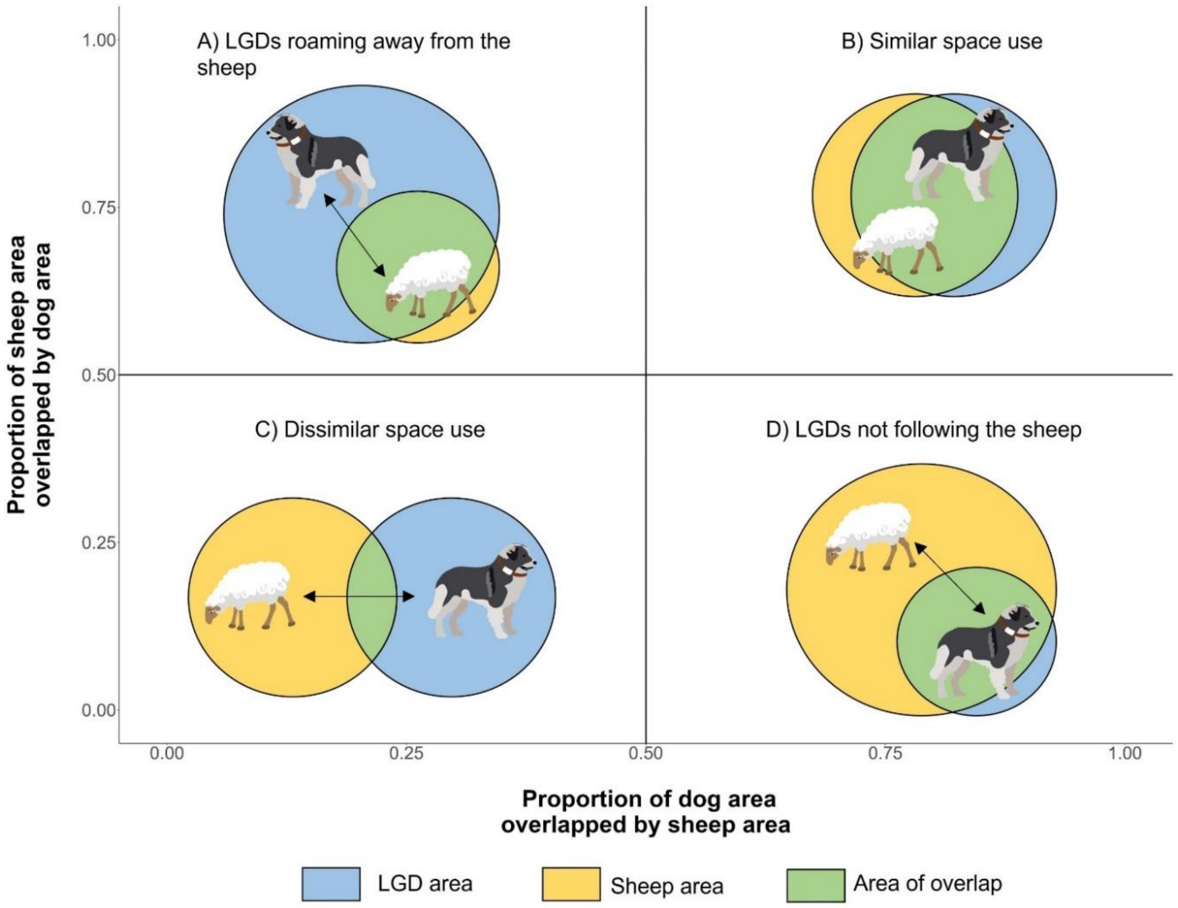

Figure 5.4. Schematic showing how the proportion of overlap of each sheep and LGD area of use was compared each day to determine whether LGDs were roaming away from the sheep (A), staying with the sheep (B), not following the sheep (D), or using completely different areas to the sheep (C). Scenario C could arise through extreme cases of either A or D whereby LGDs could roam away from the sheep and spend hardly any time with them, or they could not accompany them and their space use could just be the area around the sheepfold for example. LGD vector created by Bethany Smith.

5.2.7 Factors affecting LGD roaming

Data corresponding to when the sheep were in or out of the sheepfold were treated as two datasets. Linear mixed effects models were used to determine if the sex, breed, age, or neutered status of the LGD affected overall LGD-sheep distances or daily maximum LGD-sheep distances. Models were fitted using the '*lme4*' package in R (Bates *et al.* 2015) with LGD sex (Male/Female), breed (Carpathian/Mixed-breed), age (Juvenile/Adult), and whether LGDs were neutered (Yes/No) as explanatory variables, and site and individual LGD as nested random effects. As with the sheepfold model, LGD-sheep distance response variables were log-transformed. No step-wise selection was performed as there was cause to expect all explanatory variables could affect all of the response variables, so a full model was fitted and compared to the null model. As the proportion of the total LGD and sheep area shared by both animals was a response variable bounded by 0 and 1, similar models were run but using the '*glmmTMB*' package (Brooks *et al.* 2017) in R specifying the family as a beta family. The response variable was not transformed. This test was only conducted for the areas of use when the sheep were out of the sheepfold on the pasture as unless the LGDs were in the enclosure with the sheep, overlaps in space use during the time sheep were in the sheepfold were likely to be low and not meaningful.

To first compare the null to the full models, models were estimated using '*ML*', but all final outputs are from models estimated using '*REML*' (Bates *et al.* 2015). For all linear mixed effects models, the 95% confidence intervals (CI) were computed using the '*confint*' function in R. Computing p-values for each of the explanatory variables in linear mixed effects models is advised against (Bates *et al.* 2015), hence the statistical significance of the explanatory variables was based on several factors: comparison between the full and null models ($p < .05$ then the model fit of the full model is better); the marginal R2 of the models (how much of the variance in the data can be attributed to the explanatory variables); the 95% CIs around the effect size of each explanatory variable (if CIs include 0 then not statistically significant), and consideration of the effect sizes. The model outputs are provided with guidance from the '*report*' package in R (Makowski *et al.* 2023).

5.3 Results

5.3.1 GPS data summary

From screening the data, it was apparent that at three sites (SB02, SB03, and SB08), the cellular reception was too poor for the data to be transmitted, so these three sites were removed from the analysis, leaving data from 11 sites. In addition, one of the Carpathian Shepherd dogs from site HD01 (Brezoi), did not stay with the GPS-tracked sheep flock and instead seemed to move to another of the shepherd's flocks before returning to the homestead and so was removed from any further analysis. Only a subset of the data for one of the Carpathian Shepherd LGDs at site HD03 (Arnica) was used as she was in heat and chained at the homestead for a time. After this screening process, data for a total of 47 animals (11 sheep and 36 LGDs) remained. The 36 LGDs included in the analysis consisted of 14 purebred Carpathian Shepherd dogs and 22 mixed-breed dogs. Eleven of the mixed-breed LGDs were early generation crosses with LGD breeds, namely Carpathian Shepherd, Bucovina Shepherd, Romanian Mioritic Shepherd, and Kangal. There were 12 females (none of which were neutered) and 24 males (eight of which were neutered) ranging in age from 8 months to 10 years old (Table 5.1).

The screened dataset contained 212,180 GPS fixes. After removing the duplicates, which accounted for approximately 26% of the fixes, as well as the outliers and the first hour of data from each animal, the total number of fixes was reduced to 156,690. On average, each animal was tracked for 20 days (range: 5-33 days), generating an average of 3334 fixes per animal (range: 911 – 7580). After regularising the data to a 5-minute interval and cleaning this new dataset, each animal had an average of 5131 GPS fixes (range: 1265 – 8991). The average accuracy of the devices per tracking period, as provided by Tractive® from the raw uncleaned data, ranged from 49 m to 71 m. Details of the animals, tracking times, and number of fixes can be found in Table 5.1. Examples of the sheep and dogs' daily locations are provided for a subset of days for one site in each of the three counties: Sibiu (Figure 5.5), Alba (Figure 5.6), and Hunedoara (Figure 5.7). The selected sites and days were chosen to show a range of data from Carpathian Shepherd dogs and mixed-breed dogs of different sexes exhibiting behaviours from staying close to the sheep to roaming long distances. All locations for each site, split between when the sheep were in and out of the sheepfold, are shown in Appendix D.

Table 5.1. Breed (M = mixed-breed; C = Carpathian Shepherd), sex (M = male; F = female), and age of each LGD as well as whether neutered, along with a summary of the GPS data collected for each animal – time periods of collection, the total number of days data collected on, and the number of GPS locations (fixes) before and after the data were cleaned.

Site	Name	Animal	Breed (C/M)	Sex	Age (years)	Neutered (Y/N)	Tracking periods	No. days tracked	No. of fixes pre-clean	No. of fixes post-clean	No. of regularised fixes post-clean
AB01	Codruta	Dog	M	F	2	N	2021-08-03 - 2021-08-18 2021-08-18 - 2021-09-03	30	7966	5970	8426
AB01	Lotru	Dog	M	M	2	N	2021-08-03 - 2021-08-18 2021-08-18 - 2021-09-05	33	6022	4539	8784
AB01	Rocky	Dog	M	M	0.67	N	2021-08-03 - 2021-08-18 2021-08-18 - 2021-08-18 2021-08-21 - 2021-09-06	31	7674	6000	8133
AB01	Sheep	Sheep	-	-	-	-	2021-08-03 - 2021-08-18 2021-08-18 - 2021-09-04	32	8198	6705	8991
AB02	Tarzan	Dog	M	M	3	Y	2021-08-03 - 2021-08-16	13	2832	2244	3432
AB02	Titescu	Dog	M	M	3	N	2021-08-03 - 2021-08-14 2021-08-18 - 2021-08-29	21	5096	3839	5686
AB02	Sheep	Sheep	-	-	-	-	2021-08-03 - 2021-08-16 2021-08-18 - 2021-08-29	23	6056	4619	6204
HD01	Joia	Dog	C	F	3	N	2021-09-27 - 2021-10-05 2021-10-12 - 2021-10-18	14	2751	1969	2645
HD01	Zeta	Dog	C	F	1	N	2021-09-27 - 2021-10-04 2021-10-12 - 2021-10-20	15	3820	2416	3219
HD01	Sheep	Sheep	-	-	-	-	2021-09-27 - 2021-10-04 2021-10-12 - 2021-10-21	16	5062	2944	4500
HD02	Bradu	Dog	C	M	4	N	2021-05-27 - 2021-06-13	17	3731	2747	4432
HD02	Dina	Dog	C	F	4	N	2021-05-27 - 2021-06-11	15	3331	2474	3391
HD02	Draganu	Dog	C	M	4	N	2021-05-27 - 2021-06-11	14	3114	2436	3656
HD02	Gerula	Dog	C	M	1.5	N	2021-05-27 - 2021-06-11	15	3395	2555	3596
HD02	Sheep	Sheep	-	-	-	-	2021-05-27 - 2021-06-13	17	4294	3408	4871

HD03	Arnica	Dog	C	F	4	N	2021-06-05 - 2021-06-10	5	1131	911	1265
HD03	Dor	Dog	C	M	4	N	2021-05-27 - 2021-06-14	18	3193	2537	4637
HD03	Dumbrava	Dog	C	F	1.5	N	2021-05-27 - 2021-06-14	18	4829	3810	4846
HD03	Gruia	Dog	C	M	2	N	2021-05-27 - 2021-06-14	18	3671	2886	4467
HD03	Sheep	Sheep	-	-	-	-	2021-05-27 - 2021-06-14	18	3551	2824	5087
HD04	Badea	Dog	C	M	3	N	2021-09-27 - 2021-10-12 2021-10-12 - 2021-10-26	29	7554	5787	7842
HD04	Bistra	Dog	C	F	3	N	2021-09-27 - 2021-10-12 2021-10-12 - 2021-10-26	29	5354	3983	7438
HD04	Novac	Dog	M	M	0.67	N	2021-09-27 - 2021-10-12 2021-10-12 - 2021-10-26	29	7790	6211	7978
HD04	Tarzan	Dog	M	M	8	N	2021-09-27 - 2021-10-12 2021-10-12 - 2021-10-26	29	7022	5481	7572
HD04	Sheep	Sheep	-	-	-	-	2021-09-27 - 2021-10-12 2021-10-12 - 2021-10-26	29	8461	6643	8219
SB01	Bucalau	Dog	M	M	4	Y	2021-06-15 - 2021-06-21 2021-06-25 - 2021-07-01	12	1899	1468	3094
SB01	Galbenu	Dog	M	M	3	Y	2021-06-15 - 2021-06-22 2021-06-25 - 2021-07-01	13	1897	1471	3412
SB01	Ghiabure	Dog	M	M	5	Y	2021-06-15 - 2021-06-22 2021-06-25 - 2021-07-02	14	2181	1687	3406
SB01	Pintea	Dog	M	M	10	Y	2021-06-15 - 2021-06-22 2021-06-25 - 2021-07-02	13	1826	1238	2917
SB01	Sheep	Sheep	-	-	-	-	2021-06-15 - 2021-06-21 2021-06-25 - 2021-06-30 2021-06-30 - 2021-07-06	17	3953	2544	4588
SB04	Tisa	Dog	M	F	5	N	2021-07-16 - 2021-07-28 2021-07-29 - 2021-08-12	26	7874	5187	6684
SB04	Toflea	Dog	M	M	3	N	2021-07-16 - 2021-07-29 2021-07-29 - 2021-08-10	25	6230	4250	6411

SB04	Sheep	Sheep	-	-	-	-	2021-07-16 - 2021-07-29 2021-07-29 - 2021-08-15	29	9259	7580	8360
SB05	Ciula	Dog	M	F	3	N	2021-06-22 - 2021-06-23 2021-06-25 - 2021-07-01 2021-07-01 - 2021-07-10	16	1901	1435	3589
SB05	Codruta	Dog	M	F	2	N	2021-06-22 - 2021-07-01 2021-07-01 - 2021-07-10	18	2150	1643	4360
SB05	Neagra	Dog	M	F	6	N	2021-06-22 - 2021-07-01 2021-07-01 - 2021-07-10	18	2189	1570	4076
SB05	Sheep	Sheep	-	-	-	-	2021-06-22 - 2021-07-01 2021-07-01 - 2021-07-08	16	2129	1888	4082
SB06	Gruia	Dog	M	M	5	Y	2021-07-09 - 2021-07-17 2021-07-20 - 2021-07-30	18	3986	2606	4521
SB06	Jderu	Dog	M	M	3	N	2021-07-09 - 2021-07-18 2021-07-20 - 2021-07-30	19	4015	2992	4943
SB06	Mustata	Dog	M	M	4	Y	2021-07-09 - 2021-07-18 2021-07-20 - 2021-07-30	19	4350	3241	5233
SB06	Novac	Dog	M	M	4	Y	2021-07-09 - 2021-07-18 2021-07-20 - 2021-07-30	19	4160	2755	4616
SB06	Sheep	Sheep	-	-	-	-	2021-07-09 - 2021-07-16 2021-07-17 - 2021-07-18 2021-07-20 - 2021-07-30	18	2342	1582	4580
SB07	Arun	Dog	C	M	2.5	N	2021-08-06 - 2021-08-17 2021-08-20 - 2021-08-29	21	4449	2901	5371
SB07	Leu	Dog	M	M	4	N	2021-08-06 - 2021-08-14 2021-08-20 - 2021-08-29	18	5332	3576	4790
SB07	Luna	Dog	C	F	2.5	N	2021-08-07 - 2021-08-14 2021-08-20 - 2021-08-27	14	4176	2390	3462
SB07	Mures	Dog	M	M	2.5	N	2021-08-09 - 2021-08-17 2021-08-20 - 2021-08-28	16	4218	2648	3698

SB07	Sheep	Sheep	-	-	-	-	2021-08-06 - 2021-08-16 2021-08-20 - 2021-08-30	20	5766	4100	5647	

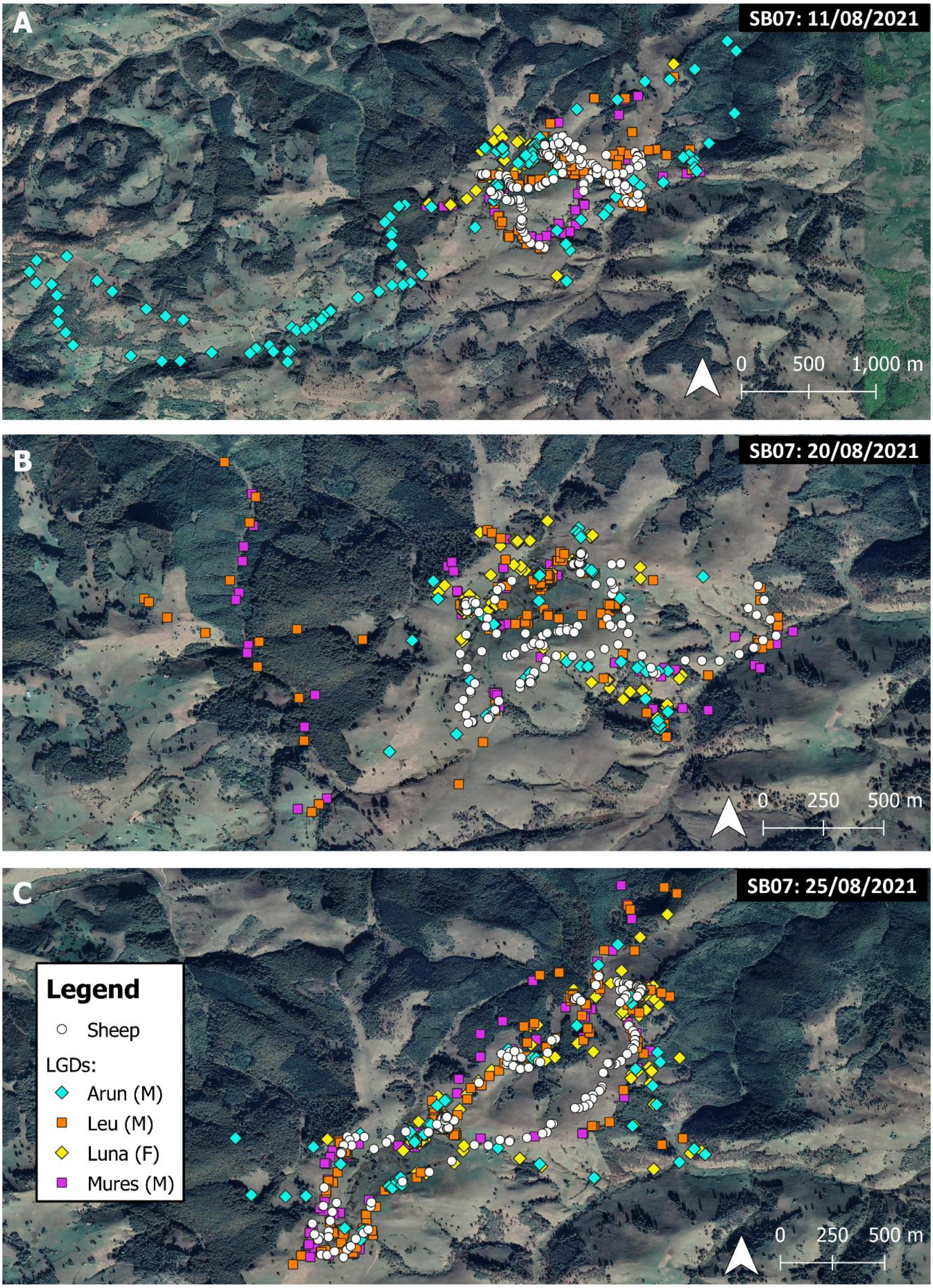

Figure 5.5. Locations of the sheep (white circles) and LGDs on three days at site SB07. Each LGD is shown with a coloured diamond for Carpathian Shepherd dogs or square for mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). All locations for the day in each panel are shown, regardless of whether the sheep were in or out of the sheepfold. The days shown were selected to be representative of the different behaviours shown by the LGDs at each site. For example, Panel A shows an instance of the LGD Arun roaming 4km from the sheep, whereas Panel C shows the LGDs in close proximity to the sheep for most of the day. Maps produced in QGIS using Google Satellite imagery.

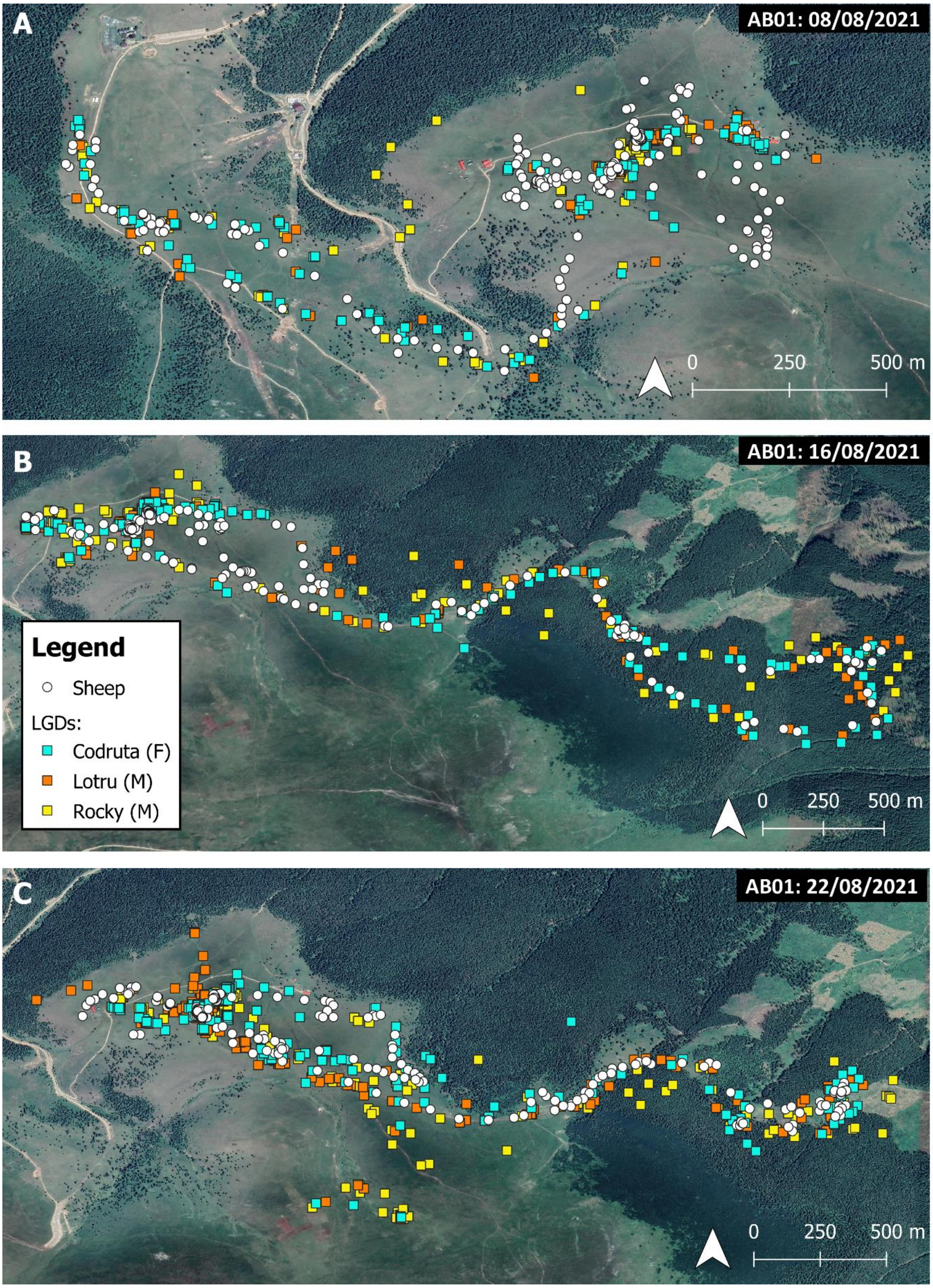

Figure 5.6. Locations of the sheep (white circles) and LGDs on three days at site AB01. Each LGD is shown with a coloured square as all were mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). All locations for the day in each panel are shown, regardless of whether the sheep were in or out of the sheepfold. The days shown were selected to be representative of the different behaviours shown by the LGDs at each site. For example, Panel A shows locations of sheep not accompanied by any of the GPS-tracked LGDs, Panel B shows the LGDs in close proximity to the sheep for most of the day, and Panel C shows some instances of LGD locations further away from the sheep. Maps produced in QGIS using Google Satellite imagery.

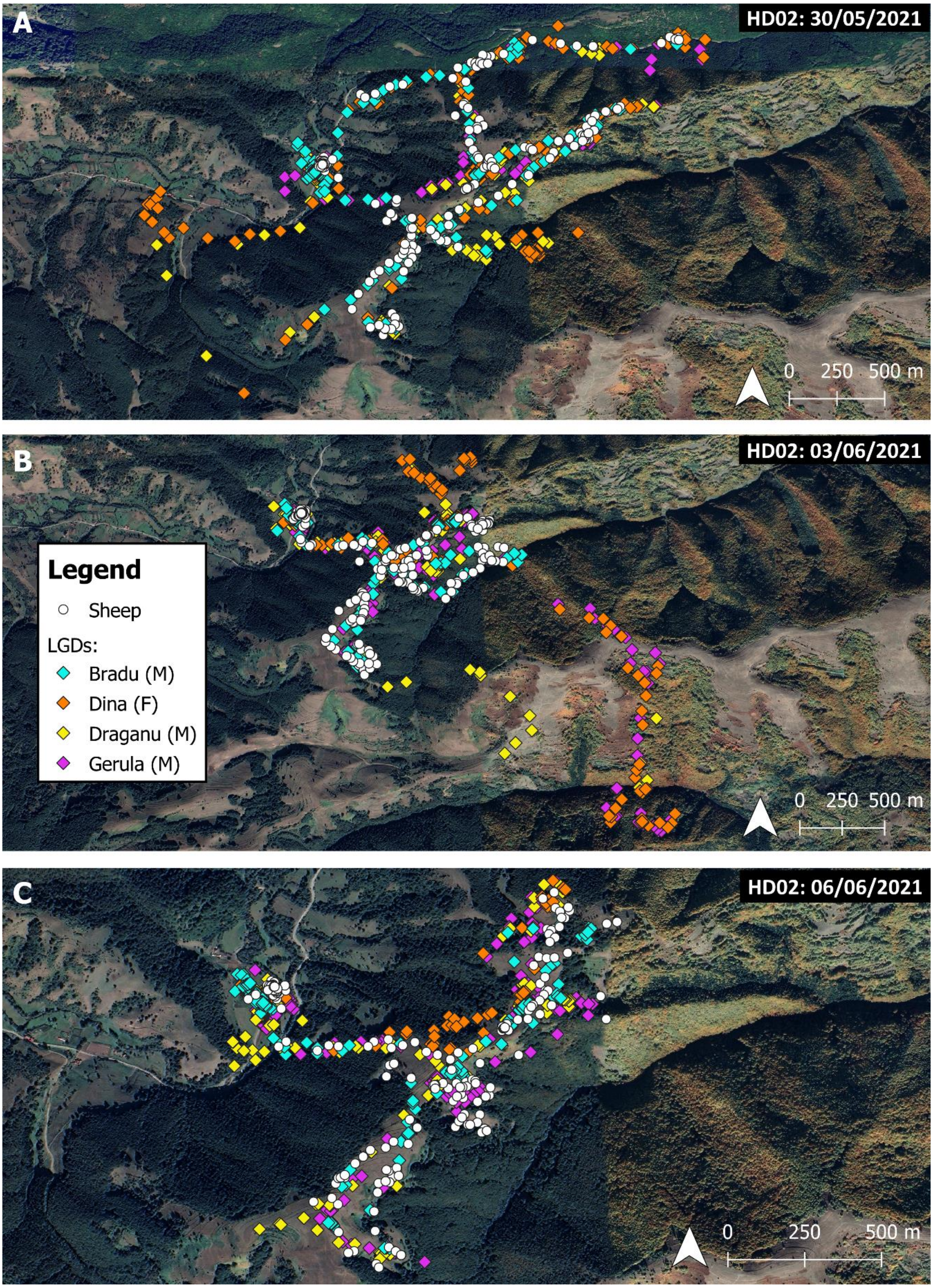

Figure 5.7. Locations of the sheep (white circles) and LGDs on three days at site HD02. Each LGD is shown with a coloured diamond as all were Carpathian Shepherd dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). All locations for the day in each panel are shown, regardless of whether the sheep were in or out of the sheepfold. The days shown were selected to be representative of the different behaviours shown by the LGDs at each site. For example, Panel C shows the LGDs in close proximity to the sheep for most of the day whereas Panels A and B show some of the LGDs roaming away from the sheep for shorter and longer distances, respectively. Maps produced in QGIS using Google Satellite imagery.

5.3.2 LGD-sheep distances

Each day LGDs were, on average, within 100 m of the sheep when the sheep were in the sheepfold (mean of the mean daily LGD-sheep distances per dog: 80 m ± 45 m SD; mean of the median daily LGD-sheep distances per LGD: 70 m ± 42 m SD) (Figure 5.8; Table 5.2). When the sheep were on the pastures during the day LGDs were, on average, within 200 m of the sheep (mean of the mean daily LGD-sheep distances per LGD: 200 m ± 127 m SD; mean of the median daily LGD-sheep distances per LGD: 154 m ± 119 m SD) (Figure 5.8; Table 5.2). Daily minimum LGD-sheep distances showed that LGDs were usually in close proximity to the sheep at some point each day during the times when the sheep were in the sheepfold (mean: 18 m ± 17 m SD; range: 0-172 m) and when the sheep were not in the sheepfold (mean: 10 m ± 6 m SD; range: 0-125 m) (Table 5.2). In contrast, daily maximum LGD-sheep distances were more variable and were larger when sheep were not in the sheepfold (mean: 699 m ± 304 m SD; range: 122-4073 m) compared to when sheep were in the sheepfold (mean: 262 m ± 149 m SD; range: 41-2543 m) (Figure 5.8; Table 5.2). Thus, on average, LGDs were approximately 700 m away from sheep at some point every day. However, differences in behaviours between individuals were apparent with some LGDs found further away than others. On a daily basis, average maximum daily distances between LGDs and sheep were <500 m for ten of the LGDs but >1000 m for eight of the LGDs (Table 5.2).

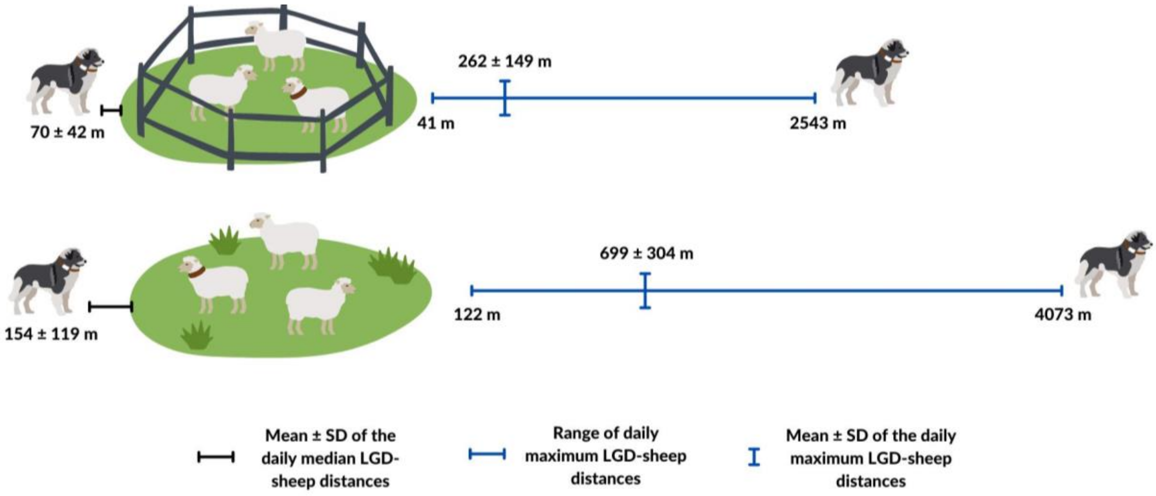

Figure 5.8. Summary of LGD-sheep distances when the sheep were enclosed overnight in the sheepfold (top) and grazing on the pastures during the day (bottom). Not drawn to scale.

Table 5.2. Summary of the daily distances between simultaneous locations of LGDs and their associated sheep during the times when the sheep were in the sheepfold and out on the pasture, approximately night and daytime, respectively. Both the median and mean values are given for information. However, due to the high variability and skew in the distance data, the median is likely to give a better representation of the central tendency. For each LGD, the mean of the daily mean, median, minimum, and maximum distances per day per sheepfold state are provided along with the range of each in brackets. The overall means for all LGDs are provided in the last row of the table.

Site	**LGD**	**# Paired locations**		**Daily mean (m)**		**Daily median (m)**		**Daily minimum (m)**		**Daily maximum (m)**	
Sheepfold state		*In*	*Out*	*In*	*Out*	*In*	*Out*	*In*	*Out*	*In*	*Out*
AB01	Codruta	3121	5113	51 (23-79)	121 (87-199)	37 (10-72)	87 (59-172)	7 (1-16)	6 (1-15)	272 (61-377)	526 (327-1416)
AB01	Lotru	3038	5290	81 (31-412)	156 (74-258)	56 (24-229)	112 (57-167)	10 (1-51)	8 (1-35)	360 (100-1383)	687 (271-1521)
AB01	Rocky	2549	4741	42 (22-107)	211 (101-638)	37 (17-69)	141 (55-540)	9 (1-27)	7 (2-34)	149 (59-264)	824 (360-1731)
AB02	Tarzan	1397	1984	71 (36-128)	102 (62-305)	69 (31-132)	71 (45-123)	28 (2-102)	5 (2-10)	152 (64-277)	488 (170-1578)
AB02	Titescu	2112	3092	53 (19-119)	116 (74-295)	43 (18-119)	86 (56-239)	12 (1-83)	8 (2-25)	164 (60-306)	478 (197-957)
HD01	Joia	86	1574	51 (51-51)	691 (86-2783)	50 (50-50)	672 (54-3330)	30 (30-30)	16 (6-52)	84 (84-84)	1550 (305-3875)
HD01	Zeta	536	1926	46 (35-58)	231 (82-581)	44 (28-58)	151 (63-540)	9 (3-19)	9 (4-23)	111 (78-163)	866 (346-1704)
HD02	Bradu	2219	2114	77 (39-105)	131 (73-219)	72 (26-100)	93 (56-113)	22 (1-53)	9 (1-20)	259 (108-576)	586 (240-1310)
HD02	Dina	1498	1787	162 (48-1299)	307 (83-1103)	151 (43-1226)	214 (49-990)	22 (12-49)	11 (1-77)	385 (106-2543)	1086 (418-2542)
HD02	Draganu	1827	1748	83 (59-159)	282 (88-896)	74 (27-116)	200 (56-880)	27 (4-67)	6 (3-13)	226 (103-702)	1070 (322-2509)
HD02	Gerula	1610	1886	74 (47-127)	398 (82-895)	73 (37-145)	340 (48-868)	18 (3-46)	13 (3-78)	183 (96-354)	1037 (338-2567)
HD03	Arnica	517	630	42 (37-54)	65 (45-89)	37 (26-47)	46 (37-66)	5 (3-10)	4 (1-7)	146 (81-278)	322 (175-607)
HD03	Dor	2428	2063	41 (21-64)	263 (72-932)	38 (21-56)	225 (40-1048)	10 (1-34)	28 (2-125)	101 (47-177)	631 (251-1319)
HD03	Dumbrava	2583	2153	29 (22-54)	63 (39-100)	22 (14-37)	36 (25-60)	3 (0-8)	2 (1-6)	102 (68-238)	287 (182-430)
HD03	Gruia	2156	2037	27 (21-36)	56 (35-83)	25 (18-31)	39 (27-67)	4 (0-9)	4 (1-9)	87 (56-153)	254 (122-514)
HD04	Badea	4197	3519	48 (21-162)	138 (50-189)	28 (18-44)	103 (32-136)	3 (1-9)	9 (1-23)	471 (41-1828)	673 (299-1717)
HD04	Bistra	3717	3576	63 (22-159)	152 (73-251)	28 (15-43)	105 (51-148)	4 (1-13)	10 (1-28)	602 (134-1934)	751 (275-1493)
HD04	Novac	4320	3588	77 (20-233)	135 (70-256)	59 (18-290)	84 (51-121)	6 (0-21)	8 (1-20)	390 (56-1752)	743 (247-2119)
HD04	Tarzan	3777	3580	70 (20-137)	88 (55-164)	45 (14-90)	65 (38-98)	7 (0-23)	6 (1-18)	641 (56-1305)	548 (208-1515)
SB01	Bucalau	1021	1763	190 (81-435)	224 (121-860)	136 (57-195)	169 (96-549)	51 (17-133)	12 (4-21)	592 (278-1915)	772 (298-2229)
SB01	Galbenu	1258	1820	145 (84-272)	170 (109-246)	131 (53-282)	139 (78-250)	62 (8-140)	13 (1-30)	330 (234-785)	559 (371-868)

SB01	Ghiabure	1193	1880	121 (91-163)	163 (93-238)	94 (51-147)	129 (66-234)	31 (9-94)	11 (3-27)	346 (242-626)	604 (290-1108)
SB01	Pintea	670	1714	147 (70-293)	126 (60-218)	155 (60-316)	99 (53-173)	69 (17-172)	8 (1-26)	257 (159-361)	421 (179-843)
SB04	Tisa	1984	4413	24 (13-40)	179 (82-331)	19 (7-36)	145 (52-330)	4 (1-11)	6 (1-14)	125 (45-552)	601 (265-1284)
SB04	Toflea	2223	3958	68 (16-165)	406 (236-759)	44 (16-183)	321 (167-661)	7 (2-16)	29 (5-86)	247 (41-633)	1088 (570-1790)
SB05	Ciula	1362	1104	77 (32-160)	188 (97-388)	68 (30-149)	114 (72-247)	9 (2-20)	4 (1-7)	274 (69-542)	754 (274-1606)
SB05	Codruta	1551	1709	87 (47-217)	252 (63-1041)	81 (36-293)	220 (46-1091)	12 (3-30)	15 (0-80)	241 (113-443)	695 (258-1496)
SB05	Neagra	1564	1387	73 (39-121)	169 (83-355)	69 (35-127)	109 (55-361)	15 (2-37)	7 (2-16)	194 (132-283)	631 (297-1392)
SB06	Gruia	1474	1959	42 (29-64)	85 (59-172)	38 (22-55)	67 (45-127)	12 (3-29)	6 (1-13)	155 (48-383)	311 (166-476)
SB06	Jderu	1696	2127	83 (23-196)	135 (92-227)	97 (19-295)	103 (56-213)	11 (2-25)	11 (1-31)	179 (53-597)	413 (268-785)
SB06	Mustata	1786	2375	50 (31-63)	106 (55-192)	48 (35-71)	72 (43-125)	9 (1-23)	7 (1-16)	156 (49-363)	350 (210-473)
SB06	Novac	1433	2029	34 (25-49)	75 (56-149)	32 (20-49)	58 (42-82)	7 (1-14)	4 (0-9)	108 (41-560)	287 (193-485)
SB07	Arun	1843	2952	180 (78-411)	357 (196-1204)	154 (62-463)	281 (108-474)	39 (10-133)	12 (2-79)	400 (148-1204)	1194 (588-4073)
SB07	Leu	1783	2957	86 (46-134)	227 (82-394)	77 (42-141)	148 (44-338)	21 (1-53)	6 (1-12)	273 (95-584)	1009 (418-1720)
SB07	Luna	1098	2167	144 (78-246)	365 (280-441)	141 (66-305)	295 (210-425)	41 (9-125)	20 (5-91)	401 (194-722)	1125 (787-1691)
SB07	Mures	1206	2156	140 (49-223)	266 (187-448)	147 (51-232)	191 (119-404)	24 (8-63)	9 (1-34)	265 (69-676)	935 (511-1438)
Mean (SD)		**1912**	**2524**	**80 ± 45**	**200 ± 127**	**70 ± 42**	**154 ± 119**	**18 ± 17**	**10 ± 6**	**262 ± 149**	**699 ± 304**

Grouping the LGD-sheep distances into ranges further showed that LGDs largely stayed in close proximity to the sheep they were guarding with an average of 78% (± 22% SD) of LGD-sheep distances per LGD ≤100 m when the sheep were in the sheepfold, and 50% (± 18% SD) when sheep were out of the sheepfold (Table 5.3). On average, less than 1% of LGD-sheep distances were greater than 500 m when sheep were in the sheepfold, and less than 10% when sheep were out of the sheepfold (Table 5.3). Considering the maximum daily distances, only eight LGDs ranged more than 1000 m away from the sheep when the sheep were in the sheepfold and did so on between 3% and 19% of the days (Figure 5.9). However, almost daily occurrences of LGDs being away from the sheep whilst sheep were on the pasture were recorded. There wasn't a single day that any of the LGDs always remained within 100 m of the sheep, and only an average of 7% of the daily maximum LGD-sheep distances per LGD fell within 250 m (Table 5.3; Figure 5.9). The LGDs were at least 500 m away from the sheep whilst the sheep were on the pasture on over half of the days, with an average of 33% of the daily maximum distances between 501-1000 m and 21% over 1000 m (Table 5.3). Examining individual differences between LGDs showed that 26 LGDs (72%) were >1000 m away from sheep on between 3% and 71% of days (Figure 5.9). Thus, only ten LGDs were never >1000 m from sheep, four of which were never >500 m from sheep (HD03 – Dumbrava, SB06 – Gruia, Mustata, and Novac) (Figure 5.9).

Table 5.3. Mean percentages and standard deviations of the LGD-sheep distances and maximum daily distances across all LGDs. Data are split between whether the sheep were in the sheepfold or not.

Distance (m)	**All distances – Sheepfold: In**		**All distances – Sheepfold: Out**		**Daily maximum – Sheepfold: In**		**Daily maximum - Sheepfold: Out**	
	%	**SD**	**%**	**SD**	**%**	**SD**	**%**	**SD**
≤100	78	22	50	18	22	29	0	0
101-250	18	17	29	7	38	26	7	15
251-500	4	6	12	8	29	26	39	24
501-1000	0.3	1	6	7	8	11	33	19
>1000	0.25	1	3	4	2	4	21	21

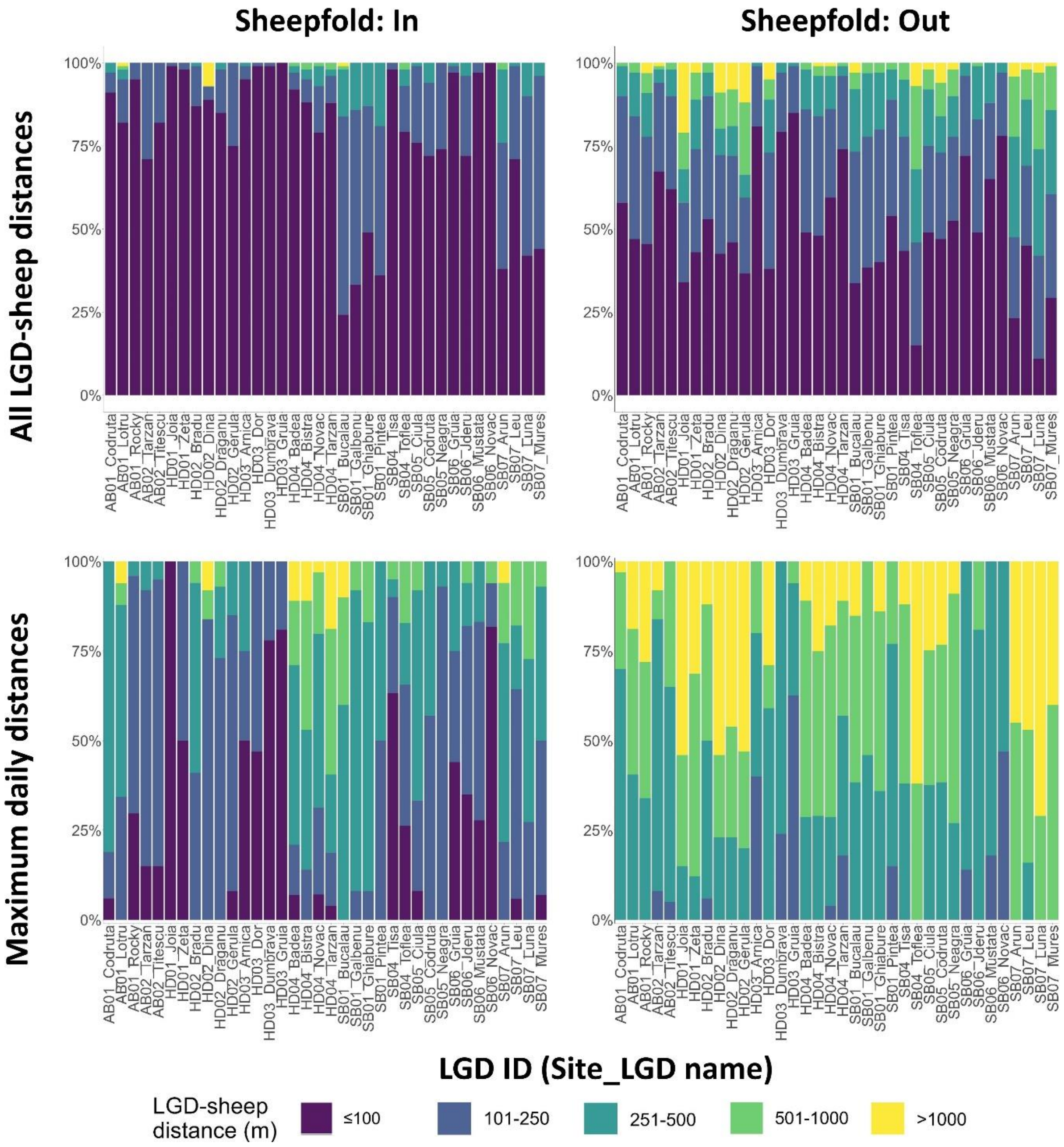

Figure 5.9. Percentage distributions of all of the LGD-sheep distances (top) and the daily maximum LGD-sheep distances (bottom) when the sheep were in the sheepfold (left) and out of the sheepfold on the pasture (right).

The percentage of time and the overall time in minutes that the LGDs were away from the sheep each day was relatively low with distances greater than 1000 m making up only 0-5% of the locations most days (Figure 5.10). In rare cases the length of time an LGD spent away from sheep in a day could be relatively long (up to 600 minutes), but on average, they only spent 2 minutes per day at distances greater than 1000 m when the sheep were in the sheepfold and 18 minutes per day at distances greater than 1000 m when the sheep were on the pasture (Table 5.4).

Table 5.4. Maximum and mean length of time that LGDs spent at different distances from the sheep each day.

Distance (m)	**Maximum per day (mins)**		**Mean per day (mins) (SD)**	
Sheepfold state	*In*	*Out*	*In*	*Out*
≤100	920	760	437 (159)	348 (122)
101-250	630	560	94 (86)	202 (56)
251-500	515	460	19 (27)	87 (59)
501-1000	145	455	2 (3)	43 (51)
>1000	530	600	2 (7)	18 (28)

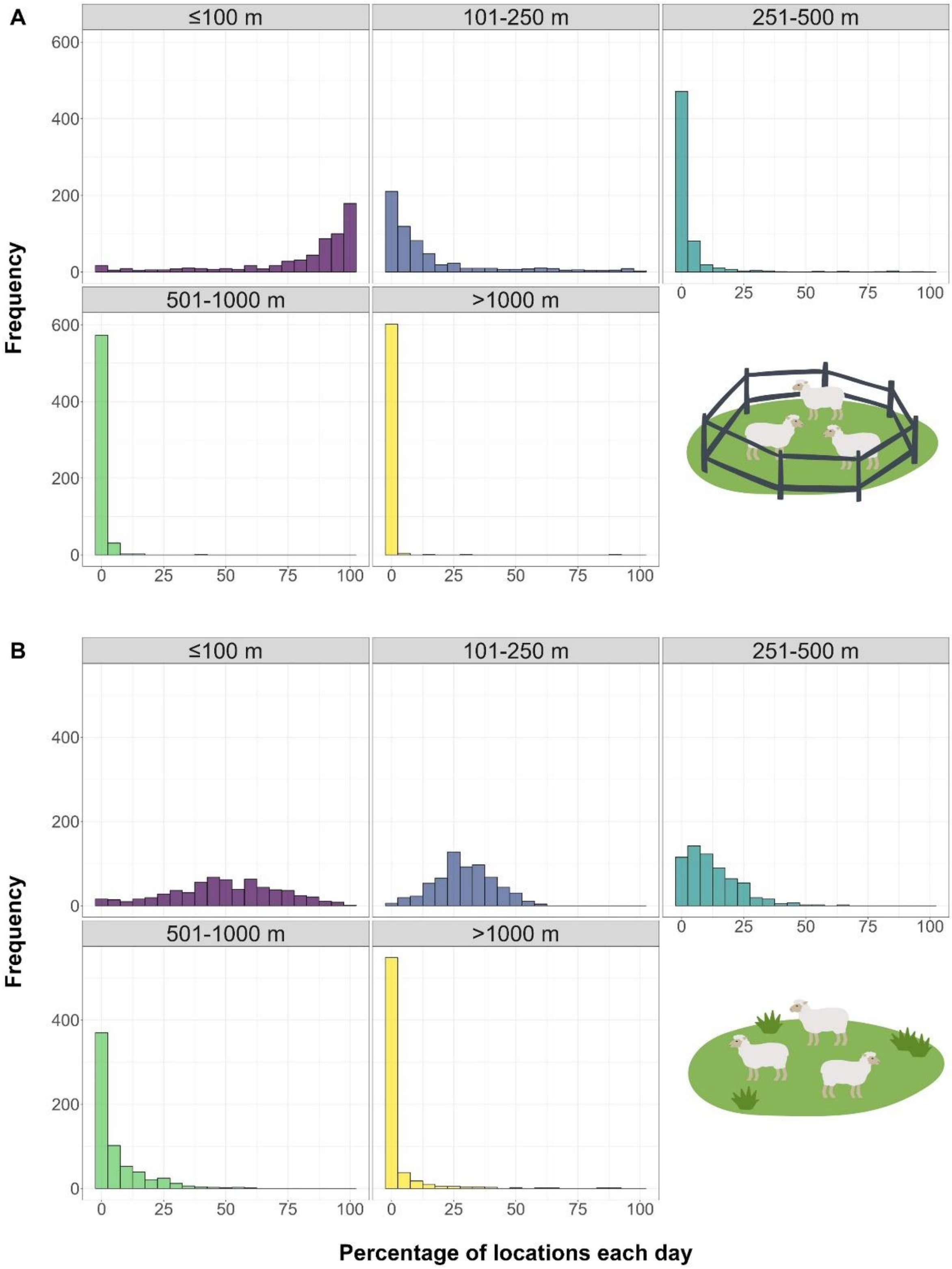

Figure 5.10. Frequency of the percentages of each LGD-sheep distance category each day when the sheep were in the sheepfold (A) and out of the sheepfold (B).

5.3.3 Daily area of use

The mean area of use by sheep each day when they were grazing on the pasture was 0.42 km^2 (± 0.21 km^2) (Table 5.5). For LGDs, this value was similar but slightly higher at 0.48 km^2 (± 0.23 km^2) and decreased to only 0.02 km^2 (± 0.02 km^2) when the sheep were in the sheepfold at night (Table 5.5). The mean daily values per LGD ranged from 0.002 km^2 to 0.07 km^2 when sheep were enclosed and from 0.15 km^2 to 0.95 km^2 when sheep were grazing on pastures (Table 5.5). When the sheep were out on the pasture, the daily area used by sheep ranged from 0.03 km^2 to 1.64 km^2, whereas the daily area used by LGDs ranged much higher from 0.007 km^2 to 4.39 km^2 (Table 5.5). The proportion of the total area covered by both the LGD and the sheep that was shared between the two was highly variable at the different sites and for different individual LGDs, with one LGD from SB04 having particularly low shared areas with the sheep (Figure 5.11).

Table 5.5. Summaries of the size of the daily areas of use per LGD.

Animal	**Sheepfold state**		**Mean daily area of use (km^2)**	**Minimum daily area of use (km^2)**	**Maximum daily area of use (km^2)**
LGD	**In**	*Mean (± SD)*	0.02 (0.02)	0.003 (0.004)	0.07 (0.10)
		Range	0.002 – 0.07	0.0001 – 0.02	0.004 – 0.36
LGD	**Out**	*Mean (± SD)*	0.48 (0.23)	1.00 (0.09)	1.20 (0.81)
		Range	0.15 – 0.95	0.007 – 0.39	0.31 – 4.39
Sheep	**Out**	*Mean (± SD)*	0.42 (0.21)	0.1 (0.1)	0.91 (0.48)
		Range	0.15 – 0.82	0.03 – 0.40	0.26 – 1.64

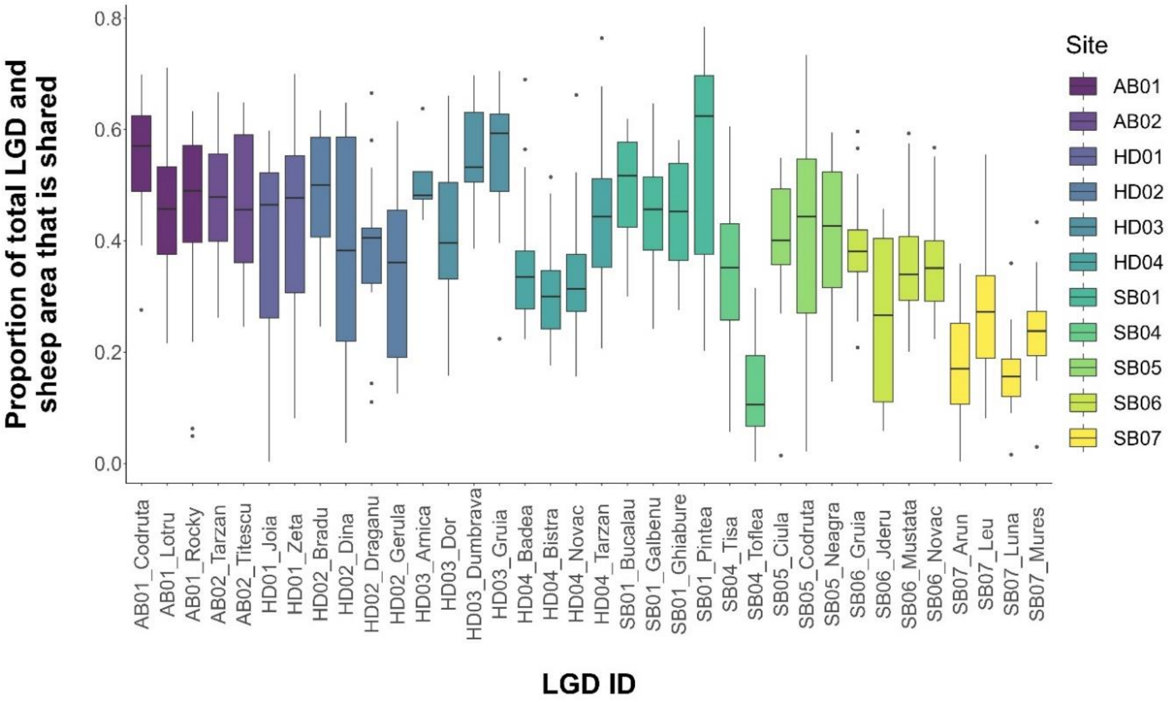

Figure 5.11. Proportion of the total LGD and sheep area used each day that was shared between the two when the sheep were out on the pasture.

Comparing the proportion of the LGD area that was shared with the sheep, to the proportion of the sheep area that was shared with the dog further showed that the LGDs largely stayed with the sheep as they overlapped large proportions of the sheep space use areas, but that the LGDs sometimes roamed away from the sheep too (Figure 5.12).

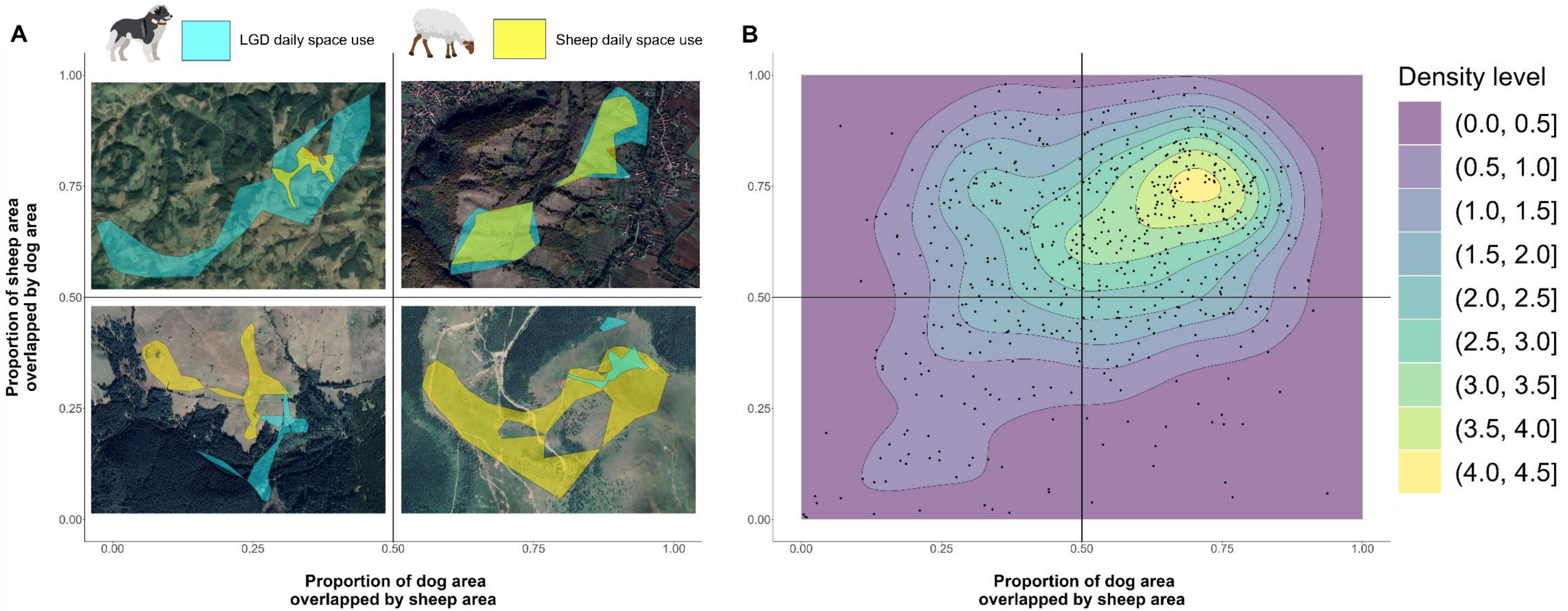

Figure 5.12. Follows on from Figure 5.4 showing: A) real examples from the data of how the four combinations of overlaps between LGD and sheep daily areas of use arise. For example, the top right shows two similarly overlapping areas where the proportion of the LGD area and sheep area that are overlapping are both high, whereas the top left shows a high proportion of overlap of the sheep area by the LGD but lower overlap of the LGD area by the sheep area caused by the LGD having roamed away from the sheep. B) Where all of the pairwise space use overlaps lie graphically with a kernel density highlighting that most days there are high overlaps between the LGDs and sheep (top-right) but there are also instances of the LGDs roaming from the sheep (top-left).

5.3.4 Factors affecting LGD roaming

Comparing the full models to the null models suggested there were no significant effects of LGD sex, breed, age, or whether neutered on overall LGD-sheep distances either whilst the sheep were in the sheepfold ($\chi^2(4, N = 71{,}837) = 2.3, p = 0.67, p > .05$) or out of the sheepfold ($\chi^2(4, N = 93{,}789) = 6.6, p = 0.16, p > .05$) and effect sizes for all explanatory variables were very low (Table 5.6). The model's explanatory power for when the sheep were in the sheepfold was substantial (conditional R2 = 0.33), but the part related to the fixed effects alone (marginal R2) was only 0.008. The model's explanatory power for when the sheep were out of the sheepfold was moderate (conditional R2 = 0.23), but the part related to the fixed effects alone (marginal R2) was only 0.04.

Similarly, there were no significant effects of LGD sex, breed, age, or whether neutered on daily maximum distances between LGDs and sheep either whilst the sheep were in the sheepfold ($\chi^2(4, N = 609) = 3.0, p = 0.56, p > .05$) or out of the sheepfold ($\chi^2(4, N = 641) = 5.6, p = 0.24, p > .05$) and effect sizes for all explanatory variables were very low (Table 5.6). The model's explanatory power for when the sheep were in the sheepfold was substantial (conditional R2 = 0.46), but the part related to the fixed effects alone (marginal R2) was of only 0.02. The model's explanatory power for when the sheep were out of the sheepfold was substantial (conditional R2 = 0.46), but the part related to the fixed effects alone (marginal R2) was only 0.05.

There was also no evidence for a significant effect of LGD sex, breed, age, or whether neutered on the proportion of the total LGD and sheep area that was shared between the two whilst the sheep were out of the sheepfold on the pasture ($\chi^2(4, N = 635) = 6.7, p = 0.15, p > .05$). There was a tendency for neutered LGDs to remain closer to the sheep (higher overlap proportions) as indicated by the larger effect size and 95% confidence intervals almost not overlapping zero (beta = 0.38; 95% CI: -0.03 – 0.80), but the effect sizes for all other explanatory variables were low (Table 5.6). The explanatory power of the model was substantial (conditional R2 = 0.81), but the part related to the fixed effects alone (marginal R2) was only 0.13.

Table 5.6. Outputs from linear mixed models fitted to predict LGD-sheep distances and daily maximum LGD-sheep distances with whether sheep were in the sheepfold or not, and LGD sex, age, breed, and whether neutered. Beta effect sizes and 95% confidence intervals (CI) are estimated from log-transformed data.

Model description	**Parameter**	**beta**	**Lower 95% CI**	**Upper 95% CI**
Distance ~ LGD characteristics (Sheepfold: In)	Intercept	3.83	3.47	4.20
	Sex (M)	0.15	-0.08	0.38
	Age (Juvenile)	-0.10	-0.35	0.14
	Breed (Mixed-breed)	-0.006	-0.32	0.31
	Neutered (Yes)	-0.02	-0.40	0.38
Distance ~ LGD characteristics (Sheepfold: Out)	Intercept	4.86	4.51	5.21
	Sex (M)	0.18	-0.11	0.45
	Age (Juvenile)	-0.15	-0.44	0.13
	Breed (Mixed-breed)	-0.32	-0.70	0.07
	Neutered (Yes)	-0.32	-0.74	0.10
Daily maximum distance ~ LGD characteristics (Sheepfold: In)	Intercept	5.38	5.02	5.76
	Sex (M)	-0.03	-0.26	0.20
	Age (Juvenile)	-0.17	-0.43	0.08
	Breed (Mixed-breed)	-0.09	-0.40	0.23
	Neutered (Yes)	-0.13	-0.51	0.25
Daily maximum distance ~ LGD characteristics (Sheepfold: Out)	Intercept	6.49	6.21	6.77
	Sex (M)	0.10	-0.11	0.31
	Age (Juvenile)	-0.10	-0.32	0.12
	Breed (Mixed-breed)	-0.16	-0.43	0.11
	Neutered (Yes)	-0.27	-0.61	0.06
Proportion of total area that is shared ~ LGD characteristics (Sheepfold: Out)	Intercept	-0.66	-0.99	-0.32
	Sex (M)	-0.16	-0.43	0.11
	Age (Juvenile)	0.18	-0.12	0.49
	Breed (Mixed-breed)	0.21	-0.17	0.59
	Neutered (Yes)	0.38	-0.03	0.80

5.4 Discussion

For livestock guarding dogs (LGDs) to be effective at reducing livestock losses, it is assumed that they need to be in close proximity to the livestock they are guarding (Gehring *et al.* 2011a). Before this study, little was documented about the proximity of LGDs to sheep in Romania or other transhumance grazing systems, especially at night whilst shepherds are sleeping and LGDs are not under direct human supervision. The LGDs in this study were typically in close proximity to the sheep they were guarding during both the day and night, but almost all of the LGDs left the sheep at least once every day, though usually only for a short duration of time.

The LGDs in this study were, on average, within 100 m and 200 m of the sheep during the night and day, respectively. Whilst there is no hard boundary for what is ‘close to’ and ‘far away’ from the livestock they are guarding, it is reasonable to assume based on the terrain and open pastures in the study area that if the dogs are within 200 m of the sheep then they can quickly respond to any threats or indications of threats such as hearing other LGDs barking. A similar distance threshold was also applied in a recent study from Israel where LGDs were said to have left the herd when they were more than 200 m away from cattle and out of sight (Gavagnach and Ben-Ami 2023). Thus, the LGDs in this study were closely associated with the sheep they were guarding in line with expectations for performance criteria required for assumed effective guarding (Lorenz and Coppinger 1986; Zingaro *et al.* 2018; Aslam *et al.* 2022). However, as GPS collars could only be attached to the least aggressive and more socialised LGDs, the findings must be treated with caution, given this potential bias. Furthermore, most LGDs did roam away from the sheep at some point every day with the average daily maximum distance between LGDs and sheep being just over 700 m during the day and extending up to 4000 m in rare instances.

If LGDs are not with the livestock, then they are not directly guarding the livestock. However, although a distance of 700 m from the sheep (the average daily maximum whilst sheep grazed) could be interpreted as far away, this distance could be covered by a running LGD in just over 1 minute (LGDs can run at speeds of up to 9 ms^{-1} (Akyazi *et al.* 2018)). This would enable the LGD to provide rapid assistance in the event of an attack, assuming they were alerted by other LGDs barking or shepherds shouting. There are also situations where roaming behaviours might be deemed beneficial for livestock protection. If LGDs roam away from livestock to establish and mark territories, then this could help deter predators from approaching the livestock (van Bommel and Johnson 2014b; van Bommel and Johnson 2014a). Livestock protection might also require engagement of LGDs with predators before predators get too close to livestock (van Bommel and Johnson 2014a; Allen *et al.* 2017b; Landry *et al.* 2020; Potet *et al.* 2021), although this behaviour can be exploited by ‘decoy’ tactics used by some social predators such as wolves (Chapter 3). As such, instead of leaving the livestock to challenge predators, it might be preferable for LGDs to remain closer to livestock to keep them tightly herded and protected, especially during dusk and dawn when predation risk increases (Gipson *et al.* 2012; Young *et al.* 2019; Roddick *et al.* 2022; Aslam *et al.* 2022). Alternatively, when multiple LGDs are used to guard livestock, some might move to challenge encroaching predators whilst others remain with the livestock (van Bommel and Johnson 2014a; Allen *et al.* 2017b; Akyazi *et al.* 2018; Landry *et al.* 2020). This is often reported as the case for Romanian LGDs whereby some remain in front of and behind the livestock, whilst others patrol further away and check forest edges for predators (per. comms.). However, this could not be confirmed within the current study design, warranting future research.

Incidents of LGDs roaming away from livestock could have implications beyond livestock protection. Given shepherd reports that the LGDs in the study did chase, and sometimes kill, both target and non-target species (Chapter 3), and some evidence of vertebrate remains detected in LGD scats (Chapter 4), it is possible that LGDs were, at times, chasing wildlife away from the sheep during this study. Whilst chasing target predators away from livestock could be viewed as LGDs protecting livestock, prolonged chases could pose a welfare concern for the animals involved in these interactions (Allen *et al.* 2019a; Allen *et al.* 2019b). However, the short duration of LGDs being away from the sheep observed in this study suggests that these LGDs were not chasing wildlife for prolonged periods of time. It is also possible that incidents of LGDs roaming were not due to engaging with wildlife and instead were due to LGDs seeking mating opportunities with neighbouring shepherds' dogs or additional food. Likewise, seeking shelter during hot periods may also explain some of the roaming observed; daily temperatures during the study duration frequently topped 30°C and LGDs were often observed lying away from the sheep in the shade of tree cover (personal observation). However, a study in Namibia found no effect of daily temperature on Anatolian Shepherd dog proximity to the livestock they were guarding (Aslam *et al.* 2022), though this breed, which originates from the Anatolian region of Turkey, may be better-suited to hot, arid climates. Shepherds were not asked to keep a record of their movements, so it is also possible that excursions from livestock could be due to LGDs following shepherds as there is evidence that LGDs can be more strongly bonded to humans than livestock in some cases (Akyazi *et al.* 2018; McKellar *et al.* 2023). However, if the LGDs were roaming in the absence of the shepherd, this could pose an issue for recreational tourism in the study area (Mosley *et al.* 2020). Shepherds at some sites did report conflicts with hikers and mountain bikers over encounters with LGDs in the mountains near public trails (per. comms.).

Therefore, whilst some level of roaming by LGDs can play a role in livestock protection, the near-daily occurrence and in rare cases, the long distance, of these excursions warrant some cause for concern from both an ecological and social perspective. As such, mitigations should be considered, which requires an understanding of what leads to different LGD behaviours. In this study, there was no evidence that LGD-sheep proximity and roaming behaviours were influenced by LGD breed, sex (including neutering status), or age. This finding mostly aligns with previous studies finding LGD proximity to livestock to be independent of breed (Young *et al.* 2019), sex (Allen *et al.* 2017b; Akyazi *et al.* 2018; Zingaro *et al.* 2018; Young *et al.* 2019) or age (Young *et al.* 2019; Mosley *et al.* 2020) of LGDs. There was a tendency for neutered LGDs to share larger proportions of space use with sheep, suggesting they remained closer to sheep than reproductively intact LGDs, but the effect was not statistically significant. Furthermore, most of the dogs were not neutered, with those that were neutered being mostly at site SB06 where three of the neutrered LGDs stayed in close proximity to the sheep. As such, it is possible that these behaviours were due to the management and training of the LGDs at this site rather than the LGDs being neutered.

Differences in LGD proximity to sheep were largely caused by individual variation, a finding concurrent with other studies on LGD movements (Allen *et al.* 2017b; Zingaro *et al.* 2018; Aslam *et al.* 2022). Thus, other factors that have not been considered in this study could be influencing LGD roaming behaviours. One such factor is habitat, as LGD-sheep distances were previously found to be larger with increasing woodland and heterogeneous areas (Zingaro *et al.* 2018). However, the landscape is largely homogeneous in the study region, with LGDs being monitored on higher altitude pastures surrounded by mixed coniferous and deciduous forests (Chapter 3). The relative risk of predation levels at each site could influence behaviours too as predator numbers were different across the study region (Chapter 3), though this would likely affect the LGDs at the site-level rather than the individual-level. Similarly, if LGDs are roaming because they are hunting or scavenging for food, then human-provisioning of food to LGDs could be influencing behaviours (Chapter 4). Furthermore, a growing body of research in recent years has acknowledged that domestic and wild animals, including dogs and specifically LGDs, have unique personalities (Svartberg and Forkman 2002; Wolf and Weissing 2012; McConnell *et al.* 2022). Thus, differences in behaviours could be due to general differences in personalities between LGDs, requiring tailored training of individual LGDs. It is clear that further investigation into what causes LGDs to roam away from livestock is required, and this would enable the implementation of effective mitigation measures that optimise LGD performance and minimise undesirable effects.

5.5 Conclusion

Overall, the LGDs monitored in this study remained in close proximity to the livestock they were guarding, even at night whilst unsupervised, and can be considered as being attentive towards livestock in this regard. However, LGDs did roam away from sheep at least once most days. Some of these excursions away from sheep covered large distances and lasted for prolonged periods of time, but mostly they were short in duration and not conducted by all LGDs. There was no evidence that these roaming behaviours were associated with the LGD-specific factors investigated here and roaming appeared largely related to individual variation, hence the circumstances under which LGDs were leaving the sheep remain unknown. Some roaming from the sheep could be beneficial in deterring predators from attacking sheep, but chasing non-target wildlife or causing a nuisance to people undertaking recreational activities whilst out of the shepherd's control are undesirable behaviours in an area with high abundances of wildlife and high levels of recreational use. As such, further investigation into why some LGDs sometimes roam from sheep in this region is required so that mitigation measures can be implemented. In addition, the methods presented in this study could be used for LGD selection and training. If LGD owners are able to fit their dogs with low-cost GPS collars they could determine how frequently their LGDs roam away from their livestock and set a threshold that helps them to select the most effective LGDs or focus correctional training efforts on those deemed to roam too far or too frequently. As the first study to GPS track LGDs in the Romanian Carpathian Mountains, these findings provide much-needed information on LGD movement behaviours to inform appropriate management of free-ranging LGDs in transhumance grazing systems.

Chapter 6: Spatial and temporal responses of wildlife to the presence of livestock guarding dogs in the Carpathian Mountains, Romania

6.1 Introduction

Predators affect prey through consumptive and non-consumptive effects. Consumptive effects are those arising from predators killing prey, thus altering prey survival and potentially prey population dynamics. Non-consumptive effects are those that arise from the fear of predation, whereby prey develop anti-predator responses that can be morphological, physiological or behavioural (Say-Sallaz *et al.* 2019). While increasing survival probability against predation, anti-predator responses can incur other costs on survival and reproduction, ultimately impacting prey population growth rates much like consumptive effects (Preisser *et al.* 2005; Allen *et al.* 2022). The fear of predation can give rise to what is known as a 'landscape of fear' - the spatial variation in prey perception of predation risk (Laundré *et al.* 2010; Gaynor *et al.* 2019). Prey responses to a landscape of fear typically manifest as behaviour modulations to reduce the chance of predation in a risky area, such as increased vigilance and reduced foraging, and spatiotemporal avoidance of high predation risk areas (Gaynor *et al.* 2019). These anti-predator strategies, in turn, can have cascading effects on populations and ecosystems (Palmer *et al.* 2021; Burgos *et al.* 2022).

A growing body of research is demonstrating that anthropogenic disturbances can also induce landscape of fear effects, even sometimes to a greater extent than wild predators (Ciuti *et al.* 2012; Clinchy *et al.* 2016; Sévêque *et al.* 2020; Lasky and Bombaci 2023). For example, humans might be thought of as 'super predators' in the environment (Smith *et al.* 2017) and by being mostly diurnal are pushing wildlife towards becoming more nocturnal (Gaynor *et al.* 2018). Animals associated with humans, such as domestic dogs (*Canis familiaris*), might also function as predators and competitors in the environment, particularly when they are feral or free-ranging (Vanak and Gompper 2009b; Young *et al.* 2011; Hughes and Macdonald 2013). Domestic dogs can affect the foraging behaviour (Mahlaba *et al.* 2017), spatial distribution (Lenth *et al.* 2008; Silva-Rodríguez and Sieving 2012; Callan *et al.* 2020; Ünal *et al.* 2020), activity patterns (Zapata-Ríos and Branch 2016; Marshall *et al.* 2023), stress indicators (Rangel-Negrín *et al.* 2023), and even social dynamics (Gall *et al.* 2022) of wildlife. As with wild predators, the fear of domestic dogs can have far-reaching consequences through ecosystems (Suraci *et al.* 2016).

Although more studies are acknowledging the effect that domestic dogs can have on wildlife, little attention has been paid specifically to the potential effects of working dogs in the environments where they are used (Smith *et al.* 2020a; Chapter 2). Livestock guarding dogs (LGDs) are used to protect livestock from being predated by wild predators and are widely considered an effective tool at preventing livestock losses or injuries from predators around the world (Scasta *et al.* 2017; Lieb *et al.* 2021; Marker *et al.* 2021; Petridou *et al.* 2023). The use of LGDs is largely supported as an effective, non-lethal livestock protection tool and advocated for by conservation organisations due to increasing farmer tolerance of predatory wildlife, thus potentially reducing persecution of these species (González *et al.* 2012; Rust *et al.* 2013). However, LGDs have been reported chasing and killing apex predators, mesopredators, and herbivores of different sizes (Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020). In fact, a review on the ecological effects of LGDs found that LGDs had been reported chasing and killing 80 different wild species, 78% of which were non-target species, i.e. animals deemed not to be a predation threat to livestock (Smith *et al.* 2020a; Chapter 2). Thus, LGDs could be perceived by wildlife as surrogate top predators in the environment (van Bommel and Johnson 2016).

If areas that LGDs use are perceived as risky locations to wildlife, then the landscape of fear theory predicts that wildlife would attempt to avoid LGDs in space, and/or time (Laundré *et al.* 2010). Spatial avoidance of LGDs by wildlife could be seen as beneficial and a method by which LGDs are effective at reducing livestock predation by excluding target predators. However, it is possible that displacing predators from areas used by LGDs simply shifts the problem elsewhere, thus exacerbating conflicts over livestock predation in other locations (e.g. Osipova *et al.* 2018). Furthermore, excluding predators from agricultural lands could be detrimental to these predators by restricting access to resources and creating a barrier to movement; similar effects to those reported for fencing (Jakes *et al.* 2018; Smith *et al.* 2020b; McInturff *et al.* 2020). Similarly, the exclusion of non-target species from habitat they would normally use could be detrimental to those species. On the contrary, the separation of wildlife from livestock is seen as a desirable outcome by some due to reducing: damages such as wild boar (*Sus scrofa*) rooting of pastures or damage to electric fences (Ballarín *et al.* 2023); competition between wild grazers and livestock (van Bommel and Johnson 2016; Ugarte *et al.* 2021), and the risk of disease transmission between wildlife and domestic animals (VerCauteren *et al.* 2008; Gehring *et al.* 2011b; VerCauteren *et al.* 2012).

To date, a few studies have demonstrated spatial and temporal avoidance of LGDs by wildlife (Gehring *et al.* 2011b; van Bommel and Johnson 2016; Kinka *et al.* 2021; Ugarte *et al.* 2021). One recent study from the USA found that the presence of sheep bands (sheep, shepherds, and LGDs together) displaced large mammals including predators and herbivores (Kinka *et al.* 2021). However, in the same study, coyotes (*Canis latrans*) were more likely to be detected whilst a sheep band was present and after one had moved through an area (Kinka *et al.* 2021), highlighting that there are likely to be species-specific responses to LGD presence. Similarly, some studies have found no evidence of spatial or temporal avoidance of LGDs by wildlife, e.g. Spencer *et al*. (2020) found that LGD presence did not affect the occurrence of leopard (*Panthera pardus*) or black-backed jackal (*Lupulella mesomelas*) on South African farms. Whilst these previous studies are important for understanding wildlife responses to LGDs, many only consider spatial responses. Wildlife might not be spatially displaced by LGDs, but they might alter the timing of their activity to avoid interactions with LGDs, thus both spatial and temporal responses must be considered together.

Furthermore, there are many environmental, biotic, and anthropogenic drivers of species' distributions and diel activity patterns (Clinchy *et al.* 2016; Gaynor *et al.* 2018; Dyck *et al.* 2022; Kellner *et al.* 2022). The relative influence of these other drivers is often not considered when assessing whether wildlife display spatial or temporal responses to LGDs. The level of concern that LGD-induced effects warrant must be considered in relative terms in the landscape. For example, if the effects of LGDs on wildlife behaviours are negligible relative to other drivers, such as other forms of anthropogenic disturbance or the presence of wild apex predators, then a focus on LGDs may be unnecessary or lower priority. With such complex potential responses by wildlife to the presence of LGDs, and differences in desirability of these responses to various stakeholder groups, it is imperative to understand the impacts of LGDs on co-occurring wildlife relative to other drivers of spatial and temporal patterns in wildlife behaviour.

The aim of this study was to determine if the presence of LGDs induced substantial spatial and temporal responses by wildlife relative to other drivers of species distribution and activity. To do so, camera traps were deployed in the southern Carpathian Mountains, Romania. In this region, shepherds practice transhumance grazing taking their livestock to higher altitude pastures in the summer months (May-October) and typically use multiple LGDs of varying breeds to guard each of their sheep flocks (Chapter 3). Whilst there is abundant wildlife, including large predators, and large swathes of natural habitat in this region, there is also a high level of anthropogenic disturbance from logging and recreational activities such as hiking and offroad motorbiking (Chapter 3). The detections of wildlife at camera sites were used to assess species distributions and activity patterns in relation to LGD presence and other anthropogenic, environmental, and biotic variables. Based on the landscape of fear theory, it was hypothesised that wildlife would perceive LGDs as surrogate top predators and 1) either avoid using high risk LGD areas or use them less frequently, 2) display increased nocturnal behaviour in high risk LGD areas considering LGDs are active during the day, and 3) exhibit spatiotemporal responses to LGDs of a similar magnitude to their responses to wild apex predators that would represent a similar level of danger (Say-sallaz *et al.* 2023). Due to the high level of anthropogenic activity in the study region and previous research suggesting considerable responses by wildlife to humans but not dogs or wild predators (Clinchy *et al.* 2016; Suraci *et al.* 2019), it was also hypothesised that wildlife would perceive humans as a greater risk than LGDs and any spatial or temporal responses to humans would be of a greater magnitude than those to LGDs. Understanding how wildlife respond to the presence of LGDs relative to other drivers of spatial and temporal patterns is of critical importance for assessing the overall effectiveness and conservation benefit of LGDs. The results from this study provide valuable insight into some of the ecological effects of LGDs in an area with long-standing traditional use of LGDs and high levels of human disturbance, which are applicable to similar systems around the world.

6.2 Methods

6.2.1 Ethical approval

This study received ethical approval from Nottingham Trent University under project code ARE192048R(21); see Chapter 3 for details.

6.2.2 Study area

This study was conducted across a 315 km^2 region of the Southern Carpathian Mountains in collaboration with the organisation Fauna & Flora. Permission to deploy camera traps was sought and received from the appropriate Game Management Units (GMU) for each area. See Chapter 3 for more details.

6.2.3 Camera trap deployment

Camera traps were deployed across 35 contiguous 3x3 km grid cells with only one camera per grid cell at any one time, and with all cameras at least 1 km apart (Figure 6.1). This spacing was based on previous methodology employed in Fauna & Flora projects and other wildlife monitoring studies in Romania (Popescu *et al.* 2017; Dyck *et al.* 2022). Cameras remained in the same location, hereafter referred to as a 'camera site' for the duration of the study, unless they were stolen (12 in total) or had to be moved to an alternative site in the same grid cell, for example when a logging camp was established in front of one of the cameras. The exact location of each camera within the grid cell was limited by road accessibility. As such, cameras could not be deployed according to a rigorous stratification of habitat types but were instead placed at varying distances from pastures that could be reached by road with limited hiking required. Camera sites ranged in elevation from 864 m to 2010 m asl (mean: 1371 m ± 255 m SD).

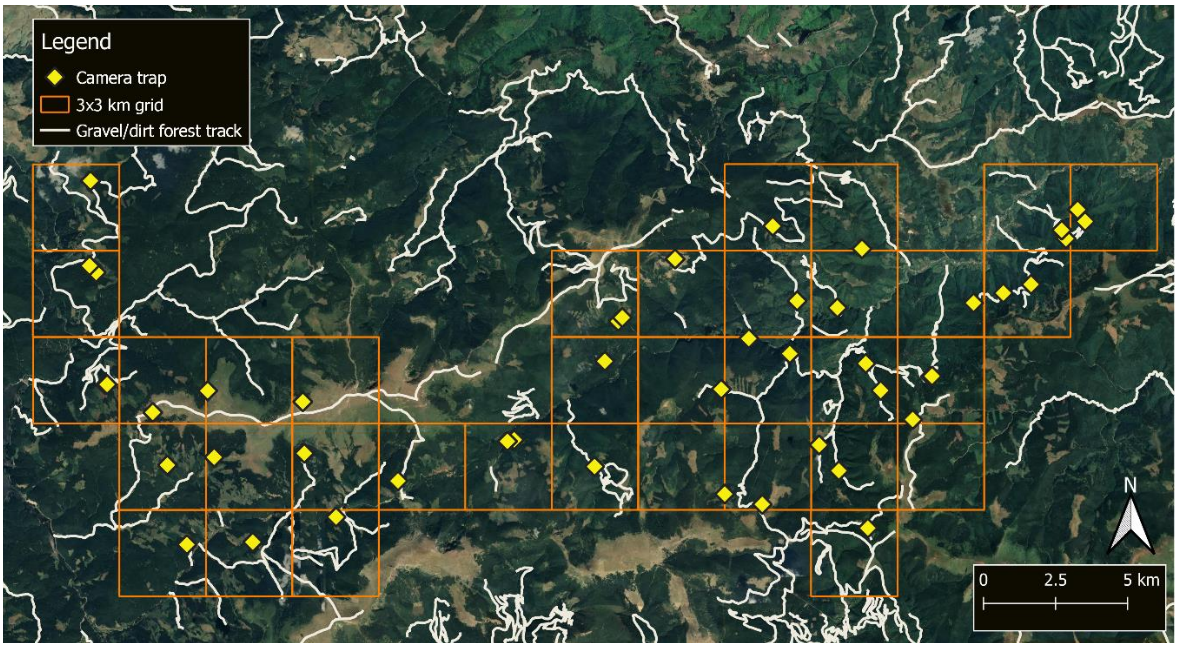

Figure 6.1. Camera trap locations within contiguous 3x3 km grid cells in the southern Carpathian Mountains, Romania. Cameras were placed facing gravel and dirt forest roads and tracks, most of which are shown here though not all have been mapped as new tracks are created by continuous logging in the area. Map produced in QGIS using Google Satellite imagery.

At each camera site, cameras were placed on trees at an angle (approximately 45°) facing towards forest tracks and no baits or lures were used. These forest tracks were classified in the field as primary, secondary, and tertiary tracks (Figure 6.2). Primary tracks were more permanent, gravel or compacted dirt tracks most commonly used by vehicles to move around the study area. Secondary tracks were dirt tracks branching off primary tracks that were used less frequently. Tertiary tracks were primarily older, overgrown secondary tracks that were rarely, if ever, used by vehicles but were still clearly a linear, open feature in the landscape. Some of the tertiary tracks were used by logging vehicles for infrequent, short periods of time during the study but overall were not frequently accessed by vehicles.

Figure 6.2. Examples of different classifications of forest tracks that cameras were situated on: primary tracks (A-B), secondary tracks (C-D), and tertiary tracks (E-F).

There is still debate over whether targeted camera trap placement along roads provides differing results to random camera trap placement. Some studies have found that non-random camera trap placement along roads biases captures of wildlife (Kolowski and Forrester 2017), whereas others have found no significant difference between random versus trail-placed cameras (Fonteyn *et al.* 2020). Ultimately, forest tracks were used to increase captures of wildlife (Di Bitetti *et al.* 2014) on the basis that any comparisons between sites would be relative for each species and not compared across species. Cameras were mounted opportunistically to trees that were close enough to the tracks to capture passing wildlife without being too obvious to passing humans, hence no standard height or distance from the edge of the trail was possible. Instead, cameras were set at what was deemed an appropriate height and distance to the track for each site based on the researchers' extensive experience setting camera traps. To deter theft of the cameras they were secured to the trunk of the tree with a chain and padlock.

All cameras deployed were Bushnell Trophy Cam HD Aggressor 20MP No-Glow (model number: 119876). These cameras have an infrared flash range of >24 m and response time of 0.2 s when triggering. "No-Glow" camera traps feature black instead of red LEDs, which reduces the visibility of the flash and minimises disturbance to wildlife (Meek *et al.* 2014; Meek *et al.* 2016), as well as to reduce the probability of cameras being seen and subsequently stolen by humans. Cameras were programmed to be active for 24 hours a day and take a series of three photos when triggered with a 0.6 s interval between subsequent triggers. After a preliminary trial to compare different combinations of settings to produce the brightest, highest quality images during both the night and day, the 'Image Size' was set to 'HD' (1920 x 1080p - to reduce motion blur on the photos), 'Sensor

Level’ to ‘Auto’ (to account for varying air temperatures both diurnally and seasonally), ‘Night Vision Shutter’ to ‘Auto’ (as images were too dark at night when set to ‘High’), and ‘LED Control’ to ‘High’ (to increase brightness of images when using No-Glow camera traps).

The first cameras were deployed on 15 July 2021 and all cameras were collected in from the field by 08 June 2022. The aim was to check camera traps every 4-6 weeks, but this was not always possible, especially during the winter months when thick snow cover prevented access to many of the sites. At each camera trap check, the following information was noted: date, time, battery level, whether the camera was working and any other notes e.g. if the camera looked to have been tampered with.

6.2.3.1 Camera site inclusion for analyses

Not all cameras were active for the entire survey period and some cameras had to be moved to different sites within the same grid cell. Thus, not all of the data from each site was useable in its raw format. In three of the cells, data were collected from two different sites after the theft of the first camera trap meant a second camera trap needed to be deployed in that cell but in a slightly different area. In these three cells, the data from the two sites were merged together as though one continuous tracking period as the two sites were similar enough in habitat type and placed on the same type of linear feature (Figure 6.3). At these three grid cells the mean of the environmental variables at each site, such as elevation and distance to pasture, was used. Due to theft, malfunctioning cameras, or poor access to sites, some camera sites were removed from any further analysis. In total, data from 30 grid cells were included in the analyses (Figure 6.3). There were seven sites on primary tracks, 11 on secondary tracks, and 12 on tertiary tracks.

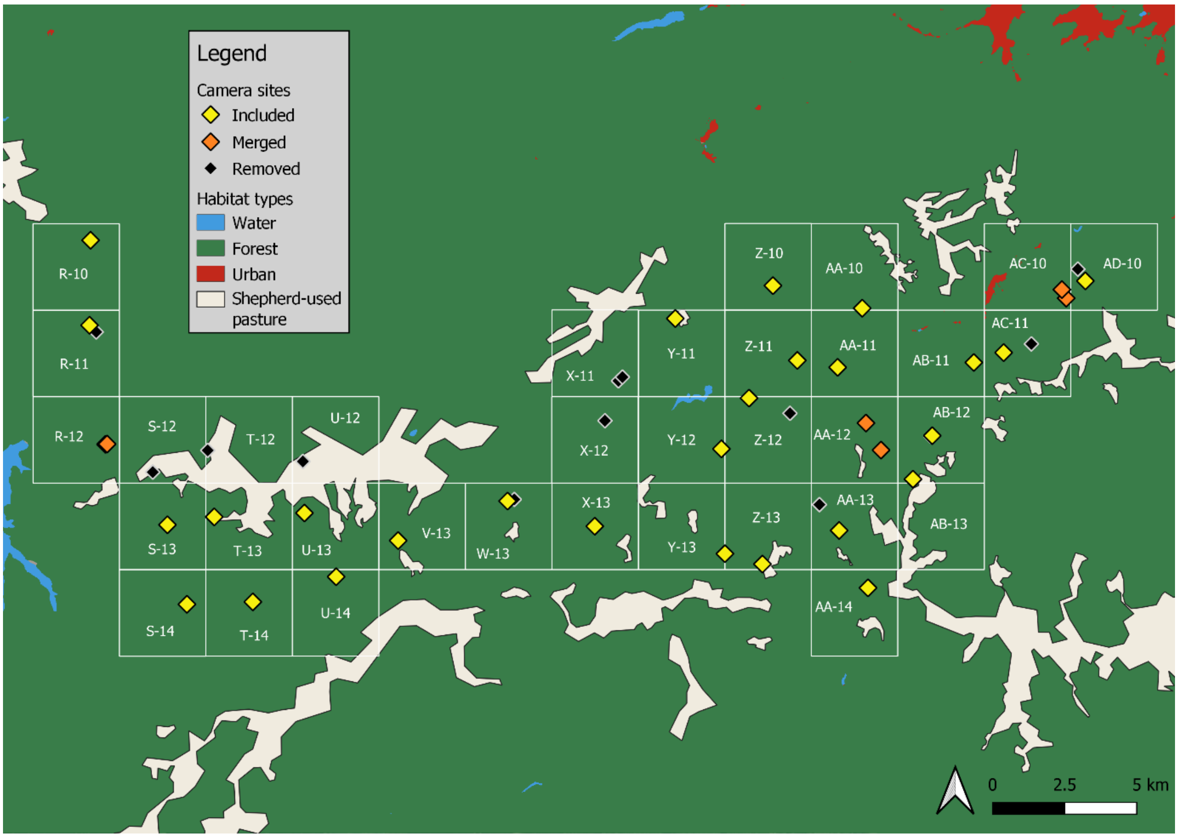

Figure 6.3. Locations of camera traps included in the analysis (yellow diamonds) and those that were merged to form a dataset as though from one site (orange diamonds). Camera sites that were removed from the analysis are depicted with black diamonds. Unique IDs for each grid cell are shown. Forest, urban, and water are simplified habitat types from 2021 Sentinel-2 10-Metre Land Cover data available at: https://livingatlas.arcgis.com/landcover/ (Karra *et al.* 2021). *Shepherd-used pasture was assigned as in Section 6.2.5.2.*

6.2.4 Photo processing

6.2.4.1 Species identification

All photos were checked manually to confirm that cameras were functioning correctly and to identify cut-off points in the images to be used if the cameras had been moved by humans, wildlife, or in one case due to a tree being uprooted. All 'useable' photos were processed using Wildlife Insights; a cloud-based camera trap data management platform with integrated automatic species detection (Ahumada *et al.* 2020). The automated detection function of Wildlife Insights identified true blank photos (where the camera may have been triggered by vegetation instead of wildlife) from photos where the animal was difficult to discern by the human eye. All species identifications were made manually and all images that were automatically-classified as blank were double-checked manually.

Photos were tagged with the species and number of individuals present. All mammals were identified to species level except for pine marten and beech marten, which were identified to genus (*Martes spp.*) due to the difficulty of distinguishing the two species in photos. As cameras were located away from human settlements and at high elevations, images of small felids with characteristic wildcat (*Felis silvestris*) markings were assumed to be wildcats as opposed to domestic cats (*Felis catus*) or hybrids. Where possible, all wildcat identifying features were considered: a bushy tail with blunt black tip; thick, distinctive tail bands; wider-set face and jaw-line; striped coat with no spots on either the flanks or hind quarters; and black dorsal stripe not extending down the tail (Kitchener *et al.* 2005). For photos where the species could not be assigned with a high level of certainty, such as where the subject was extremely blurred, no identification was given other than 'animal' to differentiate these images from blank images.

Anthropogenic activity and all domestic animals were also tagged in photos. Human presence was recorded and assigned into motorised (motorbikes, ATVs, cars, and logging trucks) and unmotorised (pedestrians, cyclists, horse riders, and horse and carts) groups. Domestic dogs were further classified into four categories: 1) LGDs - if clearly accompanying livestock, or wearing dangle sticks, or recognised by the researchers due to working with the shepherds and their dogs in the area; 2) herding dogs - small black dogs that shepherds use to herd, rather than guard, livestock); 3) pets - dogs accompanying humans other than shepherds (e.g. dogs clearly with hikers, foragers, loggers or hunters); and 4) unknown - unrecognised dogs not captured with livestock or humans, which could, therefore, have been LGDs, pet dogs, or feral dogs (Figure 6.4). Once all images were tagged, the images were checked again and any errors in species identification corrected.

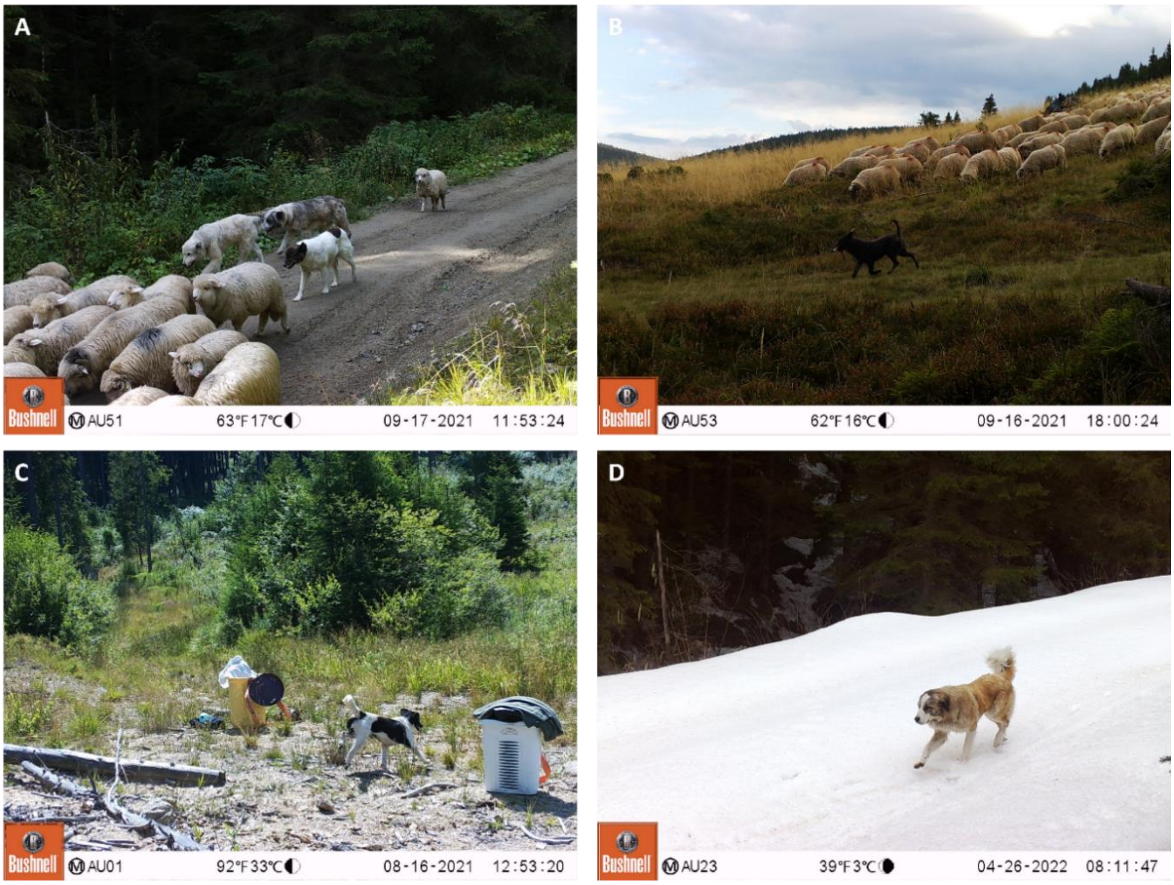

Figure 6.4. Examples of different categories of dogs tagged in the camera trap photos. A) Livestock guarding dogs accompanying sheep. B) Small black herding dog accompanying sheep. C) Pet dog accompanying humans foraging in the forest. D) Unknown dog that was not accompanying livestock or humans, not wearing a dangle stick, and not known as one of the livestock guarding dogs in the area.

6.2.4.2 Independent observations

Each image of a species does not necessarily constitute a different individual, or ‘independent observation’, especially where cameras are set to take multiple photos per trigger and where animals remain in front of cameras for extended periods. A common practice in camera trapping is to group species detections into independent observations, whereby images of the same species at the same site are considered to be the same animal if they occur within a certain time period of each other, typically 30 or 60 minutes (Peral *et al.* 2022). However, there is little scientific rationale for the time threshold used and having looked through all of the images manually, it was clear that individual animals were predominantly travelling past the cameras on the trails in one direction and were not being captured going backwards and forwards within a short period of time. It was also apparent that different individuals of the same species would pass the same camera site within 30 minutes of each other and that grouping images into independent observations based on a 30-minute time-to-independence threshold would discard unique detections. As such, a smaller time-to-independence threshold was chosen whereby photos taken at the same camera site of the same species were considered to be different detections if photos were separated by more than 5 minutes.

Currently, there is debate surrounding whether independent observations should be used at all, particularly in estimations of temporal activity as discarding images within a certain time period discards real data about when that animal was active (Peral *et al.* 2022). To investigate whether to use independent observations or all of the data in this study, the duration of independent observations (the difference between the time of the first image and the last image of those that were grouped into independent observations based on the chosen 5-minute threshold) were calculated and examined. It was clear that most animals simply moved past the camera within a matter of seconds or minutes and that only some individuals of a few species on occasion stayed in front of the camera for longer periods of time, the longest being wild boars at 26 minutes (Table E.1). As such, including all of the images would have inflated activity patterns around the few time periods when animals remained in front of the camera, compared with animals passing the cameras. Thus, it was decided to keep images grouped into independent observations based on the 5-minute threshold, and the timestamp of the first image within each group of photos was used to record the time each species was detected.

6.2.5 Spatial and temporal presence of LGDs

6.2.5.1 Temporal

The transhumance grazing season when shepherds, livestock, herding dogs, and LGDs occupy pastures in the study area is typically May through October each year. As such, the grazing season was defined as the first day of May until the last day of October. Although it was not possible to know exactly when all of the shepherds had entered or moved out of the area, the end date was largely confirmed by the cessation of continual captures of LGDs, herding dogs, and sheep on the camera traps towards the end of October (Figure 6.5). The few captures in November were at the lowest elevation camera sites and so were likely some of the last shepherds to be moving their sheep and dogs down off the higher altitude pastures. These captures of LGDs were not included in the analyses as they occurred outside of the defined transhumance grazing season.

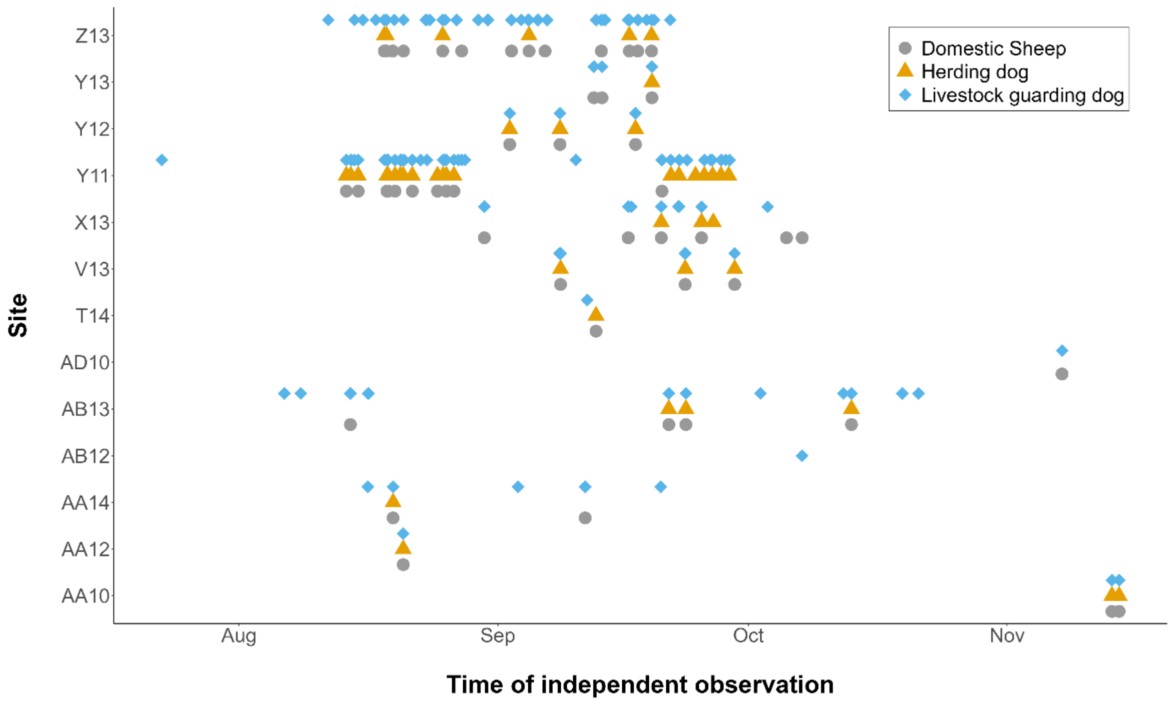

Figure 6.5. Times of independent observations of livestock guarding dogs, herding dogs, and sheep at each of the sites they were detected at throughout the study. The x-axis is for 2021 only as none of these animals were detected on camera traps whilst active in 2022.

6.2.5.2 Spatial

The exact distribution of LGDs throughout the study area was unknown. Some locations of active sheepfolds – locations known to be in use by shepherds during the summer of 2021 – were recorded in the field. However, it was not possible to find all of the areas used by shepherds for grazing sheep in the study area whilst in the field. Instead, open areas of habitat were searched on Google Earth for structures resembling sheepfolds. These were often easily identifiable as rectangular or circular fencing surrounding different-coloured ground, often situated next to a small human-made structure, and sometimes with sheep nearby (Figure 6.6).

Figure 6.6. Examples of sheepfolds found using Google Earth satellite imagery.

No detailed Google Earth satellite imagery was available for the region for 2021, so available imagery between 2017 and 2022 were searched and any sheepfold locations noted with the year they were present. It was clear that most identifiable sheepfolds were present for several years, and, therefore, were likely to have been in use during the summer of 2021 too. As sheep range over pastures during the day (Chapter 4), it was likely that the entirety of any grassland habitat with a sheepfold would be used for grazing at some point over the summer. Thus, polygons were drawn manually around these whole grassland areas and this habitat type classed as shepherd-used pasture (Figure 6.7). These shepherd-used pastures mostly encompassed all open grassland in the study area with the exception of some small fragments, which were deemed negligible in terms of habitat classification. For each camera site, the Euclidian distance to the edge of the nearest shepherd-used pasture was measured and interpreted as the minimum distance to the nearest potential LGD-frequented area.

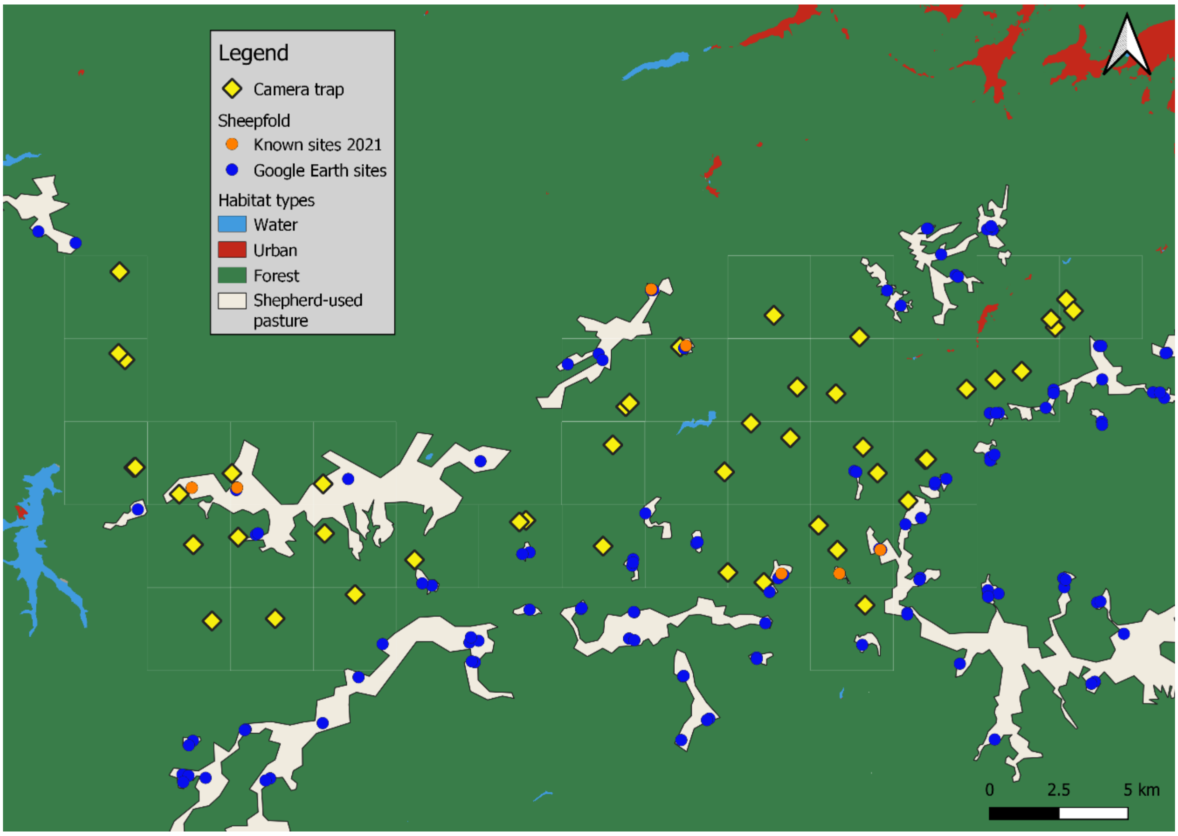

Figure 6.7. Simplified landcover map showing camera trap locations (yellow diamonds) in relation to forest and shepherd-used pastures habitat types. The locations of sheepfolds that were known to be in use in 2021 (orange circles) and those found from Google Earth satellite imagery from surrounding years (blue circles) are also shown. Shepherd-used pasture habitat type was determined manually from the locations of the sheepfolds. Forest, urban, and water are modified habitat types from 2021 Sentinel-2 10-Metre Land Cover data available at: https://livingatlas.arcgis.com/landcover/ (Karra *et al.* 2021). *The forest classification here contains both 'trees' and 'rangeland' habitat types from the original dataset as the remaining rangeland (after manually accounting for shepherd-used pastures) was predominantly small fragments of clear-cut forests which have been classed as forest for simplicity in this study.*

In addition, the detection rates of LGDs throughout the grazing season – the number of independent detections per 100 camera trapping days – were calculated for each site. The relative presence of LGDs across the camera trapping area was then represented at the landscape scale by combining detection rates and the distance to the nearest shepherd-used pasture to classify sites as high or low likelihood of continuous LGD presence (hereafter referred to as high or low LGD sites). First, camera sites with LGD detections were classed as high LGD sites with the exception of some sites with fewer detections that were inspected manually. Eleven camera sites captured LGDs during the grazing season but at five of these sites the number of independent detections was extremely low: three sites had one detection, one site had three and another had six. At the site with six detections, these were captured on three days within one week in September. Further manual inspection of these images, in combination with the date they were taken, elevation of the camera site, and firsthand knowledge of the study area, strongly suggested that these images were captures of LGDs, shepherds, and sheep sporadically passing by the camera whilst moving between pastures or whilst on their way back to the lower altitude pastures and villages at the end of the grazing season. As such, these captures did not represent high likelihood of LGD presence at these locations throughout the grazing season based solely on LGD detection rates. Second, it was expected that relative LGD presence would be higher closer to shepherd-used pastures, and this was confirmed by the occupancy analyses (detailed later). As cameras were not guaranteed to detect LGDs even if LGDs were nearby, camera sites close to pastures were, therefore, classed as high likelihood of continuous LGD presence sites regardless of the LGD detection rate. All camera sites within 700 m of pastures were designated as high LGD sites as previous GPS tracking of LGDs in the region showed that LGDs could be, on average, a maximum of 700 m from livestock every day (Chapter 5). Following this, all sites within 700 m of shepherd-used pasture, plus those with higher detection rates of LGDs, were classed as high LGD presence sites. In total, 20 sites were classified as low LGD sites and nine were classified as high LGD sites (six of which captured LGDs, and three of which did not capture LGDs but were within 700 m of pasture). Of the high LGD sites, two were on primary tracks, four secondary, and three tertiary. For the low LGD sites, there were four on primary tracks, seven on secondary, and nine on tertiary.

6.2.6 Habitat and anthropogenic variables

Cameras were deployed across an elevational gradient. Elevation can affect species' distributions due to differences in habitat and climatic conditions such as reduced tree cover or increased snow cover at higher elevations. Thus, elevation was a variable of interest and recorded in the field at each site using a handheld GPS device. The percentage of forest cover within a 500 m buffer around each camera site was extracted from 2018 Corine Land Cover (CLC) data. Forest was a grouped category comprising the CLC categories broadleaved, coniferous, mixed forest, and transitional woodland shrub. The only other two CLC categories contained within the 500 m buffers were natural grasslands, and moors and heathland. The detection rates (number of detections per 100 camera trapping days) of all human activities (both motorised and unmotorised combined) at each camera trap site were used as a proxy for the relative level of human activity across the sites.

6.2.7 Analysis of spatial and temporal responses of wildlife to LGD presence

Species that were detected most frequently across the camera trap sites were included for further analysis, specifically: grey wolf (*Canis lupus*), brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), red deer (*Cervus elaphus*), and wild boar. Only images of these species captured during the grazing season when LGDs were present in the study area were used to assess the spatial and temporal responses of wildlife to LGD presence. Several measures were employed to determine if the presence of LGDs affected wildlife distribution and activity.

6.2.7.1 Habitat use: single season, single species occupancy models

Single season, single species occupancy models were initially used to determine the relative influence of different variables on LGD and wildlife occurrence throughout the study area. Occupancy models account for the detectability of a species and so can account for the imperfect detection of a species across sites (MacKenzie *et al.* 2002) and are frequently used to assess the effect of variables on species occurrence using camera trap data (Burton *et al.* 2015; Sollmann 2018). Accounting for detectability requires sites to be visited repeatedly to build detection histories for each site. In this study, detection histories were built for each species using a 7-day sampling window whereby a species was classed as present at a site if it was recorded by the camera trap at any point during those 7 days. Instances of cameras operating for less than 7 days per visit (e.g. the last week of sampling) were removed from the detection history to keep sampling effort consistent. One assumption of occupancy models is site closure, whereby sites are assumed to be either always occupied or unoccupied (MacKenzie *et al.* 2006). This assumption is extremely unlikely to be validated in camera trapping studies, and the cameras in this study were spaced at distances shorter than the focal species' home ranges e.g. average home ranges for brown bears in Romania are approximately 65 km^2 (Cristescu *et al.* 2019) up to 200 km^2 (Pop *et al.* 2012; Pop *et al.* 2018) and 128.5 km^2 for grey wolves (Cristescu *et al.* 2019). Thus, occupancy in this study is considered to be 'habitat use' rather than occupancy in the traditional sense (MacKenzie *et al.* 2006). As well as site closure, single season occupancy models assume closure of the study area during each season, so only data collected during the transhumance grazing season (May-October) were used.

Before running the occupancy models, collinearity between the variables hypothesised to affect species' occupancy (habitat use) was investigated (Figure E.1). The percentage of forest cover at each site was largely uniform (83% of the 29 sites with 100% forest cover) and was correlated with LGD presence (i.e. sites that were not 100% forest cover were those near to pastures and were, therefore, the high LGD sites). Hence, forest cover was removed from the analysis. Human detection rates and the forest track type were also correlated with higher human detection rates on primary tracks than secondary and tertiary tracks, hence forest track type was removed from the analysis. As expected, since the LGD presence variable was assigned in part due to the distance to pasture, LGD presence and distance to pasture were correlated. This relationship was further confirmed by including the distance to pasture in occupancy models for LGDs. Distance to pasture was, therefore, not used as an explanatory variable for the wildlife occupancy models as the low versus high LGD presence classification of each site was included. Although the detection rates of a species' predator, competitor, or prey could affect the occurrence of this species, these were not included as covariates in these models so as to avoid overparameterising the models since the number of sampled sites was relatively low. Instead, two-species interactions were modelled with single season, multispecies occupancy models (see below). Thus, there were three remaining variables included in the single species models: elevation, LGD presence (high/low), and human detection rates.

Single season, single species occupancy models were fitted using the package '*unmarked*' in R (Fiske and Chandler 2011; Fiske and Chandler 2015) with the site-level covariates of elevation, LGD presence, and human detection rates. In all models, the formula for detection was set to be constant as common variables affecting detectability were not applicable in this study (e.g. same camera trap models used, similar habitat types). The formula for occupancy was allowed to vary with the three covariates hypothesised to influence occupancy probability. Elevation and human detection rates were scaled within the model formulae. All possible combinations of these three covariates were fitted to build a set of eight candidate models (including the null and global model). Candidate models were first ranked by AICc and all models with delta AICc < 10 kept as a subset. Top-ranked models with delta AICc < 2 were considered to not vary significantly from each other (Burnham and Anderson 2002). To help determine the best model, variable weights from each of the models that ranked within ten AICc were calculated using the '*sw*' function in the R package '*MuMIn*' (Bartoń 2023). Variable weights help to inform of the relative influence of each covariate whereby values closer to 1 hold greater influence. The delta AICc, model weights, and variable weights were then examined together to select the best model (Table E.2; Table E.3). The fit of each of the best models was inspected with a Chi-squared test, whereby the model was deemed a poor fit if p < .05.

6.2.7.2 Habitat use: single season, two-species occupancy models

The LGD presence variable used in the single season, single species occupancy models is a binary variable that approximates the relative risk of LGDs being in the vicinity of a camera trap site. For a more direct comparison of the effect of LGDs on species' occupancy, single season, multispecies occupancy models were also run. In this analysis, all multispecies models were run as two-species models. Two-species occupancy models take into account whether a site is occupied by just species A, just species B, both species A and B, or neither species A nor B to infer whether there is co-occurrence between species (Mackenzie *et al.* 2004; Rota *et al.* 2016). Multispecies models generalise the single species occupancy model framework, and are commonly being used to assess interactions between multiple species and whole communities (Devarajan *et al.* 2020). To assess the relative magnitude of any effects of LGD occupancy on the occupancy of the five wild species, multispecies occupancy models were also fitted to assess the effects of apex predators (grey wolves and brown bears) on mesopredators (red fox) and prey (red deer and wild boar). Occupancy of the wild species was not compared to human occupancy in this manner as humans occupied all sites so there was no opportunity for a wild species to occupy a site without humans.

Single season, two-species occupancy models were fitted on the same detection history data as the single species occupancy models using the '*unmarked*' package in R (Fiske and Chandler 2011; Fiske and Chandler 2015). For all models, both the detection and occupancy formulae were held constant with no covariates in the models, both for simplicity and as a direct result of finding none of the studied variables affected wild species' occupancy in the single species models. Models were fitted specifying first independence (i.e. single species models) and then dependence between the two species in each paired dataset. The model outputs were examined and where large standard errors were produced around the estimates, the models were rerun as a penalised likelihood model (Clipp *et al.* 2021). This was achieved by adding a Bayes penalty term to the model. The optimal penalty value was determined from a range of possible values using K-fold cross validation (Clipp *et al.* 2021), specifically by using the function '*optimizePenalty*' within the '*unmarked*' package. Models with independence and dependence were then compared using AIC. Where independence was favoured (dependence model AIC > 2), no further investigation of interaction between the two species was conducted. Where dependence was favoured (independence model AIC > 2), or there was no difference between the models (AIC < 2), further investigation of the interaction between the two species was conducted. For the latter, the log odds estimate, 95% confidence intervals (CIs) and p-value of the two-species interaction were examined to assess the direction and statistical significance of the interaction. The interaction was deemed statistically significant where $p < .05$ and 95% CIs around the log odds estimate did not overlap zero. For each interaction, the conditional occupancies (occupancy probability of species A given species B is present or absent) and 95% CIs were estimated. Finally, an interaction term (η) was calculated as:

$$\psi AB / (\psi A * \psi B)$$

where ψA is the probability of occupancy of species A, ψB the probability of occupancy of species B, and ψAB the probability of occupancy of both species A and B. Values of $\eta < 1$ suggest avoidance between the two species whereas values of $\eta > 1$ suggest attraction between the two species. When η is 1 or close to 1, this suggests there is independence between the two species (Karanth *et al.* 2017).

6.2.7.3 Habitat use: detection rates

Occupancy models help determine how wildlife are distributed through the study area but cannot inform if sites are used more frequently than others. Thus, to test differences in the frequency of habitat use by wildlife, the monthly number of detections for each species were modelled as a function of elevation, LGD presence (high/low), and human activity (monthly detection rates per site). Models were constructed within a negative binomial generalised linear mixed model framework using the package '*glmmTMB*' in R (Brooks *et al.* 2017). Collinearity between explanatory variables was tested using the '*performance*' package in R (Lüdecke *et al.* 2021) and found to be low, hence all three explanatory variables were included in the models. Camera site was added as a random effect to account for repeated measures per site. The number of days each camera was active at each site each month was included as an offset in the model to account for any variation in survey effort across sites and months. Elevation and monthly human detection rate were scaled within the model formulae to allow for comparison across sites. Model residuals were checked using the '*DHARMa*' package in R (Hartig 2022). Due to the high number of zero values in the data, zero-inflation was tested for using the '*DHARMa*' package and models with and without a single zero-inflation parameter compared using AIC (Hartig 2022). None of the data displayed zero-inflation and adding a zero-inflation parameter did not significantly improve any of the model fits. Models were constructed as the full global models and no model simplification was performed. The statistical significance of variables in explaining the monthly counts of species at each site was determined according to a threshold of $p < .05$ and by examination of the effect sizes and 95% CIs. Confidence intervals were calculated using the '*confint*' function in R and explanatory variables deemed significant where the confidence intervals did not overlap zero.

6.2.7.4 Activity patterns

To determine if wildlife alter their activity in response to relative levels of LGD or human presence, activity patterns of each species were estimated and compared between sites with high and low LGD presence, as well as between sites with high and low human activity. High and low LGD presence was determined as above, whereas human activity was determined from the detection rates of humans at each camera site. Specifically, sites with human detection rates higher than or equal to the mean human detection rate (106 human detections per 100 camera trap days) were classified as high human activity sites (n = 7), and those below the mean classified as low human activity sites (n = 22) (Figure E. 2).

Activity patterns were estimated using the '*overlap*' package in R (Ridout and Linkie 2009) following a nonparametric kernel density approach whereby the time of detections was considered a random sample from a circular distribution (Ridout and Linkie 2009; Rowcliffe *et al.* 2014). Clock time was first converted to solar time to account for the differences in sunrise and sunset times throughout the year, which affect when animals are active (Nouvellet *et al.* 2012; Rowcliffe *et al.* 2014). Activity patterns were compared by calculating the coefficient of overlap (Δ) of two activity patterns; a value that ranges from 0 (no overlap i.e. completely different activity curves) to 1 (complete overlap, i.e. the same activity curve) (Ridout and Linkie 2009). The coefficient of overlap (Δ) was estimated using the Δ_1 estimator when the smaller of the two sample sizes was less than 50, and Δ_4 when both sample sizes were greater than 50 (Lashley *et al.* 2018; Meredith and Ridout 2021). For each coefficient of overlap, 95% CIs were estimated by generating 10,000 smoothed bootstrap samples using the '*bootCI*' function in the '*overlap*' package and extracting the adjusted 95% CIs (basic0) (Meredith and Ridout 2021). Activity patterns were compared statistically using the Watson's U^2 test in the R package '*circular*' (Agostinelli and Lund 2022), which tests the null hypothesis that the two underlying circular populations are identical. This test has previously been used for comparing activity patterns and has generally been identified as one of the tests offering the best power when comparing circular distributions (Landler *et al.* 2021). The threshold for rejecting the null hypothesis was $p < .05$.

6.2.7.5 Spatiotemporal responses: time-to-encounter & avoidance-attractance ratios

Several studies have used the time interval between successive detections of different species at camera trap sites to assess more fine-scale spatiotemporal interactions between species (Harmsen *et al.* 2009; Parsons *et al.* 2016; Karanth *et al.* 2017; Niedball *et al.* 2019). First, time intervals between LGD detections and the next focal species detections were measured (equivalent to T2 in Figure 6.8). Second, the distribution of T2 time intervals at each site was compared to a simulated distribution of T2 time intervals generated by randomly assigning times of detections of LGDs and the focal species to camera trap locations over 1000 simulations (Karanth *et al.* 2017). Larger median values of T2 than observed at random, whereby the random distribution represents independence between species, suggests avoidance of LGDs by the focal species, and vice versa.

Finally, the avoidance-attractance ratio (AAR) method laid out in Parsons *et al.* (2016) was used to compare the time interval between detections of the focal species with (T3) and without (T4) LGD detections between successive detections of the focal species (Figure 6.8). The ratio of T4 to T3 was calculated for each site using the average values of T4 and T3 per site. Values of T4/T3 equal to 1 suggest independence of the two species, whereby the detection of an LGD does not affect the average spacing between detections of the focal species. Where T4/T3 was >1 this suggests avoidance of LGDs by the focal species as there was a larger than average interval between detections of the focal species, and vice versa (Figure 6.8). It is also possible to compare the time interval between detections of the focal species before (T1) and after (T2) an LGD detection (Figure 6.8), but this was not conducted as T1 can be biased by avoidance or attractance by LGDs to the focal species (Parsons *et al.* 2016). Both T1 and T2 are shown in Figure 6.8 despite the ratio of T2/T1 not being calculated in order to show consistency between studies, and to demonstrate T2 for the time-to-encounter analysis above. Only sites where LGDs were detected (n = 13) could be included in these two analyses of spatiotemporal responses.

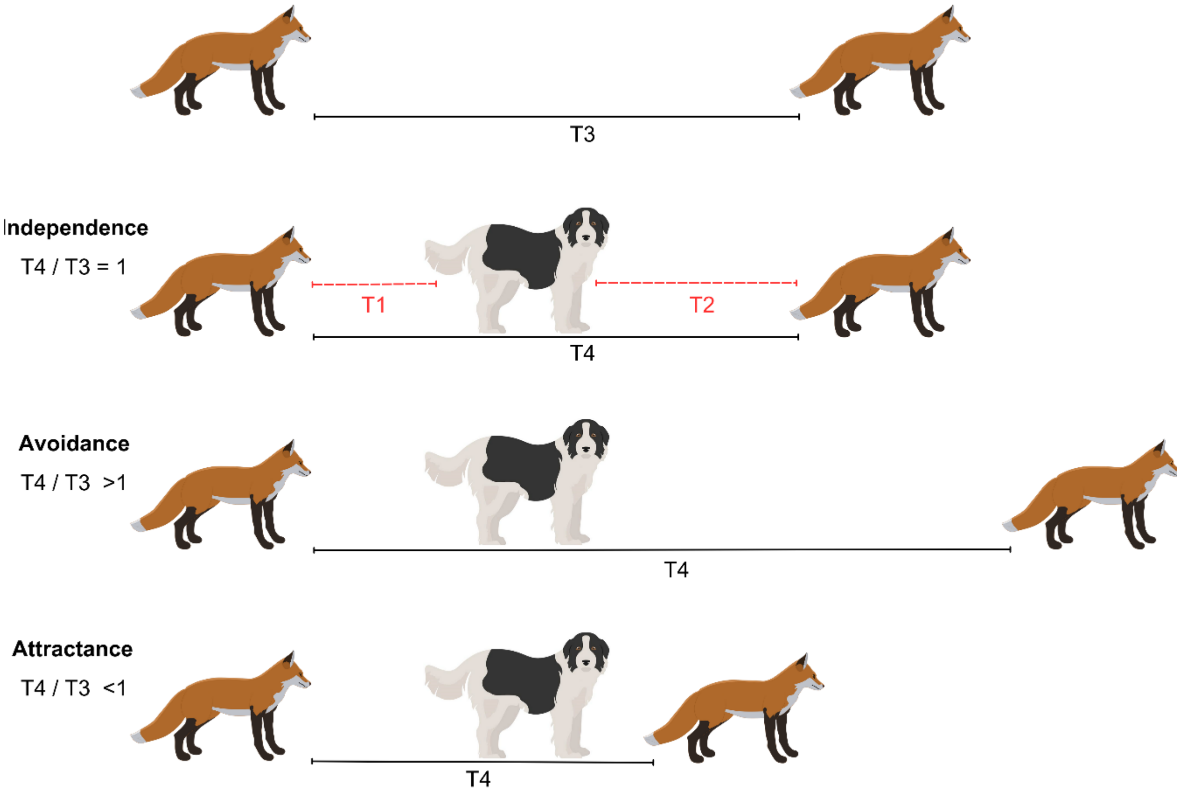

Figure 6.8. Avoidance-attractance ratios (AARs) schematic whereby T1 is the time between an LGD detection and previous detection of the species of interest, T2 is the time between an LGD detection and subsequent detection of the species of interest, T3 is the average time between successive species detections without an LGD detection in between, and T4 is the time between successive species detections with an LGD detection between them (it is the sum of T1 and T2).

6.3 Results

6.3.1 Data summary

All cameras were deployed between 15 July 2021 and 08 June 2022 but only data from the 2021 transhumance grazing season were used for the analyses presented in this study. Of the 30 sites chosen for inclusion, 29 had functioning cameras during the grazing season ranging from 15 July 2021 until 31 October 2021. These cameras were active for a total of 1940 trapping days. Individual cameras were active for on average 67 days (± 27 days SD) though this ranged from 11 to 109 days (Table 6.1). The time period over which each camera was deployed is shown in Figure E.3. Details about each camera site, including environmental, and LGD- and human-related, variables are provided in Table 6.1.

Table 6.1. Locations of cameras and site-level covariates.

Camera site	Latitude	Longitude	No. survey days	Elevation (m)	Road type	Distance to pasture (m)	No. LGD detections	LGD detection rate (/100 days)	LGD presence	Human detection rate (/100 days)	Forest cover (%)	Natural grasslands (%)	Moors & heathland (%)
AA10	45.62046	24.00188	103	943	tertiary	1420	0	0	low	3.9	100	0	0
AA11	45.60232	23.98999	104	862	primary	2700	0	0	low	310.6	100	0	0
AA12	45.57993	24.00484	89	1146	primary	730	1	1.2	low	466.3	100	0	0
AA13	45.55146	23.98795	29	1274	secondary	600	0	0	high	27.6	100	0	0
AA14	45.53323	23.99981	53	1574	primary	730	9	17	high	179.2	100	0	0
AB11	45.60223	24.05055	109	1153	tertiary	1050	0	0	low	8.3	100	0	0
AB12	45.57991	24.03086	41	1339	tertiary	750	1	2.4	low	14.6	100	0	0
AB13	45.56658	24.02157	89	1450	secondary	190	22	24.7	high	42.7	84	16	0
AC10	45.62202	24.0907	85	938	primary	1455	0	0	low	81.2	100	0	0
AC11	45.60496	24.06397	109	1102	secondary	970	0	0	low	80.7	100	0	0
AD10	45.62632	24.10149	41	1091	secondary	1140	0	0	low	65.9	100	0	0
R10	45.65015	23.65999	44	1514	tertiary	1750	0	0	low	27.3	100	0	0
R12	45.58643	23.66392	21	1513	secondary	1140	0	0	low	152.4	100	0	0
S13	45.56064	23.68992	11	1536	tertiary	1070	0	0	low	9.1	100	0	0
S14	45.53565	23.69739	53	1508	secondary	3100	0	0	low	62.3	100	0	0
T13	45.56261	23.71081	53	1608	tertiary	100	0	0	high	3.8	91	9	0
T14	45.53571	23.72667	61	1589	tertiary	2270	1	1.6	low	41.0	100	0	0

U13	45.56287	23.75092	61	1767	secondary	400	0	0	high	34.4	82	3	15
U14	45.54266	23.76402	61	1566	tertiary	1240	0	0	low	4.9	100	0	0
V13	45.55326	23.79208	61	1776	tertiary	350	10	16.4	high	67.2	69	31	0
W13	45.56438	23.84127	81	1413	tertiary	730	0	0	low	7.4	100	0	0
X13	45.55556	23.87958	70	1451	primary	1000	9	12.9	high	475.7	100	0	0
Y11	45.6194	23.91867	72	1646	secondary	100	47	65.3	high	311.1	100	0	0
Y12	45.57824	23.93705	81	1376	primary	2300	3	3.7	low	311.1	100	0	0
Y13	45.54553	23.93689	82	1620	secondary	1130	6	7.3	low	76.8	100	0	0
Z10	45.62854	23.96259	91	1480	tertiary	3090	0	0	low	24.2	100	0	0
Z11	45.60494	23.97219	104	1081	secondary	3550	0	0	low	60.6	100	0	0
Z12	45.59375	23.95013	35	1146	secondary	3330	0	0	low	37.1	100	0	0
Z13	45.54187	23.95336	46	1608	tertiary	0	46	100	high	95.7	65	32	3

In total, 8692 independent observations of wildlife, domestic animals, and humans were captured across the entire camera trapping survey. When constraining the data to only the grazing season, there were 4198 independent observations, 2272 of which were humans, 1394 were identifiable as wild species, and 155 as LGDs. Sixteen distinct species or taxa (14 species plus Martes spp. and Aves groupings) were identified in the photos. The five most commonly detected wild species were brown bear, grey wolf, red fox, red deer, and wild boar, hence, these were chosen for the analyses. The number of detections of each species included in the analysis are provided in Table 6.2. A full breakdown of all species detections is provided in Table E.4.

Table 6.2. Number of independent observations of the species included in the analyses across 29 sites during the 2021 transhumance grazing season.

Species	**Independent observations (IO)**	**IOs (LGD presence - high)**	**IOs (LGD presence - low)**	**IOs (Human presence - high)**	**IOs (Human presence - low)**	**Site x week periods - present**	**Site x week periods - absent**
LGD	155	143	12	69	86	34	224
Brown bear	163	9	154	14	149	44	214
Grey wolf	91	36	55	29	62	67	191
Red fox	447	169	278	248	199	127	131
Red deer	378	49	329	36	342	125	133
Wild boar	72	5	67	4	68	39	219

6.3.2 Spatial and temporal responses of wildlife to LGD presence

6.3.2.1 Habitat use: single season, single species occupancy models

Livestock guarding dogs made use of just over a third of the sites monitored with an average occupancy probability of 0.36 (0.34 – 0.52 95% CI) (Table 6.3). Occupancy probability of LGDs decreased significantly as the distance from pasture increased (beta = -3.48 ± 1.68, 95% CI: -6.78 – -0.18, $p = 0.04$, $p < .05$) and increased as human activity increased (beta = -3.48 ± 1.68, 95% CI: -6.78 – -0.18, $p = 0.04$, $p < .05$) (Table 6.4; Figure 6.9). Four of the focal wild species were widely distributed across the study area with average occupancy probabilities of 0.79, 0.89, 0.99, and 0.90 for brown bear, grey wolf, red fox, and red deer, respectively (Table 6.3). In comparison, wild boar were less widely distributed occupying only approximately 50% of the sites monitored (Table 6.3).

None of the tested variables explained red fox or wild boar occupancy probabilities (Table E.2; Table 6.4). The best model for grey wolves and brown bears included elevation, and elevation and human activity levels, respectively (Table E.2; Table 6.4). However, none of these variables had a statistically significant effect on the occupancy probabilities for either of these species (Table 6.4; Figure 6.9). The best model for red deer included LGD presence but produced large standard errors around the estimate. This was due to a boundary estimate issue and so the model was run again as a penalised likelihood model (Clipp *et al.* 2021). This penalised model suggested that red deer occupancy probability significantly increased at low LGD sites compared to high LGD sites (beta = 4.12 ± 0.82, 95% CI: 2.52 – 5.72, p < .0001) (Table 6.4; Figure 6.9).

Table 6.3. Occupancy and detectability estimates for livestock guarding dogs (LGDs) and the five focal wild species computed from single season, single species occupancy models. The occupancy estimates and 95% CIs were estimated from the best model using empirical Bayes methods after model selection (Fiske and Chandler 2015).

Species	**Naïve occupancy (ψ)**	**Null model occupancy probability (ψ)**	**Null model detection probability (*p*)**	**Best model averaged occupancy probability (ψ) [95% CI]**
LGD	0.34	0.37	0.36	0.36 [0.34 – 0.52]
Brown bear	0.69	0.77	0.32	0.79 [0.72 – 0.86]
Grey wolf	0.79	0.90	0.20	0.89 [0.83 – 0.97]
Red fox	0.93	0.99	0.50	0.99 [0.93 – 1.00]
Red deer	0.86	0.90	0.52	0.90 [0.90 – 0.93]
Wild boar	0.45	0.49	0.30	0.49 [0.44 – 0.79]

Table 6.4. Model outputs from single season, single species occupancy models fitted to determine the effect of habitat and anthropogenic variables on occupancy of livestock guarding dogs (LGDs), brown bears, grey wolves, red foxes, red deer, and wild boars. Only the outputs from the models deemed to be the best models during model selection are given here. Statistically significant variables are highlighted in bold.

Species	**Variable**	**Log odds**	**Standard error**	**z**	**Lower 95% CI**	**Upper 95% CI**	**p value**
LGD	Intercept	-1.29	0.78	-1.64	-2.82	0.25	0.10
	Distance to pasture	-3.48	1.68	-2.06	-6.78	-0.18	**0.04**
	Human activity	3.52	1.69	2.08	0.21	6.83	**0.04**
Brown bear	Intercept	4.91	3.13	1.57	-1.22	11.04	0.12
	Elevation	-5.50	3.39	-1.62	-12.15	1.15	0.11
	Human activity	-1.81	1.24	-1.46	-4.25	0.62	0.14
Grey wolf	Intercept	4.61	3.07	1.50	-1.40	10.62	0.13
	Elevation	2.98	2.06	1.45	-1.05	7.01	0.15
Red fox	Intercept	4.28	3.41	1.26	-2.39	10.96	0.21
Red deer	Intercept	0.80	1.06	0.76	-1.27	2.87	0.45
	LGD presence [low]	4.12	0.82	5.05	2.52	5.72	**<0.001**
Wild boar	Intercept	-0.85	0.21	-4.10	-0.82	0.77	**<0.001**

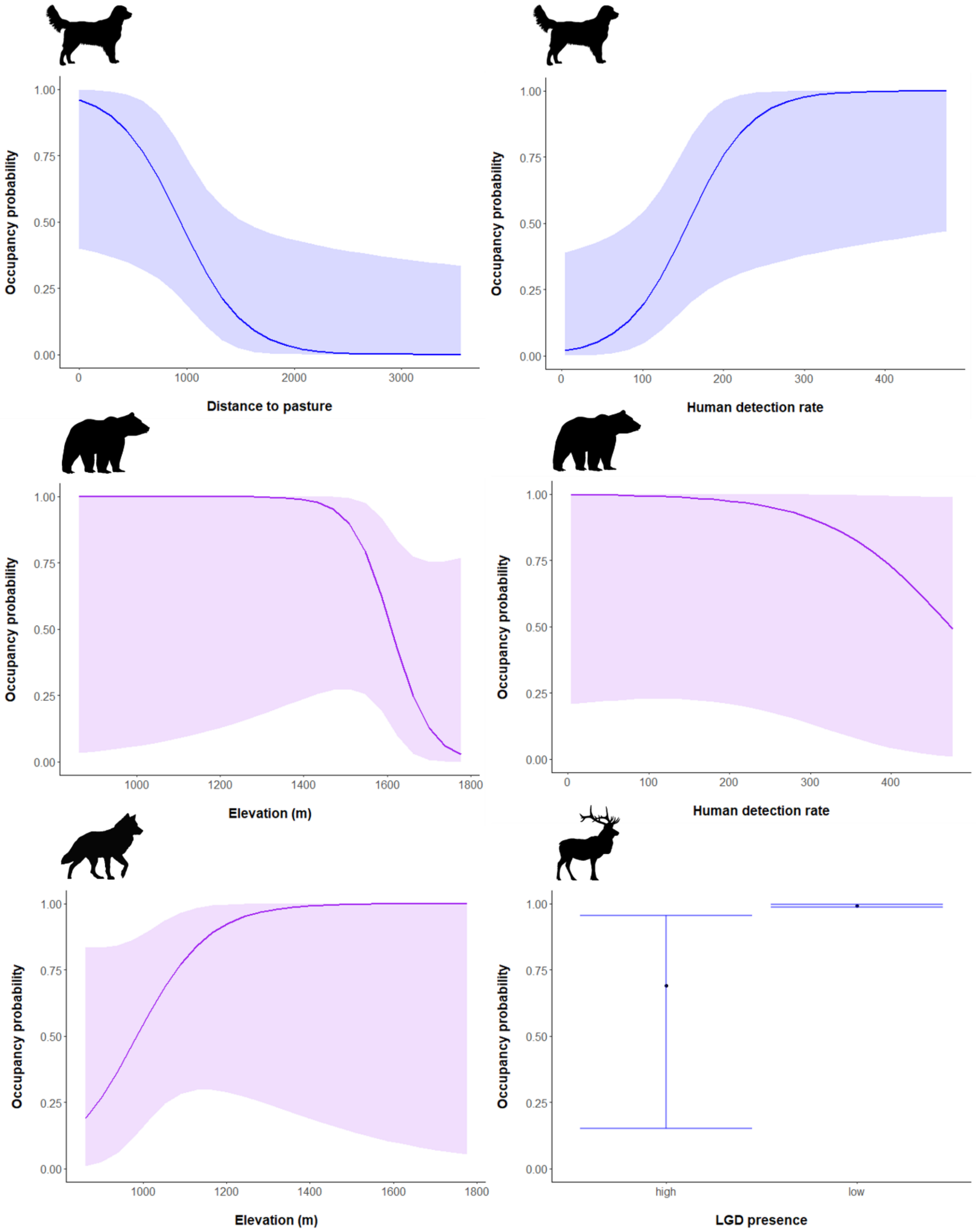

Figure 6.9. Estimated effect on occupancy of the variables included in the top-ranking models for livestock guarding dogs (top), brown bears (middle), grey wolves (bottom left) and red deer (bottom right). Effects in blue are statistically significant, those in purple are not.

6.3.2.2 Habitat use: single season, two-species occupancy models

Comparing the AIC and weights of models for species occupancy with and without dependence on LGDs suggested that dependence between LGDs and the focal species was favoured for brown bears, grey wolves, and red deer, but that there was little difference between the two states for red foxes and wild boars. Comparing the AIC for the other species pairings of 'prey: apex predator', 'mesopredator: apex predator', and 'apex predator: apex predator' suggested that independence was favoured for 'brown bear: grey wolf' and 'wild boar: grey wolf' interactions. Dependence was favoured for 'red deer: grey wolf', but for the remaining species pairings there was no difference in model AICs when species were dependent versus independent of each other.

Grey wolves appeared to be attracted to LGDs (η = 1.12) and grey wolf occupancy significantly increased with LGD occupancy (beta = 2.38 ± 0.80, 95% CI: 0.82 – 3.95, $p < .01$) (Table 6.5; Figure 6.10). Where LGDs were absent, conditional grey wolf occupancy was 0.82 (95% CI: 0.41 – 0.97) compared to 0.98 (95% CI: 0.95 – 0.99) where LGDs were present (Figure 6.11). There was a trend for both brown bear and red deer occupancy to decrease where LGDs were present, with brown bear conditional occupancy reducing by almost half when LGDs were present (Figure 6.11). Interaction terms for brown bear and red deer also suggested avoidance of LGDs (bear η = 0.68, red deer η = 0.88), but the effects were not statistically significant (Table 6.5; Figure 6.10). Red deer and brown bears occurred together more frequently than by chance (beta = 1.07 ± 0.21, 95% CI: 0.65 – 1.48, $p < .01$), but there was no interaction between red deer and grey wolf occupancy (Table 6.5; Figure 6.10). Red fox occupancy was not affected by LGD presence (Table 6.5; Figure 6.10), and the interaction term suggested independence of the two species (η = 0.97). In contrast, red foxes occurred together more frequently than by chance with both brown bears (beta = 1.70 ± 0.41, 95% CI: 0.90 – 2.50, $p < .01$) and grey wolves (beta = 1.98 ± 0.59, 95% CI: 0.82 – 3.15, $p < .01$) (Table 6.5; Figure 6.10). Wild boar occupancy decreased by almost 50% where LGDs were present (Figure 6.11) and the interaction term suggested avoidance of LGDs by wild boars (η = 0.63), but the interaction was not statistically significant (Table 6.5; Figure 6.10). Wild boar occupancy was also not determined by brown bear or grey wolf occupancy (Table 6.5; Figure 6.10).

Table 6.5. Model outputs from single season, two-species occupancy models assessing whether the occurrence of a species is dependent on the occurrence of another species. Where large standard errors around the log odds estimates were produced, the models were rerun as a penalised likelihood model and the optimal value for the penalty used is given. The interaction term (η) between each species pairing is also provided. Spatial partitioning between species is suggested when η < 1 and vice versa. When η is close to or equal to 1, this suggests the two species occur independently of each other. Statistically significant interactions are highlighted in bold.

Species interaction	**Log odds**	**Standard error**	**z**	**Lower 95% CI**	**Upper 95% CI**	**p value**	**penalty**	**η**
Brown bear: LGD	-2.30	1.41	-1.64	-5.06	0.46	0.10	NA	0.68
Grey wolf: LGD	**2.38**	**0.80**	**2.98**	**0.82**	**3.95**	**< .01**	**0.03**	**1.12**
Brown bear: Grey wolf	NA	NA	NA	NA	NA	NA	NA	NA
Red fox: LGD	-1.39	1.18	-1.19	-3.70	0.91	0.24	0.03	0.97
Red fox: Brown bear	**1.70**	**0.41**	**4.15**	**0.90**	**2.50**	**< .01**	**0.25**	**1.03**
Red fox: Grey wolf	**1.98**	**0.59**	**3.34**	**0.82**	**3.15**	**< .01**	**0.13**	**1.02**
Red deer: LGD	-2.08	1.13	-1.84	-4.31	0.14	0.07	0.03	0.88
Red deer: Brown bear	**1.07**	**0.21**	**5.03**	**0.65**	**1.48**	**< .01**	**2.00**	**1.05**
Red deer: Grey wolf	-0.68	1.26	-0.54	-3.14	1.79	0.59	0.03	0.99
Wild boar: LGD	-1.23	0.90	-1.36	-3.00	0.54	0.17	NA	0.63
Wild boar: Brown bear	0.90	1.18	0.76	-1.42	3.21	0.45	NA	1.10
Wild boar: Grey wolf	NA	NA	NA	NA	NA	NA	NA	NA

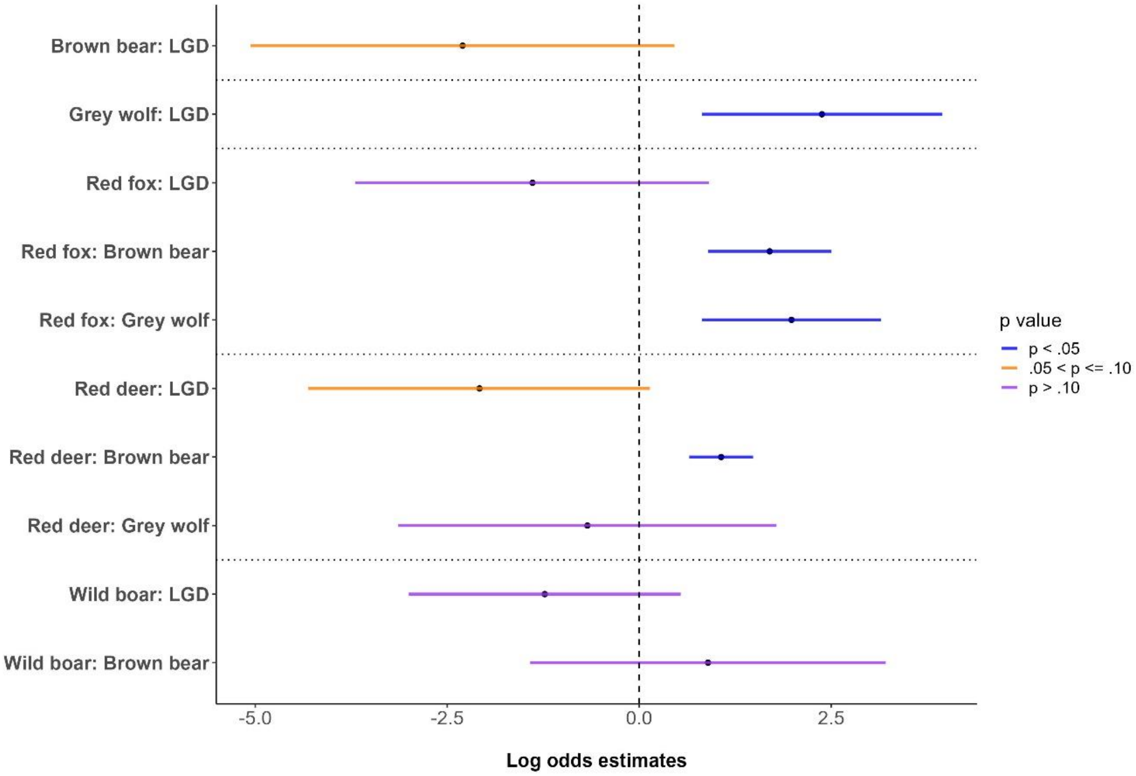

Figure 6.10. Log odds estimates and 95% CIs of occupancies of potentially interacting species pairs. Positive log odds estimates suggest species occur together and vice versa. The probability of this interaction occurring by chance is denoted by the p value from single season, two-species occupancy models. In addition, the interaction is statistically significant when 95% CIs do not incorporate zero (black, dashed line). Grey wolf interactions with brown bear, and wild boar interactions with grey wolf are not shown as the models with independence were favoured over dependence during model selection suggesting no interactions between the two species.

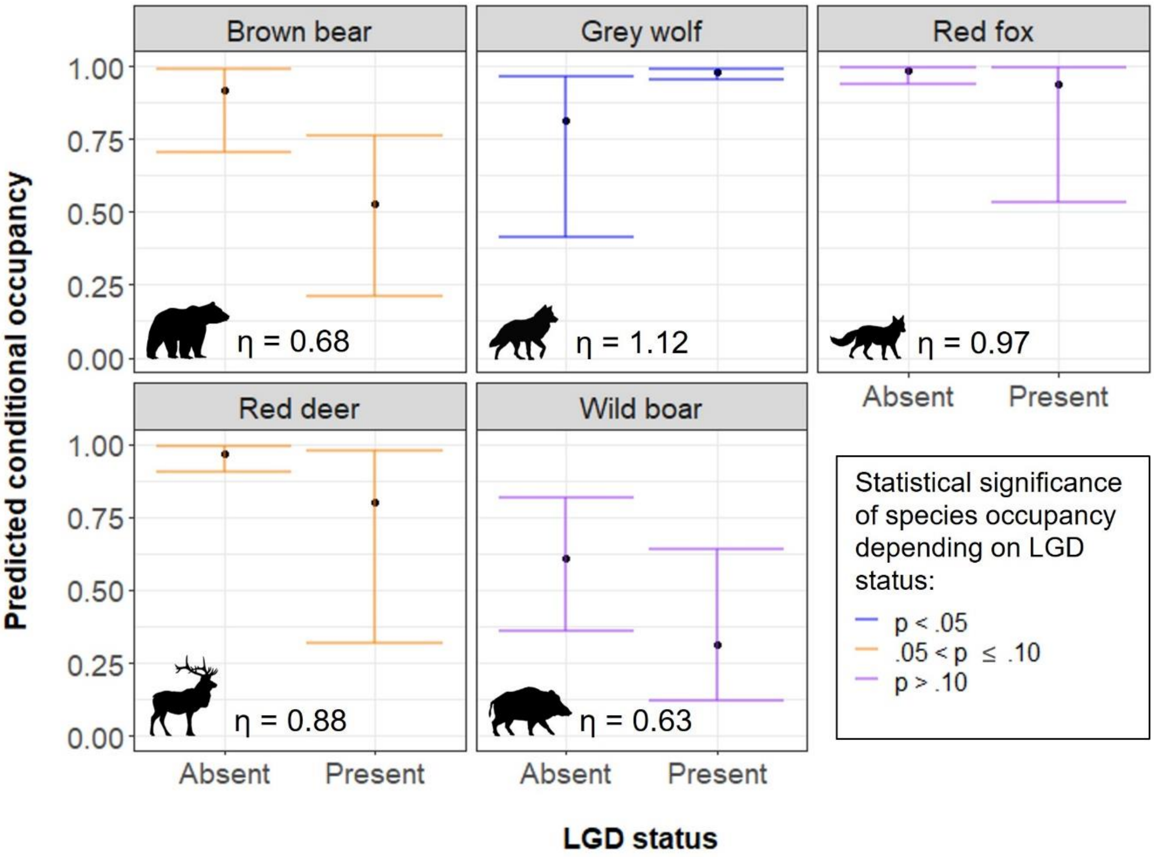

Figure 6.11. Predicted conditional occupancy and 95% CIs of the five focal species (left-right: brown bear, grey wolf, red fox, red deer, wild boar) when livestock guarding dogs (LGDs) were present or absent at sites. These conditional occupancies are estimated from single season, two-species occupancy models. The statistical significance of the dependence of each species' occupancy on LGD occupancy is shown by the different colours (blue – p <.05, orange – p > .05 but ≤ .10, and purple – p > .10). The interaction term (η) between LGDs and each species is also provided. Avoidance of LGDs is suggested when η < 1, whereas attractance is suggested when η > 1. When η is close to or equal to 1, this suggests independence of the two species.

6.3.2.3 *Habitat use: detection rates*

Grey wolf and wild boar monthly detection rates were not influenced by elevation, human activity levels, or the presence of LGDs as the null models ranked higher than the global models (Table 6.6). For brown bear, red fox, and red deer, the global models all ranked higher than the null models and were a better fit to the data. Examining the model residuals for the brown bear model highlighted an outlier in the data where there were 56 independent observations of brown bears at one site one month (the next highest being 10 detections). Models were run including and excluding this outlier, with little difference in overall model predictions (Figure E.4). Model residual comparison suggested that the model including the outlier was a better fit, so it is the results of this model that are presented. The explanatory power of the global models for brown bear, red fox, and red deer were 0.32, 0.28, and 0.39, with the parts relating to the fixed effects alone being 0.17, 0.20, and

0.10, respectively. At higher elevations there was a reduction in brown bear detection rates (beta = -0.60 ± 0.27, 95% CI: -1.13 – -0.08, p = 0.03, p < .05) and an increase in red fox detection rates (beta = 0.50 ± 0.20, 95% CI: 0.11 – 0.89, p = 0.01, p < .05) (Figure 6.12). Red fox detection rates also increased as human detection rates increased (beta = 0.62 ± 0.17, 95% CI: 0.29 – 0.95, p < .001) (Figure 6.12). Red deer detection rates were slightly lower in areas of higher human activity (beta = -0.35 ± 0.19, 95% CI: -0.72 – 0.03, p = 0.07) and higher in areas of low LGD presence (beta = 1.01 ± 0.61, 95% CI: -0.19 – 2.22, p = 0.1), but the effects were not statistically significant (Table 6.6; Figure 6.12).

Table 6.6. Outputs from negative binomial generalised linear mixed models fitted to determine the effect of elevation, human activity, and LGD presence on monthly detection rates of grey wolves, brown bears, red foxes, red deer, and wild boar.

Species	**Best model**	**Variables**	**beta**	**Standard error**	**z**	**P value**	**Lower 95% CI**	**Upper 95% CI**
Grey wolf	Null	Intercept	-3.49	0.28	-12.43	<.001	-4.23	-2.83
Brown bear	Global	Intercept	-3.89	0.55	-7.04	<.001	-4.98	-2.81
	Global	**Elevation**	**-0.60**	**0.27**	**-2.24**	**0.03**	**-1.13**	**-0.08**
	Global	Human activity	-0.27	0.23	-1.16	0.25	-0.72	0.19
	Global	LGD presence [low]	0.86	0.64	1.34	0.18	-0.40	2.11
Red fox	Global	Intercept	-1.84	0.33	-5.58	<.001	-2.49	-1.19
	Global	**Elevation**	**0.50**	**0.20**	**2.53**	**0.01**	**0.11**	**0.89**
	Global	**Human activity**	**0.62**	**0.17**	**3.64**	**<.001**	**0.29**	**0.95**
	Global	LGD presence [low]	-0.05	0.40	-0.12	0.90	-0.84	0.74
Red deer	Global	Intercept	-3.02	0.53	-5.72	<.001	-4.05	-1.98
	Global	Elevation	-0.06	0.28	-0.24	0.81	-0.60	0.47
	Global	Human activity	-0.35	0.19	-1.82	0.07	-0.72	0.03
	Global	LGD presence [low]	1.01	0.61	1.65	0.10	-0.19	2.22
Wild boar	Null	Intercept	-4.51	0.49	-9.22	< .001	-5.46	-3.55

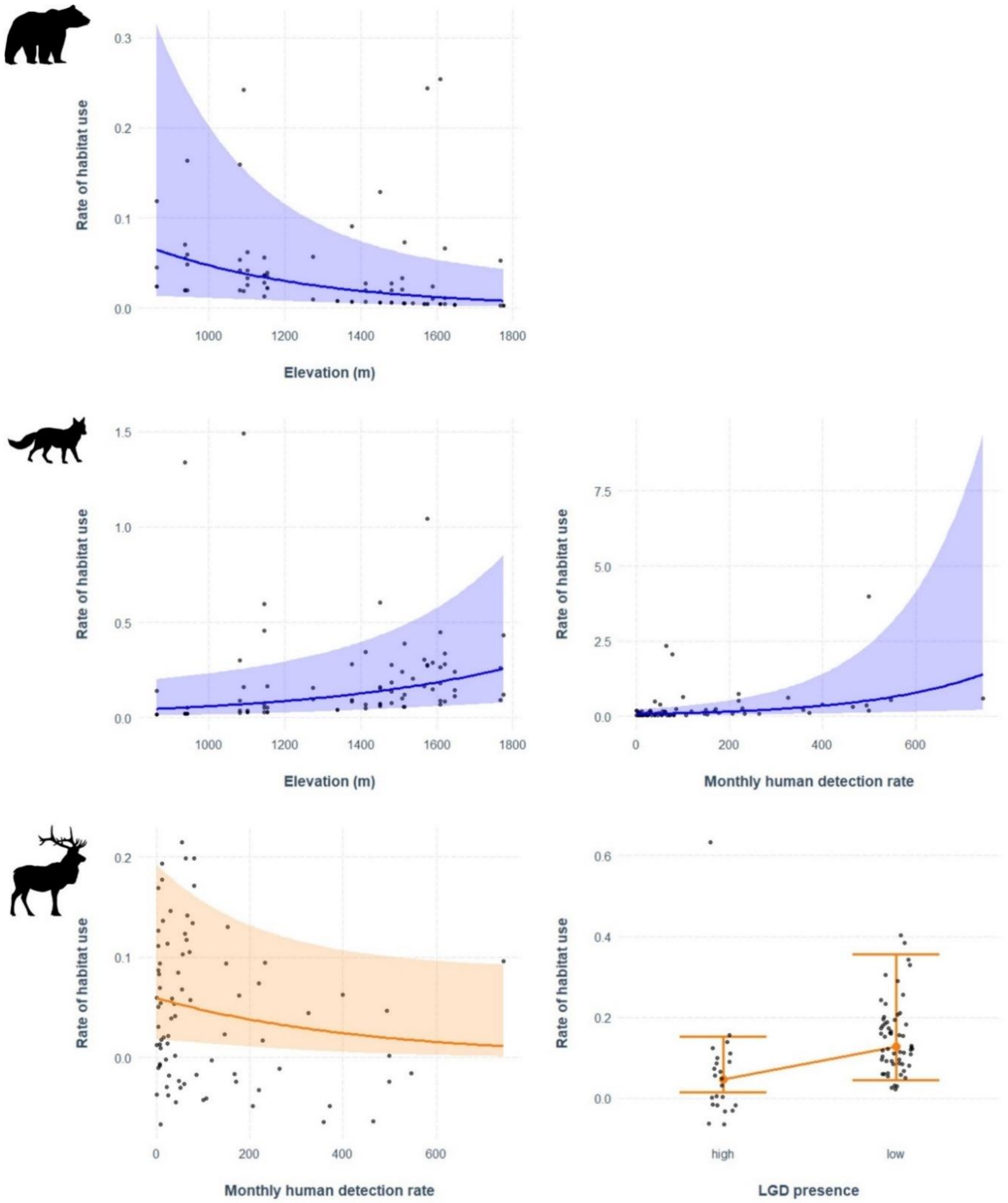

Figure 6.12. Partial residual plots showing model outputs from negative binomial generalised linear mixed models fitted to determine the effect of elevation, human activity, and LGD presence on monthly detection rates of wild species. Only variables determined to affect monthly detection rates are shown, with those in blue having a statistically significant effect ($p < .05$) and those in orange showing a trend towards statistical significance ($.05 \leq p \leq .10$). Top – brown bear, middle – red fox, bottom – red deer.

6.3.2.4 Activity patterns

Comparisons of LGD activity patterns to other species showed that LGDs were predominantly active at the same time as sheep (Δ = 0.90; 95% CIs: 0.81 – 0.98; $p > .10$) between the hours of 06:00 and 22:00 with a dip in activity just after noon (Figure 6.13). Activity patterns of grey wolves, brown bears, red foxes, red deer, and wild boar were all significantly different from LGDs, with low overlap values for shared periods of activity (Figure 6.13). There were no differences in grey wolf, brown bear, or red fox activity patterns between low and high LGD sites (Figure 6.14). However, activity patterns of red deer were significantly different between low and high LGD sites (Δ = 0.80; 95% CIs: 0.68 – 0.90; $.01 < p < .05$). At the low LGD sites, red deer activity remained relatively constant throughout the day with a peak between 18:00 and midnight, whereas at high LGD sites there was a marked decrease in diurnal activity coinciding with when LGDs are active (Figure 6.14). Wild boar activity patterns were not compared between low and high LGD sites due to a small sample at high LGD sites ($n = 5$). Comparing animal activity patterns to those of humans showed that LGDs and the five focal species all had significantly different activity patterns to humans (Figure 6.15) and none of grey wolf, brown bear, red fox, or red deer had significantly different activity patterns at sites with high human activity compared to low human activity (Figure 6.16). Wild boar activity patterns were not compared between low and high human activity sites due to a small sample at high human activity sites ($n = 4$).

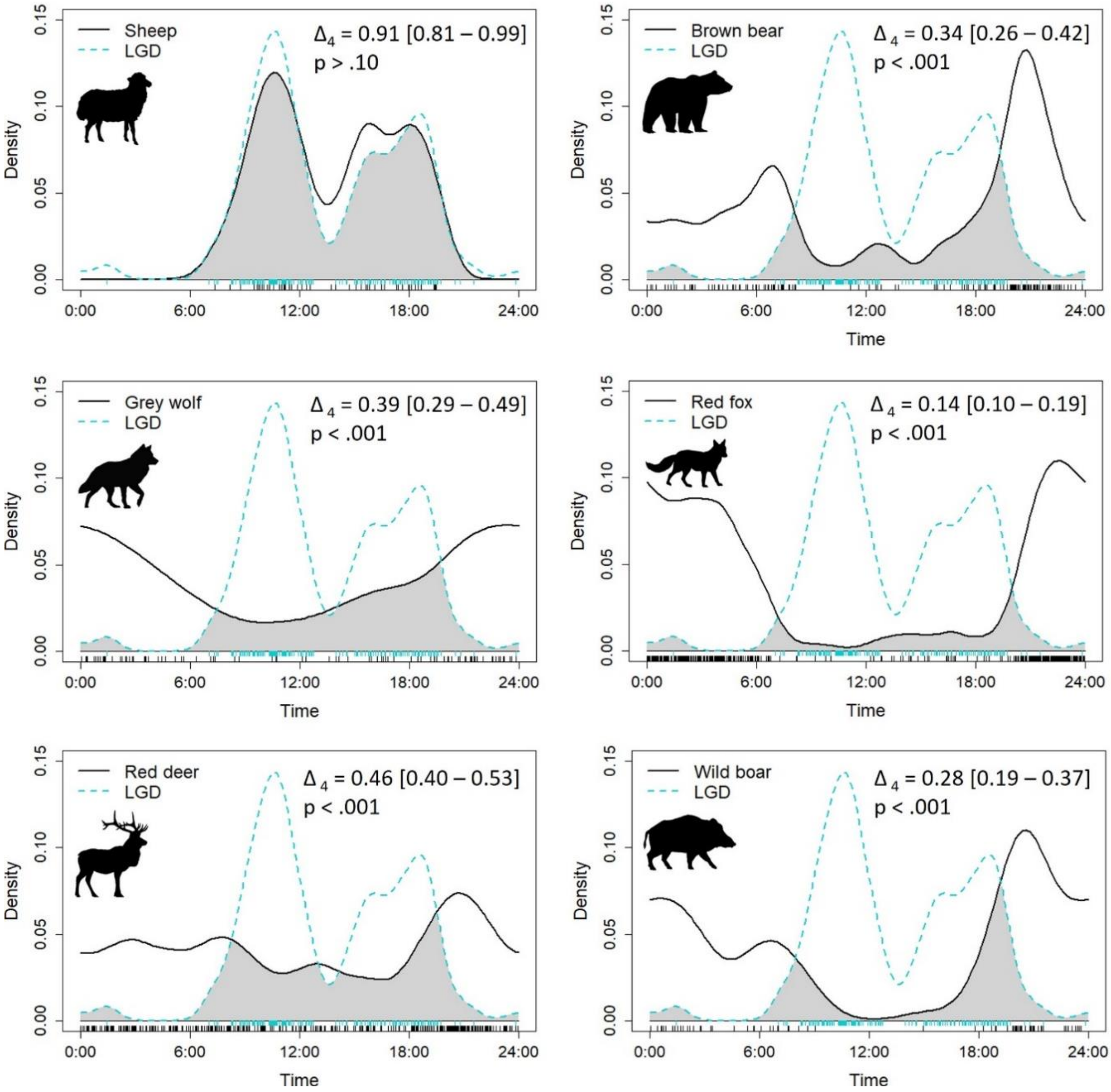

Figure 6.13. Activity patterns estimated from the times of independent detections. Each graph depicts the activity patterns of LGDs (blue dashed line) compared to sheep, brown bears, grey wolves, red foxes, red deer, and wild boars (black solid lines). The area of overlap is shaded in grey. The estimate of the overlap value is given alongside bootstrapped confidence intervals and the probability that the two distributions are the same. This p-value is calculated from a Watson's U^2 test for circular data.

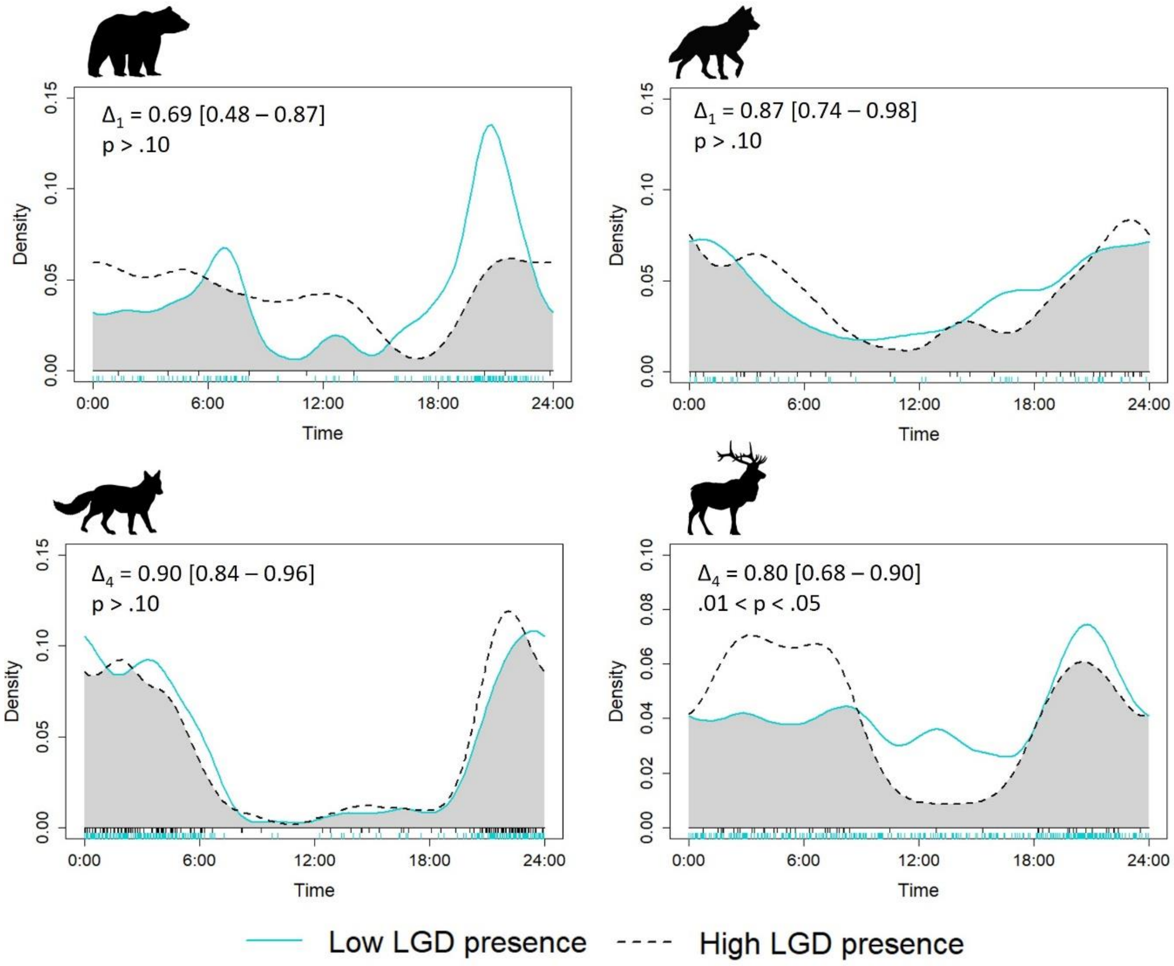

Figure 6.14. Activity patterns estimated from the times of independent detections. Each graph depicts the activity patterns of a single species at low (blue solid line) and high (black dashed line) LGD sites. The area of overlap is shaded in grey. The estimate of the overlap value is given alongside bootstrapped confidence intervals and the probability that the two distributions are the same. This p-value is calculated from a Watson's U^2 test for circular data. Individual species graphs are brown bear (top left), grey wolf (top right), red fox (bottom left), and red deer (bottom right).

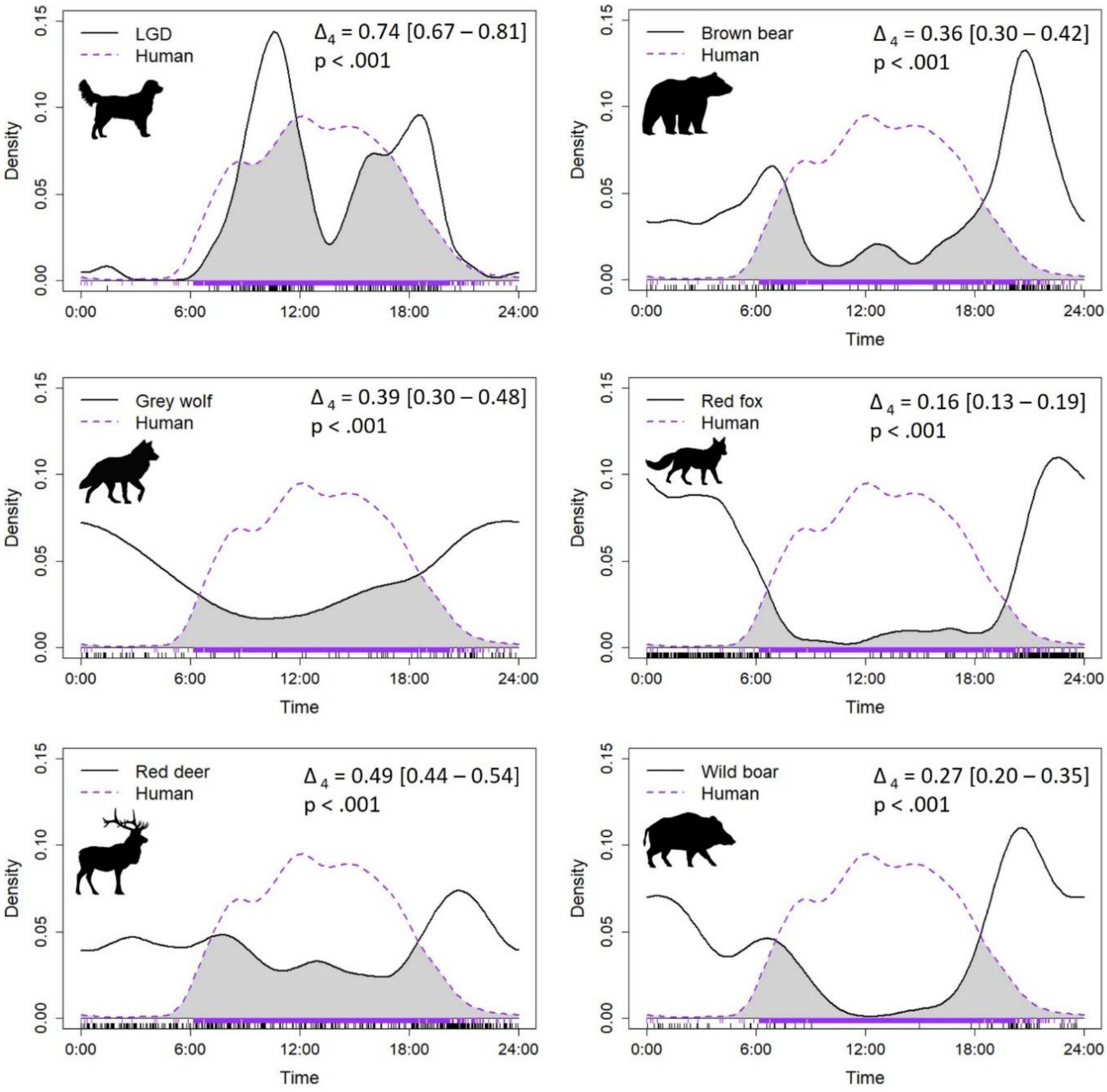

Figure 6.15. Activity patterns estimated from the times of independent detections. Each graph depicts the activity patterns of humans (purple dashed line) compared to LGDs, brown bears, grey wolves, red foxes, red deer, and wild boars (black solid lines). The area of overlap is shaded in grey. The estimate of the overlap value is given alongside bootstrapped confidence intervals and the probability that the two distributions are the same. This p-value is calculated from a Watson's U^2 *test for circular data.*

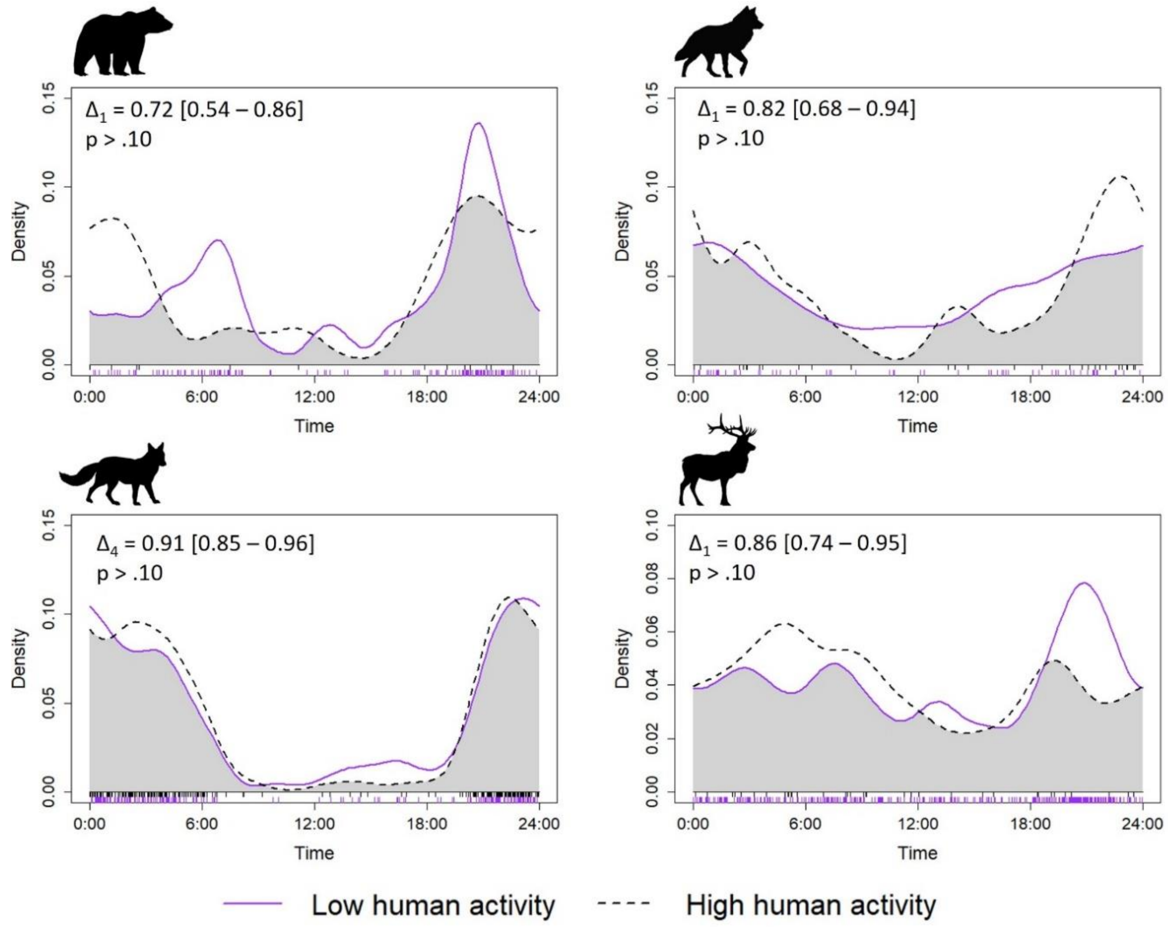

Figure 6.16. Activity patterns estimated from the times of independent detections. Each graph depicts the activity patterns of a single species at low (purple solid line) and high (black dashed line) human activity sites. The area of overlap is shaded in grey. The estimate of the overlap value is given alongside bootstrapped confidence intervals and the probability that the two distributions are the same. This p-value is calculated from a Watson's U^2 test for circular data. Individual species graphs are brown bear (top left), grey wolf (top right), red fox (bottom left), and red deer (bottom right).

6.3.2.5 Spatiotemporal responses: time-to-encounter & avoidance-attractance ratios

These analyses were attempted, but ultimately the sample sizes of T2 and T4 were too small at each site for all species. This was mainly due to the pattern of detections meaning there were too few instances of successive species detections being intersected by LGDs at each site. Although sites may have had plenty of detections of LGDs and focal species, these detections were largely separated in time with detections of LGDs clustered in time with no other species detections, which reduced the sample sizes of both T2 and T4 to one or two occasions at most sites.

6.4 Discussion

This study is the first to assess how the seasonal presence of livestock guarding dogs in the Romanian Carpathian Mountains affects the space use and activity patterns of co-occurring wildlife and is one of few studies to assess both the spatial and temporal dimension of wildlife responses to LGDs in the same study. Spatial and temporal responses to LGDs by grey wolves, brown bears, red foxes, red deer, and wild boars were assessed in relation to the effects of other habitat variables and anthropogenic activity. A full dissection of all of the results found (e.g. effects of elevation and human activity on species distribution) is beyond the scope of the study but these factors are discussed in relation to the findings on how LGDs influence wildlife. Overall, there was limited evidence for any investigated variables affecting wild species occurrence and timing of activity, though there was an indication that grey wolves might be attracted to LGD-occupied areas, whereas red deer might avoid LGDs in space and time.

Wolf attraction to LGDs was suggested by two-species occupancy models but not by single species occupancy models or modelling of the detection rates of wolves at each site in relation to LGD presence. As such, it is difficult to determine how conclusive this finding is and it contradicts previous studies that have found reductions in grey wolf activity related to the presence of LGDs (Gehring *et al.* 2011b; Kinka *et al.* 2021). However, some studies have suggested LGDs to be an attractant to other predators, including brown hyaenas (*Hyaena brunnea*) (Spencer *et al.* 2020) and coyotes (Kinka *et al.* 2021) and there are several reasons why wolves might associate with LGDs. As two closely-related canid species, grey wolves might be attracted to LGDs for play or mating opportunities (Landry *et al.* 2020) as hybridisation between wolves and dogs is not uncommon (Salvatori *et al.* 2020b). Wolves could also see LGDs as another potential prey species. Wolf predation of LGDs has previously been reported as a serious issue in Romania (Mertens and Schneider 2005) and elsewhere (Bangs *et al.* 2005; Landry *et al.* 2020), and dogs do form part of the wolf diet in Romania (Sin *et al.* 2019). The LGDs in this study region have been shown to remain largely with the sheep (current study and Chapter 5). Shepherds in the region report frequent interactions with wolves, including losses of livestock (Chapter 3, per comms.). A previous study has also found that grey wolves are attracted to pastures in Romania (Cristescu *et al.* 2019), hence it is most likely that wolves are attracted to areas with sheep flocks where there also happen to be LGDs.

In contrast to wolves, several analyses in this study suggest that red deer might avoid LGDs in space and time. Though it was expected that red deer would respond more strongly to predator presence (Creel *et al.* 2005; Hernández and Laundré 2005; van Beeck Calkoen *et al.* 2021) or human activity (Sibbald *et al.* 2011; Coppes *et al.* 2017; Müller *et al.* 2017), this was not found to be the case as the sizes of the effect of LGDs on red deer detection rates and occupancy were approximately three times those of humans on red deer detection rates and of wolves on red deer occupancy. It is possible that red deer avoid LGDs as previous studies have found spatial and temporal avoidance of LGDs by red deer in the USA (VerCauteren *et al.* 2012) and other large herbivores including white-tailed deer (*Odocoileus virginianus*) in the USA (VerCauteren *et al.* 2008; Gehring *et al.* 2011b; Kinka *et al.* 2021), and sambar deer (*Rusa unicolor*) in Australia (van Bommel and Johnson 2016). However, only two shepherds in the general study region reported that their LGDs chase red deer (Chapter 3) and no evidence of red deer remains were found in the scats of nearby LGDs (Chapter 4), making it unlikely that red deer would perceive LGDs as an apex predator in the environment. Instead, red deer might avoid areas with LGDs as these areas were near open pastures whereas red deer prefer more forest cover, especially in high-predation risk areas (Jayakody *et al.* 2008; Müller *et al.* 2017). If grey wolves are attracted to LGD- and sheep-occupied areas, then red deer could be avoiding these areas due to also avoiding wolves, one of their main predators in the Carpathian Mountains (Nowak *et al.* 2005; Sin *et al.* 2019). However, there was no relationship between red deer and wolf co-occurrence in the two-species occupancy models, and this would not explain the reduction in diurnal activity as wolf activity patterns were predominantly nocturnal and were not different between high and low LGD sites. As with wolves, red deer could also have been responding to the presence of sheep and shepherds as well as LGDs. Although there were no statistically significant effects of human activity on red deer in this study, previous studies have shown that red deer avoid humans, sometimes on a much finer scale than was investigated here (Sibbald *et al.* 2011). As both sheep and red deer are grazers, red deer could avoid sheep in space and time to limit competition during the summer months; a phenomenon not well-documented but recently demonstrated in Germany (Weiss *et al.* 2022).

If the responses by wolves and red deer are caused by the presence of LGDs rather than sheep, then there could be ecological, conservation, and management implications. For wolves, if LGDs act as an attractant for wildlife, this could exacerbate human-wildlife conflicts if predatory species are observed more frequently in the proximity of livestock, or if LGDs are preyed upon; either of which could further reduce farmer tolerance of predators (Bangs *et al.* 2005; Mertens and Schneider 2005). If LGDs are displacing red deer from grazing habitat, this could have knock-on effects on red deer foraging (Hernández and Laundré 2005) and reproduction (Creel *et al.* 2007; Creel *et al.* 2009), as well as potentially causing human-human conflicts between shepherds and game managers who believe that LGDs detrimentally affect game species (Ivaşcu and Rakosy 2017). There was also an unexpected co-occurrence of red deer with brown bears, a predator of red deer that red deer were observed on camera traps running away from. Although the effect was not statistically significant, brown bear occupancy of sites reduced by almost half when LGDs were present, hence an overlap in space use between red deer and brown bear could be due to mutual avoidance of LGDs. Such changes in species' spatial distribution and timing of activity in response to LGD presence can, therefore, lead to an increase in niche overlap between wild species potentially increasing interspecies interactions (Manlick and Pauli 2020). Given the potential implications, future studies should aim to disentangle whether changes in wildlife behaviours are caused by LGDs or the presence of livestock and/or shepherds so that appropriate mitigations can be sought.

Despite some indication of red deer and wolves responding to LGDs, there was, overall, little evidence of any of the variables investigated affecting the spatial distribution or temporal activity of the wildlife studied. The lack of effect of other drivers could have been due to including simplified variables that missed more complex relationships. It was not possible to include more variables in the models as the small number of camera trap sites would have meant that the models were overparameterised. For instance, despite previous evidence that wolves and bears are associated with different types of forest in different seasons (Pop *et al.* 2018; Cristescu *et al.* 2019), in this study it was only possible to group coniferous, broadleaved, and mixed forests into one 'forest' category. Terrain ruggedness has also been found to affect wolf and bear occupancy in Romania (Cristescu *et al.* 2019; Dyck *et al.* 2022) and whether human activity is motorised or unmotorised has previously been found to induce differing spatial responses by bears (Ladle *et al.* 2019). Overall though, the lack of effect of LGDs on wildlife aligns with other studies that have not found evidence of spatial or temporal avoidance of LGDs by wildlife. For example, LGD presence did not seem to affect the activity of several mesopredators in the USA (Bromen *et al.* 2019), or the occupancy of leopards (*Panthera pardus*) or black-backed jackals (*Lupulella mesomelas*) in South Africa (Spencer *et al.* 2020). In this study, the species most commonly reported to be chased, injured, and killed by LGDs, and, therefore, the most likely to perceive LGDs as predators and avoid them, was the red fox (Chapter 3). In all analyses conducted in this study, red foxes showed complete independence from LGDs. It is, therefore, possible that wildlife do not perceive LGDs as top predators in the environment. If LGDs can be used with limited displacement of wildlife this helps to establish their overall conservation benefit as a livestock protection measure that facilitates human-wildlife coexistence.

Whilst results from this study can be considered as evidence to advocate for continued LGD use in Romania, there were some limitations to the study that must be acknowledged. First, relatively few sites were surveyed in this study, which is a common limitation in previous studies which have found no effect of LGDs on wildlife occupancy (Spencer *et al.* 2020). It is possible that the number of sites and sample sizes were too small to discern clear relationships between wildlife distribution and activity and any covariates, including LGDs. This is particularly pertinent for the activity pattern analyses. As a result of splitting the data between high and low LGD or human sites, some of the sample sizes were relatively low. For reliable activity pattern estimates it is recommended to have a sample size of at least 100 detections of each species (Rowcliffe *et al.* 2014; Lashley *et al.* 2018), though estimates have also been shown to be highly correlated down to sample sizes as low as 10 detections (Lashley *et al.* 2018). Bear activity patterns were estimated from a small sample size (n = 9) at high LGD sites; hence this result must be interpreted with caution. In light of the reduction in bear conditional occupancy observed where LGDs were present, it is possible that differences in behaviour might start to emerge with larger sample sizes. In addition, having few camera sites also led to small sample sizes for wildlife detections, meaning that some of the species reportedly chased and killed by LGDs - primarily roe deer (*Capreolus capreolus*), European hare (*Lepus europeaus*), and wildcat (Chapter 3) - and which, therefore, might feasibly perceive LGDs as top predators, could not be investigated in this study. In a previous study, European hares were found to avoid even just LGD odours (Ugarte *et al.* 2021), but it is not known how these species, or other wildlife including non-mammalian taxa, responded to the presence of LGDs in this study.

The analyses were also conducted over a broad spatial and temporal scale with relatively few camera traps meaning any fine-scale avoidance or attraction to LGDs will have been missed in this study. For example, a study in a similar transhumance system in the USA looked at short time periods before, during, and after LGDs and sheep were present and found short-term displacement of several species, including apex predators and large herbivores, after LGDs and sheep had passed through an area (Kinka *et al.* 2021). It was not possible to conduct similar analyses in this study as shepherds tended to stay in the same area with their sheep and LGDs throughout the summer rather than passing through different areas, and it was not known exactly when they vacated each area. Furthermore, the USA study was able to integrate GPS collar locations from wild animals and LGDs into their detection histories for a clearer depiction of each species distribution. This was not possible in this study due to not being granted permission from land managers to deploy camera traps in the same areas where LGDs were GPS-collared (Chapter 5), and there being no collared wild animals in the study area. Where possible, future studies incorporating the addition of GPS tracking to monitor finer scale interactions between LGDs and wildlife, and the outcome of these interactions, would significantly enhance understanding of wildlife responses to LGDs.

Caution is also advised in generalising the results from this study to other habitats and LGD management systems outside of the Romanian Carpathian Mountains. Occupancy analyses showed that wildlife were widely distributed throughout the entire area, which could be due to the largely homogeneous, heavily forested habitat (Cristescu *et al.* 2019; Dyck *et al.* 2022). Although logging takes place, the high level of forest cover likely provides ample refuge for wildlife so they are unlikely to need to move far to avoid detection by humans or LGDs. Alternatively, or in addition, wildlife in this area may be somewhat habituated to LGDs. Unlike most other European countries where large carnivores were extirpated, the use of LGDs never ceased in Romania due to the continual presence of large carnivores through the years (Chapter 3). Furthermore, LGDs in Romania are always accompanied by shepherds, who can correct any undesired behaviours such as chasing non-target species, whereas LGDs are left free-ranging and unsupervised in many other countries (Chapter 3). As such, co-occurring wildlife in this study area might be less influenced by the presence of LGDs and stronger responses might be displayed by more naïve wildlife in countries where LGDs have more recently been introduced or reintroduced, in areas with more fragmented and disturbed habitat, or where LGDs are left unsupervised and potentially interact with wildlife more frequently. Thus, more research is needed on wildlife behavioural responses to LGD presence under different environmental contexts.

6.5 Conclusion

This study aimed to determine if the presence of LGDs affected the spatial distribution or timing of activity of co-occurring wildlife in the Romanian Carpathian Mountains. It was predicted that if LGDs were perceived as apex predations in the environment by wildlife, that wildlife would attempt to avoid LGDs in space and time to lower the risk of predation and competition. Of the five species investigated, only red deer potentially displayed avoidance of LGDs in space and time whereas grey wolves were possibly attracted to LGD-occupied areas. As LGDs were rarely documented far from their sheep flocks, it is possible that both red deer and wolves were responding to the overall presence of sheep, shepherds, and dogs on pastures rather than just LGDs. Overall, there was limited evidence that LGDs, or any other variables studied, including anthropogenic activity, affected wildlife distribution or timing of activity in the study area. This study provides the first evidence that LGDs can be used with limited displacement of wildlife or disruption to their diel activity patterns in the Carpathian Mountains. Whilst further research on a finer spatial and temporal scale and for a broader array of species is needed, this study provides preliminary support for a positive role to be played by LGDs in facilitating human-wildlife coexistence in Romania and potentially elsewhere.

Chapter 7: Discussion and conclusions

7.1 Summary of findings

Livestock guarding dogs (LGDs) are used around the world to protect livestock, and even endangered wildlife, from wild predators (Rigg 2001; King *et al.* 2015), but the ecological consequences of their use have been overlooked until recently (Smith *et al.* 2020a). This is one of the few studies to directly investigate the ecological effects of using LGDs and the first to monitor LGD behaviours in the Carpathian Mountains, Romania. The first objective of this research was to provide a detailed overview of the potential and currently reported ecological effects of using LGDs worldwide. The remaining three objectives, relating specifically to the use of LGDs in Romania, were to: 1) determine the wildlife species chased, killed, and/or consumed by LGDs, 2) quantify LGD roaming behaviours in relation to the sheep they guard by breed, sex, age, and reproductive status, and 3) quantify spatial and temporal responses of wildlife to LGD presence relative to other drivers of spatial and temporal patterns.

The literature review in Chapter 2 found that LGDs were widely reported to chase and kill wildlife (Smith *et al.* 2020a); behaviours that have recently been highlighted as a cause for concern with regard to wild animal welfare (Allen *et al.* 2019a; Allen *et al.* 2019b). The chasing and killing of wildlife could also cause wildlife to perceive LGDs as top predators (van Bommel and Johnson 2016). Some behavioural responses in concurrence with this theory, including spatial and temporal avoidance of LGDs, and increases in anti-predator behaviours in the presence of LGDs, were reported in the literature (Smith *et al.* 2020a; Chapter 2). Whilst it might be expected that LGDs should chase target predators (species that pose a predation threat to livestock) in the process of protecting livestock, killing more predators than typical lethal control methods would be an undesirable outcome of their use if they are to be advocated for as an alternative to lethal methods. However, such a scenario has been reported at least once (Potgieter *et al.* 2016). Moreover, there have been reports of LGDs chasing, injuring, and killing non-target species, i.e. animals that should not be perceived by LGDs as a predation threat to livestock (Gehring *et al.* 2011b; Whitehouse-Tedd *et al.* 2020). From the literature review it was calculated that 78% of the 80 species reported to interact with, or be affected by, LGDs were non-target species. Overall, these findings suggest that any benefits arising from the use of LGDs likely occur simultaneously with some mortality of target predators as well as unintended ecological effects for other co-occurring wildlife.

However, the magnitude of such ecological effects arising from the use of LGDs has rarely been quantified. The field study element of this thesis, carried out in the Romanian Carpathian Mountains, is one of few attempts to purposefully quantify LGD-wildlife interactions, and the only study to combine several lines of investigation including both LGD behaviours and wildlife responses to LGDs in the same study area. In the first instance, interviews with shepherds (presented in Chapter 3) largely aligned with the literature review results in Chapter 2: all shepherds reported antagonistic interactions between LGDs and target predators - grey wolves (*Canis lupus*) and brown bears (*Ursus arctos*) - and all reported that their LGDs also chased non-target species including European hares (*Lepus europaeus*), red foxes (*Vulpes vulpes*), wildcats (*Felis silvestris*), wild boars (*Sus scrofa*), roe deer (*Capreolus capreolus*), and red deer (*Cervus elaphus*). More rarely reported were instances of LGDs killing these species, and such cases typically involved red foxes and wild boars, which have been reported as affected by LGDs in previous studies (Gehring *et al.* 2010; van Bommel and Johnson 2016; Nayeri *et al.* 2022). Whilst all shepherds said they encouraged the chasing of target predators, the responses to non-target species were mixed. Some shepherds said they enjoyed seeing wildlife on their pastures and did not want their LGDs to chase species such as roe deer, whereas others encouraged their LGDs to chase all wildlife to reduce damages by wildlife and limit competition and disease transmission between wildlife and livestock. Similar reasoning has been given in previous studies, such as the idea that LGD-induced displacement of wild boars could help to reduce rooting of pastures and damage to electric fences (Ballarín *et al.* 2023), or reduce disease transmission between wild ungulates and livestock (VerCauteren *et al.* 2008; Gehring *et al.* 2011b; VerCauteren *et al.* 2012).

Human perspectives and behaviours likely influence LGD management, and could, therefore, affect the ecological impact that LGDs have. To begin to investigate this in Chapter 4, results of LGD scat analysis determined that the frequency of occurrence of wildlife in LGD scats largely aligned with self-reported shepherd responses to LGD-wildlife interactions. Although no statistical analysis could be conducted for the scat analysis, findings indicated that more wildlife was detected in the scats of LGDs supervised by shepherds who did not actively discourage the chasing of wildlife. Another study on LGD diets in South Africa found that the occurrence of birds, reptiles, and wild mammals in LGD scats were higher when accompanied by a human (although not statistically significantly so) (Drouilly *et al.* 2020). Overall, as in Drouilly et al. (2020), the frequency of occurrence of wildlife in LGD scats was relatively low with wildlife remains found in less than a third of scats and almost 70% of these wildlife occurrences were of insects. Wild boar were the most frequent vertebrate remains in the scats and were found in five scats, all from the same site on the same day, so likely all originated from the same predation or scavenging event. In combination with the results from Drouilly et al. (2020), this study suggests that the consumption of wildlife by LGDs is not of major concern. For the few LGDs that do consume wildlife, mitigation of this behaviour might be best focused on human perspectives of LGD-wildlife interactions and LGD management by shepherds when present.

Whilst the scat analysis results suggested that the LGDs in the study region were not consuming vast amounts of wildlife, there were still the reports from the shepherds that all of their LGDs chased non-target wildlife. Previous studies have reported LGDs chasing wildlife, particularly predators, for long distances away from livestock, e.g. LGDs chasing wolves for 2 km (Sedefchev 2005) and the welfare implications of such long pursuits have recently been questioned (Allen *et al.* 2019a). The results from the GPS tracking of LGDs and sheep in Chapter 5 showed that the LGDs in this study remained mostly in close proximity to the livestock, with the time spent away from livestock each day being minimal. As such, it was unlikely that if the LGDs in the study were chasing wildlife that they were doing so for long periods of time over long distances. One of the key determinants of the effectiveness of LGDs as protectors of livestock is their attentiveness – the tendency to stay with the livestock (Lorenz and Coppinger 1986; Gehring *et al.* 2011a; Aslam *et al.* 2022) – and the LGDs in this study met this criterion. However, LGDs did roam away from sheep almost daily, with some LGDs more prone to this behaviour than others. Differences in roaming were not related to the age, sex, or breed of the LGD, or whether the LGD was neutered, as expected from other studies (Timm and Schmidt 1989; Green and Woodruff 1990; van Bommel and Johnson 2014b). Instead, the tendency to roam away from livestock was largely individual-specific, in concurrence with several recent studies (Allen *et al.* 2017b; Zingaro *et al.* 2018; Aslam *et al.* 2022).

Roaming from livestock increases the area over which any ecological consequences of LGDs might take effect. However, in agreement with the results in Chapter 5, which shows that LGDs stayed in close proximity to the sheep, the camera trapping results in Chapter 6 also showed that LGDs were mostly found near to pastures and were active during the day at the same time as the sheep. It was expected that if LGDs were perceived as predators, that co-occurring wildlife would employ spatial and/or temporal avoidance of LGDs (Laundré *et al.* 2010; van Bommel and Johnson 2016). There was some suggestion that red deer avoided LGDs in both space and time, and that grey wolves were attracted to areas used by LGDs, although it was not possible to distinguish whether these effects were due to LGDs alone, to the presence of LGDs, sheep, and shepherds combined, or to these species independently selecting habitats that correlated with LGD use. Brown bears, wild boars, and red foxes did not show any substantial spatial or temporal responses to LGD presence. This finding was unexpected for several reasons; shepherds reported wild boars and red foxes to be chased and killed most frequently by LGDs, wild boar remains occurred in LGD scats, and previous studies have shown spatial and temporal avoidance of LGDs by species of fox (van Bommel and Johnson 2016;

Bromen *et al.* 2019; McKellar *et al.* 2023) and bear (Kinka *et al.* 2021). Overall the results from Chapter 6 highlight how responses by wildlife are likely to be species and context-specific with other studies also finding differences in how different species respond to LGD presence in the same environment (van Bommel and Johnson 2016; Bromen *et al.* 2019; Spencer *et al.* 2020).

7.2 Implications for conservation and LGD management

Whilst the literature review revealed many anecdotal reports of LGDs chasing and killing wildlife, especially non-target species, limited evidence was found for any substantial effects of LGDs on wildlife in a field setting. In summary, there were low occurrences of wildlife remains in LGD scats, LGDs largely remained in close proximity to livestock, and of the five species studied only red deer showed potential avoidance of LGDs in space and time. Although the spatial and temporal avoidance of LGDs by red deer could be concerning, it is likely that red deer were responding to the large flocks of sheep and shepherd presence on the pastures alongside the LGDs, rather than just the LGDs (Weiss *et al.* 2022). Overall, this thesis provides some of the first evidence, alongside Spencer et al. (2020), that LGDs can be used successfully with minimal displacement of, and effects on, wildlife. This is a particularly pertinent finding as this study was conducted in a region where large numbers of LGDs are used to guard single flocks and so where it would be expected that any impacts on wildlife would be felt the strongest. Furthermore, the results help to alleviate some human-human conflict between shepherds and game managers over whether LGDs negatively impact game species. As such, the results further help to establish LGDs as a livestock protection tool with a net benefit outcome for wildlife.

However, there are some results from this study that do warrant some concern with regard to using LGDs for conservation. First, the literature review highlighted many reports of antagonistic LGD-wildlife interactions. Sometimes these interactions involved species of conservation concern; populations of which could be detrimentally impacted from relatively few interactions with LGDs. Second, although there were low occurrences of wildlife in the LGD scats, this does not necessarily reflect how often wildlife are chased and killed if the LGDs do not consume the wildlife they kill, as has been reported for free-ranging domestic dogs and cats (Martinez *et al.* 2013; Home *et al.* 2017; Cecchetti *et al.* 2021; Piontek *et al.* 2021) and specifically for LGDs (Potgieter *et al.* 2013). The magnitude of any impacts on wildlife welfare caused by being chased by LGDs is also still unclear as such effects and their consequences are difficult to measure in the field (Allen *et al.* 2019a; Allen *et al.* 2019b). There are also welfare implications for the LGDs, with reports of LGDs killed by predators when defending livestock. This has previously been a serious issue in Romania (Mertens and Schneider 2005) and several of the shepherds interviewed for this study mentioned that their LGDs had been injured or killed by wolves and bears. In fact, two LGDs were injured in the summer of 2021 whilst the study was ongoing. Although LGDs might protect livestock and help to increase human tolerance towards predators, this tolerance could be reduced when LGDs are killed by predators as this incurs both a financial and emotional cost to the owners of the LGDs (Mertens and Schneider 2005; Bangs *et al.* 2005). Whilst this was not a focus of the study or the interviews, it is clear that the prevalence of LGDs being killed and the impacts of this on human attitudes towards predators should be addressed in more depth.

In addition, the use of LGDs poses some potential issues surrounding human-human conflicts as well as human-wildlife conflicts. Although the LGDs in this study did not frequently roam far away from livestock for long periods, any roaming could be problematic depending on the circumstances. Roaming away from the sheep could make the LGDs less effective at protecting livestock, leading to farmer dissatisfaction (Aslam *et al.* 2022), resulting in farmers resorting to lethal control methods that they might deem more effective. Second, roaming LGDs are more likely to be involved in antagonistic interactions with recreational users of the environment, such as hikers (Mosley *et al.* 2020), and interfere with hunting dogs (Ballarín *et al.* 2023), both of which can exacerbate human-human conflict but can also lead farmers to abandon the use of LGDs (Ballarín *et al.* 2023). The LGDs did not frequently roam far or for long periods but they did leave the sheep (>500 m away) at some point on most days. Therefore, this behaviour requires further investigation to understand the causes and consequences of roaming and test potential mitigations.

This study aimed to explore the impacts of LGDs on wildlife and assess the potential conservation implications, yet the findings also offer valuable insight into LGD management and selection. Notably, some of the methods employed in the study could be adopted by LGD owners to monitor and manage their dogs' behavior. For instance, individuals concerned about their LGDs consuming wildlife could periodically inspect the animals' scats for any signs of wildlife remains. While identifying wildlife remains to species level might be challenging, recognising materials like unknown bones, feathers, or hairs unlikely to be of dog or livestock origin can still be achieved by an untrained eye. If suspected wildlife remains are detected, LGD owners can further investigate and attempt adjusting the quality or quantity of food provided as a potential mitigation measure. Additionally, fitting LGDs with affordable GPS tracking devices allows owners to establish personalised thresholds for determining whether their LGDs roam too far or too frequently, based on their unique circumstances such as habitat type, predator load, attack frequency, proximity to roads and hiking trails, etc. Many commercially available pet GPS trackers, similar to those used in this study, offer live-tracking information and virtual fence features, triggering alerts if the animal moves beyond a user-defined area. This information not only aids in selecting and training LGDs, focusing efforts on those prone to roaming too far, but also brings peace of mind to owners concerned about their LGDs' whereabouts, especially following predator encounters. As an example from this study, a shepherd contacted the researcher seeking the location of a GPS-tracked LGD that had been missing for several hours after chasing away wolves from the livestock. The researcher was able to check the live locations and reassure the shepherd that the LGD was travelling back in his direction.

Moreover, one consistent finding throughout this study was that variations in behaviour among LGDs stem from individual differences rather than factors such as age, sex, reproductive status, or breed (Carpathian Shepherd versus local mixed-breed LGDs). Despite the limitations of a relatively small sample size, these findings are particularly important in discussions surrounding LGD breed selection. There is a widespread belief that purebreds make superior LGDs due to behavioural traits honed over generations of specialised breeding, and this belief has shaped the practices of conservation organisations that predominantly favour the placement of purebred LGDs like the Carpathian Shepherd in Romania (Fauna & Flora per comms.), the Anatolian Shepherd in southern Africa (Marker *et al.* 2021) and the Maremma in Australia (van Bommel and Johnson 2023). Given the typically higher costs associated with acquiring and maintaining purebred LGDs in comparison to mixed-breeds (Horgan *et al.* 2021), coupled with the limited access of most livestock owners to formal LGD placement programmes, it is crucial to assess the effectiveness of both types. A recent study in Botswana found that mixed-breed (or landrace) dogs are better adapted to local conditions and can be as, if not more, effective at guarding livestock than imported Anatolian Shepherd dogs (Horgan *et al.* 2021). Similar successes with local mixed-breed LGDs have been documented in North and South America (Black and Green 1985; González *et al.* 2012). Although the current study in Romania specifically focused on comparing the behaviour of Carpathian Shepherd and mixed-breed LGDs rather than evaluating their effectiveness in guarding livestock, it contributes additional evidence supporting the idea that LGDs should be evaluated on their individual merits rather than solely based on their breed. Overall, it appears increasingly likely that while breeding purebred LGDs with the right traits is advantageous, proper socialisation and training play a crucial role in developing LGDs tailored to the specific needs and preferences of each livestock owner. If the use of local, mixed-breed LGDs proves to be a more cost-effective and practical alternative to employing purebreds, all options should be carefully considered regardless of breed.

7.3 Limitations

This study provides much-needed synthesis of the ecological impacts of LGDs and quantitative information on their interactions with wildlife, but there are some limitations to the study that must be acknowledged. The LGDs that were monitored for Chapters 4 and 5 were the LGDs of shepherds known to the project collaborators, Fauna & Flora. Fauna & Flora have previously provided some of the shepherds in the study with electric fences and LGDs, and provided training to shepherds on best practice for LGD management. Although consent was gained from all shepherds, and reassurances were given that the data would be anonymised and not lead to repercussions regarding future help received from Fauna & Flora, the existing relationship between the shepherds and the Fauna & Flora field team could have influenced how shepherds answered the interview questions. Similarly, shepherds provided with LGD management training might have had a greater understanding of how to use their LGDs in an effective manner least likely to impact wildlife (as advocated by Fauna & Flora). However, more prominent roaming behaviours and scats containing wildlife were found at sites with and without LGDs provided by Fauna & Flora suggesting these potential biases were not realised in the study.

More specific to the methods of Chapters 4, 5 and 6 are the generally small sample sizes used in this study. Fewer than 150 scats were analysed and were collected from only a few time periods at each location providing only a snapshot of information in time. For example, all of the scats containing wild boar remains were collected from a site that was only searched twice so it was not possible to determine if the consumption of wild boar by the LGDs at this site was a common occurrence or not. The results in Chapter 6 were also obtained from relatively few camera sites due to equipment and time constraints. Only those species with larger numbers of detections were used for the analyses, which did not include some of the species reportedly chased by LGDs, notably roe deer and wildcat. However, red foxes and wild boars were the most commonly chased and killed species according to shepherd reports and neither of these species showed spatial or temporal avoidance of LGDs. This finding suggests that perhaps wildlife do not perceive LGDs as predators and that the other species not included in the analyses also might not display spatial or temporal avoidance of LGDs.

The small number of camera sites and numbers of detections also limited the complexity of the statistical models and meant that the effect of LGDs on wildlife would have needed to have been quite large for this to be detected in the models. It is, therefore, possible that small effects of LGDs on wildlife, especially at a finer spatial and temporal scale as in Kinka et al. (2021), could have been missed. Similarly, in Chapter 6 it was not possible to disentangle any effects of LGDs from those of livestock and shepherd presence from the camera trap data alone. Initially, the study was designed so that camera traps would be deployed in areas where LGDs were GPS-tracked to compare fine-scale LGD movements with wildlife activity. However, this was not possible as land managers denied permission to deploy camera traps in these areas.

The sample size used in the GPS tracking study was not particularly small, but there was a slight bias in the selection of LGDs as only the LGDs that were least aggressive and most socialised with humans could be handled safely. This could have meant that the data obtained were from LGDs that were most likely to be bonded with the shepherd and so less likely to roam away from the shepherd and livestock (Akyazi *et al.* 2018; McKellar *et al.* 2023). Although this was unavoidable, the results showed variations in behaviours from the individuals that were selected with some still roaming more than others, helping to establish that it is not only the more aggressive dogs that roam and that the process of LGD selection did not affect the results substantially.

Finally, how generalisable the results are to different systems of LGD use in other countries is not clear without more studies. Shepherds in Romania practice transhumance grazing, where they graze their livestock on lower elevation pastures during the winter and higher elevation pastures during the summer. They also remain with their livestock throughout this time, even sleeping in small shelters next to the sheepfold and can correct any undesired behaviours such as chasing of non-target wildlife. There are other countries and regions that use similar transhumance grazing practices, such as in the western USA (Kinka *et al.* 2021), where the results from this study are more likely to be applicable. However, there are also many places where livestock and LGDs are left unsupervised with food provided from self-feeders, such as in the French Pyrenees and on Australian ranches (van Bommel and Johnson 2014b). In addition, Romania is one of the few countries in Europe that has sustained LGD use through the centuries as large carnivores were never extirpated there meaning that wildlife in Romania might be habituated to LGD presence. As such, co-occurring wildlife in this study area might be less influenced by the presence of LGDs and stronger responses might be displayed by more naïve wildlife in countries where LGDs have more recently been introduced or reintroduced, or where LGDs are left unsupervised and potentially interact with wildlife more frequently.

7.4 Opportunities for future research

To address some of the limitations of this study, more research is needed on LGDs in countries where they are used unsupervised and where their use has more recently been reinstated or newly introduced. Where possible, studies should employ longer-term monitoring of LGDs and wildlife populations to determine more robust trends in the frequency by which LGDs interact with wildlife and how wildlife respond to these interactions. Though difficult to observe in the field, more direct observations of LGDs, such as those in Landry et al. (2020), could help to determine the frequencies of LGDs chasing and killing wildlife and the context under which different interaction types occur. In addition, the analysis of scats only provides a snapshot of an LGD's diet during a short period, and the scats could not be assigned to individuals. Advancing from the traditional scat analysis methods to faecal DNA metabarcoding (Shores *et al.* 2015; Gosselin *et al.* 2017; Oja *et al.* 2017) or stable isotope analysis of dog whiskers (McDonald *et al.* 2020; Wilson-Aggarwal *et al.* 2021) would provide a wealth of additional information on longer-term consumption of different food items and the likely impact of such consumption on affected wildlife populations.

With regards to the roaming behaviours of LGDs, more research is needed to establish under what context this occurs and how to minimise this behaviour. Differences in behaviour were largely due to individual differences suggesting a deeper understanding of LGD personality, behaviour, and the context under which roaming occurs is required to minimise this mostly undesirable behaviour. One potential factor that could influence behaviours such as roaming from livestock and predation of wildlife is the nutritional quality of human-provisioned food. It was beyond the scope of this study to conduct a thorough investigation on this topic; hence future studies should assess LGD behaviours in relation to different quantities and qualities of food. If undesirable LGD behaviours are linked to their diets, then this could be a simple recommendation to shepherds that would mitigate some negative effects of using LGDs. Other studies have shown correctional training to successfully reduce undesirable behaviours (Whitehouse-Tedd *et al.* 2020), so this is an option to be assessed in more depth.

Finally, more studies should be conducted addressing not just LGD behaviours but how wildlife respond to LGD presence. Other anti-predator responses should be considered as well as looking at spatial and temporal responses by wildlife and conducting these analyses on a finer scale by potentially incorporating GPS tracking data (e.g. Kinka et al. 2021). Wildlife might use the same areas at the same times as normal, but they might increase the amount of time they are vigilant, potentially at the expense of foraging or other important behaviours (Say-Sallaz *et al.* 2019). Changes in anti-predator behaviours can have knock-on effects on survival and reproduction and, therefore, on population dynamics (Preisser *et al.* 2005; Allen *et al.* 2022). For example, mountain gazelles (*Gazella gazella*) in enclosures with LGDs spent more time running instead of resting and fawn survival decreased (Gingold *et al.* 2009). Domestic dogs can also affect the production of hormones associated with stress in animals (Rangel-Negrín *et al.* 2023) and can transmit diseases to wild animals (Laurenson *et al.* 1998; Doherty *et al.* 2017). All of these potential effects of LGDs were beyond the scope of the current study but offer areas for future research to delve further into the effects of LGDs on co-occurring wildlife. Likewise, this study and all previous studies have focused predominantly on medium- to large-bodied mammals. Some older studies have reported LGDs chasing and killing other wildlife including small rodents, reptiles and birds (Black 1981;

Coppinger *et al.* 1988; Timm and Schmidt 1989; Hansen and Smith 1999; Hansen *et al.* 2002; Rigg 2004). As such, there is an opportunity to broaden the current scope of research on LGD-wildlife interactions to include a more diverse range of effect types and taxa to gain a more holistic view of the ecological impacts of LGDs.

7.5 Conclusions

This is one of the first studies to directly investigate the ecological effects of using livestock guarding dogs (LGDs) and the first to monitor LGD behaviours in the Carpathian Mountains, Romania. The many anecdotal reports of LGDs chasing and killing wildlife in the literature validate the concern over the ecological effects of using LGDs and confirm that LGD use should be carefully considered and managed. However, there was little empirical evidence to suggest that LGDs have substantial effects on co-occurring wildlife in the Romanian Carpathian Mountains. Behaviours of LGDs were not particularly concerning - shepherds reported that LGDs killed wildlife only rarely, and this was partly corroborated by the low frequency of occurrence of wildlife remains in LGD scats. The LGDs in this study, regardless of age, sex, or breed, stayed mostly in close proximity to the livestock they were guarding, although short excursions away from livestock did occur on an almost daily basis. Of the five wild species studied with the use of camera traps, only red deer showed potential avoidance of LGDs in space and time, and grey wolves were potentially attracted towards LGDs. However, it was not possible to disentangle the effects of LGDs alone from the effects of LGDs, sheep, and shepherds combined; hence it was feasible that both red deer and wolves were responding to the latter. Future studies should attempt to isolate responses to LGDs from responses to the presence of livestock associated with LGDs. More research is also needed on the behaviours of LGDs being used in different countries under different management regimes to determine the ecological effects of LGDs specific to each context they are used. Any future research should also broaden the types of anti-predator responses and the wildlife taxa studied. Overall, the results from this thesis help to establish that LGDs can be used to reduce livestock depredation (one of the key drivers of human-wildlife conflict globally) without substantially impacting co-occurring wildlife and are, therefore, a suitable candidate tool for efforts to facilitate human-wildlife coexistence or reduce the need for lethal control of wild predators.

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Chapter 9: Appendix

Appendix A

Published version of Chapter 2:

Journal of Vertebrate Biology
Open Access
J. Vertebr. Biol. 2020, 69(3): 20103
DOI: 10.25225/jvb.20103
SPECIAL ISSUE: DOGS AND CONSERVATION: CURRENT AND EMERGING CONSIDERATIONS

The ecological effects of livestock guarding dogs (LGDs) on target and non-target wildlife

Bethany R. SMITH*, Richard W. YARNELL, Antonio UZAL and Katherine WHITEHOUSE-TEDD

School of Animal, Rural and Environmental Sciences, Nottingham Trent University, United Kingdom;
e-mail: beth.smith@ntu.ac.uk, richard.yarnell@ntu.ac.uk, antonio.uzal@ntu.ac.uk, katherine.whitehousetedd@ntu.ac.uk

▸ Received 11 September 2020; Accepted 3 October 2020; Published online 2 December 2020

Abstract. Livestock guarding dogs (LGDs) are used across the world to reduce livestock depredation by free-ranging predatory wildlife. In doing so, they reduce the need for lethal predator control and are considered beneficial for conservation. However, LGDs might be perceived as predators by wildlife and induce a multitude of both positive and negative ecological effects. We conducted a literature review to evaluate the ecological effects of LGDs and found 56 publications reporting LGDs interacting with or affecting wildlife. Featuring in 77% of the publications, LGDs were widely reported to chase and kill wildlife, leading to species-specific behavioural responses. A total of 80 species were affected by LGDs, 11 of which are listed as Near Threatened or higher on the IUCN Red List. Of the affected species, 78% were non-target species, suggesting that any benefits arising from the use of LGDs likely occur simultaneously with unintended ecological effects. However, the frequency of LGD-wildlife interactions and the magnitude of any resulting ecological effects have rarely been quantified. Therefore, more empirical studies are needed to determine the net ecological outcome of LGD use, thereby ensuring that negative outcomes are minimised, while benefiting both farmers and wildlife.

Key words: conservation, free-ranging domestic dogs, human-wildlife coexistence, human-wildlife conflict, livestock protection dogs, predator control

Introduction

Livestock depredation by free-ranging predatory wildlife is one of the most widespread issues hampering human-wildlife coexistence (Thirgood et al. 2005, Torres et al. 2018). Livestock losses have substantial social and economic impacts (Moreira-Arce et al. 2018). Likewise, lethal predator control methods used on some farmlands are amongst the top causes of population declines for many threatened predator species (Inskip & Zimmerman 2009, Treves & Bruskotter 2014). Identifying and implementing livestock protection measures that can reduce livestock losses, increase farmer tolerance and promote associated positive (or neutral) behaviours towards predators are, therefore, key priorities for the conservation of these species and the sustainability of livestock farming (Torres et al. 2018).

Whilst commonly used to protect livestock, lethal predator control is often expensive and not always successful (McManus et al. 2015, Moreira-Arce et al. 2018, Bruns et al. 2020), unless targeting "problem animals" (Swan et al. 2017). For some species, particularly mesopredators, the efforts of lethal control are sometimes offset by compensatory processes such as increased reproduction and immigration (Minnie et al. 2016), and can even result in an increase in livestock

* *Corresponding Author*

depredation (Nattrass et al. 2020). Several forms of lethal control, such as poisoning and some forms of trapping, are also indiscriminate (Ogada 2014). Furthermore, the use of lethal control is often controversial (e.g. Martínez-Espiñeira 2006). Alternatives to lethal control are non-lethal, or "deterrent-based", methods of mitigating livestock depredation. These non-lethal methods typically involve reducing interactions between predators and livestock through protecting specific areas, improving husbandry techniques, and modifying predator behaviour through disruptive stimuli, such as scarecrows, noise, odour repellents and fladry (Eklund et al. 2017).

One method for modifying predator behaviour that is employed across the world is the use of livestock guarding dogs (LGDs, *Canis familiaris*; Rigg 2001). Usually, LGDs are bonded to livestock from an early age then accompany the livestock as they roam, protecting them from predators by alerting farmers to the presence of a threat, or directly deterring predators with visual, olfactory and auditory displays. The same breeds of dog have also recently been used in this way to protect threatened wildlife, including little penguins (*Eudyptula minor*), Australasian gannets (*Morus serrator*) and Eastern barred bandicoots (*Perameles gunnii*) from predation (van Bommel 2010, King et al. 2015, Parrott et al. 2017). Of the deterrent-based methods currently available, LGDs are often considered to be one of the most effective in the long term (Marker et al. 2005, Scasta et al. 2017, Khorozyan & Waltert 2019), although effectiveness can be highly varied (Smith et al. 2000, Bruns et al. 2020). Reductions in livestock losses while LGDs are in use, whether perceived or measured, can increase farmer tolerance of predators on their land resulting in a reduction of lethal control (González et al. 2012, Rust et al. 2013, Horgan 2015, Binge 2017). Thus, the use of LGDs is often considered beneficial for conservation and encouraged by conservation organisations to facilitate human-wildlife coexistence.

However, it is possible that benefits arising from the use of LGDs occur simultaneously with unintended ecological effects. The underlying ecological theory of LGD use is the disruption of optimal predator foraging by increasing the real and perceived risk to the individual of preying on livestock (Bagchi 2019, Haswell et al. 2019, Gaynor et al. 2020). As such, LGDs could be perceived as predators by both target and non-target species (van Bommel & Johnson 2016, Wilkinson et al. 2020). Through predation effects and competition, LGDs could, therefore, alter the perception of risk for co-occurring wildlife, which in turn could induce physiological and behavioural responses from affected species (Preisser et al. 2005, Say-Sallaz et al. 2019). As a form of free-ranging domestic dog, LGDs might also affect co-occurring species via disease transmission and hybridisation (Young et al. 2011, Hughes & Macdonald 2013, Ritchie et al. 2013). Overall, these effects could lead to changes in the survival, reproduction, health, and ultimately the population dynamics of the species involved (Preisser et al. 2005, Say-Sallaz et al. 2019). Furthermore, altering the behaviour or populations of some species could result in knock-on effects to other species, such as the prey and competitors of the directly affected species. Subsequently, whether or not LGD-mediated ecological effects are beneficial or detrimental will likely be species and context specific.

Following this, the use of LGDs as biological control agents has recently been challenged. For example, adverse effects on valuable non-target wildlife, such as some game species in southern Africa, are undesirable to farmers and likely influence whether they choose to use LGDs to protect their livestock (Potgieter et al. 2016). Furthermore, as LGDs have been reported to chase and kill target and non-target species (Urbigkit & Urbigkit 2010, Potgieter et al. 2016, Whitehouse-Tedd et al. 2020), some authors have raised welfare concerns over their use (Allen et al. 2019a, b, Allen & Hampton 2020). In these studies, the authors argue that the welfare impacts imposed by LGDs on wildlife are potentially greater than traditional methods of lethal control. On the contrary, others have refuted these claims on the basis that LGDs rarely engage in direct aggressive interactions with wildlife and when they do, it is in defence of livestock, hence helping to reduce livestock losses and increase farmer tolerance of predators (Johnson et al. 2019, Whitehouse-Tedd et al. 2020). However, these claims require evidence that wildlife is not adversely affected by LGDs (Allen et al. 2019b). Few studies have actually quantified the frequency and outcome of LGD-wildlife interactions, hence the full extent of LGD impacts on wildlife are relatively unknown.

For LGDs to be truly beneficial for conservation, the ecological consequences of using LGDs must be evaluated and any undesirable outcomes mitigated. In this review, we provide an overview of the current scientific knowledge about LGD interactions with target and non-target species and how these species respond to these interactions. Furthermore, we use the conservation status of each species known to interact with, or be affected by, LGDs to highlight interactions of conservation concern. Overall, we identify key knowledge gaps in the understanding of the ecological effects of LGDs, provide a platform for future research and urge relevant stakeholders to consider the unintended, as well as intended, consequences of using LGDs to protect livestock from free-ranging predators.

Material and Methods

We conducted a literature search in July 2020 using Scopus (https://www.scopus.com) and Web of Science (WoS; https://www.webofknowledge.com). The following key-word Boolean combinations were used to search peer-reviewed articles from 1970 onwards: ALL "livestock guard* dog*" OR "livestock protect* dog*" OR "guard* dog*" OR "livestock dog*" OR "guard* animal*" OR "herd* dog*"). A simplified version of these search terms was used in Google Scholar (https://scholar.google.co.uk) and the first 500 results were screened by reading the title and abstract. We also searched the Large Carnivore Initiative for Europe (LCIE) database (https://www.lcie.org/Publications – accessed: 19/06/2020) and the IUCN SSC Human-Wildlife Conflict Task Force (HWCTF) Digital Library (http://www.hwctf.org/resources/document-library – accessed: 19/06/2020) under the themes "Livestock guarding dogs" and "Livestock guarding", respectively. We conducted a snowball search by checking the reference lists of relevant publications. Where it was clear that the results included in a report, thesis or book chapter were later published in a journal, only the peer-reviewed article was included to avoid duplication. Any non-English publications returned by our search were translated using online translation engines (e.g. Google Translate). However, we acknowledge that non-English reports and some grey literature have likely been overlooked.

Publications studying or discussing the use of LGDs for protecting animals, whether livestock or wildlife, anywhere in the world were included for full screening. Publications relating to the use of LGDs to protect agricultural crops were not included. We took this decision as LGDs are not bonded to crops in the same way that they are bonded to animals; hence their defence mechanisms and any resulting ecological effects may not be comparable. The full text of these publications was then read and publications were retained for analysis if they reported any of the following: 1) LGD-wildlife interactions (e.g. chasing and killing of wildlife by LGDs, disease transmission, hybridisation). 2) Behavioural or physiological responses by wildlife to LGD presence (e.g. changes in land use spatially and/or temporally, or altered stress levels). 3) LGD-mediated effects on the survival, reproduction, or population dynamics of wildlife. 4) Reductions in lethal predator control associated with LGD use.

Although following the structure by which free-ranging domestic dogs have been suggested to affect wildlife (predation, competition, disturbance, disease transmission and hybridisation (Young et al. 2011, Doherty et al. 2017), we altered this ecological framework to tailor it specifically to LGDs (Fig. 1). We split predation effects into two categories that encompass direct interactions (chasing and killing wildlife) and indirect interactions (visual, olfactory and auditory cues). As LGDs are not typical predators, the "Chasing and killing wildlife" category also accounts for incidences of LGDs chasing and killing wildlife in defence of livestock without consuming them. Furthermore, we included incidences where LGDs were associated with a reduction in lethal predator control by farmers as this could directly affect the survival, reproduction, and population dynamics of species and affects whether LGDs are considered a net benefit for predator conservation. We did not include any studies or reports of LGDs altering farmer tolerance of predators unless this was explicitly linked to changes in lethal control.

Each individual report of a species interacting with, responding to, or being affected by LGDs was extracted and classified according to our conceptual ecological framework (Fig. 1). Dietary studies showing the consumption of wildlife by LGDs were classed as "Chasing and killing" wildlife, though we concede that these results could be caused by scavenging in the next section. Next, each individual effect was categorised as present or absent for interactions, or as negative, neutral or positive according to the outcome reported for the wildlife species, for responses and effects (Fig. 1). Where the effect on a species was categorised

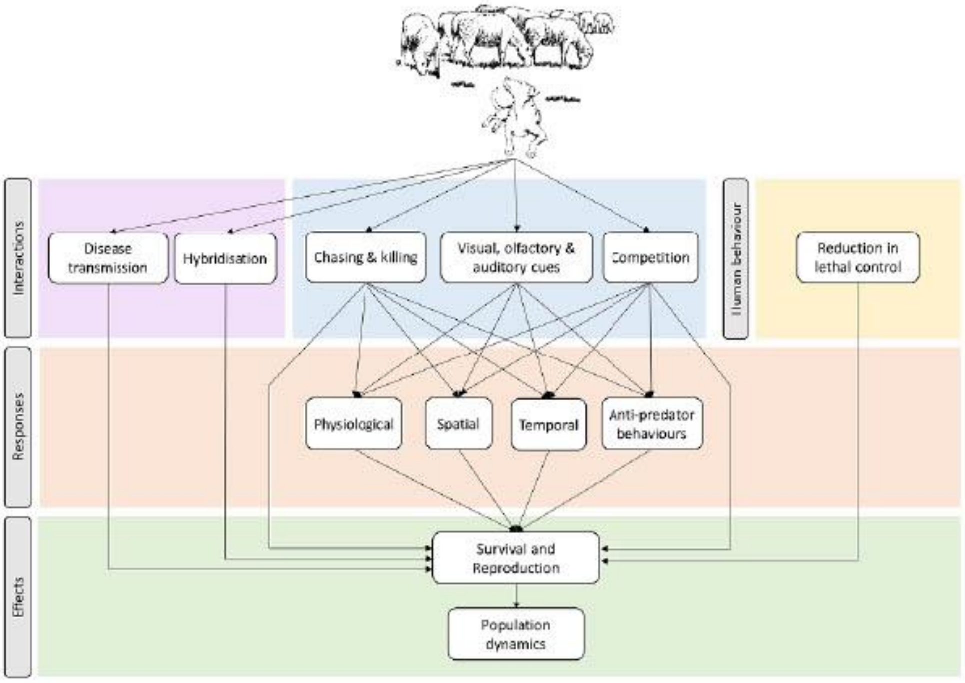

Fig. 1. Conceptual ecological framework of the pathways by which livestock guarding dogs (LGDs) could affect wildlife. As a form of free-ranging domestic dog, LGDs could interact with wildlife and affect species via disease transmission and hybridisation (purple), or by acting as predators or competitors and altering risk perceptions of wildlife (blue). Similarly, LGDs are also thought to cause changes in human behaviour, predominantly a reduction in lethal control methods (yellow). Changing the level of risk for wildlife, via predation and competition effects, can induce physiological and behavioural responses in species (pink). Overall, all of these interactions, responses and changes in human behaviour could affect survival, reproduction and ultimately population dynamics of co-occurring wildlife (green). The direction of responses are not given in this figure but all could be positive, neutral or negative depending upon the context of the interaction and the species involved.

as present, negative or positive, we classed the species as having been affected by LGDs. For each species we noted whether it was a target species (responsible for livestock depredation) or non-target species (not responsible for livestock depredation) in the study area. The IUCN Red List was then consulted to determine each species' conservation status (as relevant to the region of reported effect).

The following information was also extracted from each publication: country of study, total number of LGDs studied, number or percentage of LGDs involved in LGD-wildlife interactions, number of LGDs per farm or per livestock herd, breed of LGDs studied. In publications that did not provide the percentage of LGDs that chased or killed wildlife, where possible we calculated it from data reported. Instead of categorising these percentages as LGDs that chase or kill wildlife, we used the terms "lethal" or "non-lethal" interactions to match the terminology used in previous papers (e.g. Whitehouse-Tedd et al. 2020). We then calculated the mean and standard error of the percentages of LGDs that were reported to have lethal and non-lethal interactions with target and non-target wildlife across all of the relevant studies.

Results and Discussion

Publications summary

We found 145 publications in Scopus and WoS studying or discussing the use of LGDs to protect livestock or wildlife around the world. After applying our selection criteria, 27 publications were retained. A further 27 publications were sourced from the LCIE and HWCTF digital libraries, Google Scholar and a snowball search of relevant reference lists. Two more publications were included from this special issue after the initial search was conducted. In total, 56 publications were included that reported wildlife to interact with, respond to, or be affected by LGDs (Table S1). These 56 publications consist of peer-reviewed journal articles (n = 34), magazine articles from Carnivore Damage Prevention News (n = 9), unpublished theses (n = 5), conference proceedings (n = 3), project reports (n = 3), and book chapters (n = 2). Together, these 56 publications studied LGD use in 18 countries, mainly in Europe and Asia (n = 25). The remaining publications studied LGDs in North America (n = 15), southern Africa (n = 10), Australasia (n = 4), and South America (n = 2). Although searching from 1970 onwards, the earliest publication date was 1980. Over half of the publications (n = 31) were published between 2010 and 2020 inclusive, suggesting a growing interest in the ecological effects of LGDs in the last decade. The current literature is skewed towards reporting and studying incidences of LGDs chasing and killing wildlife, with 45 of the 56 publications reporting that LGDs chase, kill or consume wildlife (Fig. 2). In comparison, there was only one study investigating how olfactory cues from LGDs affect wildlife, and two studies reporting on hybridisation between LGDs and wild canids. No studies have explicitly investigated the transmission of disease from LGDs to wildlife, or the occurrence and effects of competition between LGDs and wildlife. Despite many reports of LGDs chasing and killing wildlife, little attention has been paid to how these interactions might affect wildlife. There were no studies on physiological responses induced by LGDs and only 10 publications that studied behavioural responses. All 10 behavioural response publications reported on spatial responses; two also reported temporal responses and one reported an effect on anti-predator behaviours. A single study

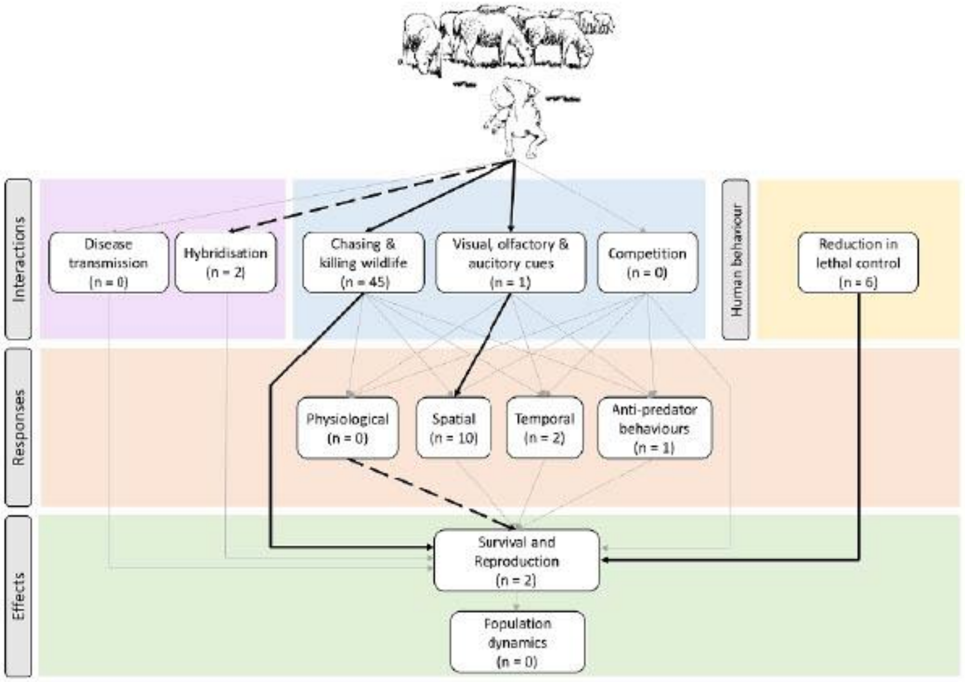

Fig. 2. Representation of the 56 studies found investigating each of the pathways by which livestock guarding dogs (LGDs) could theoretically affect wildlife. The number of publications (n) reporting each interaction, response or effect is given in each associated box. These publication numbers are not mutually exclusive as publications could have reported multiple interactions, responses or effects. Solid black arrows represent situations where a direct link from one stage of the framework to another was reported by at least one study. Dashed black arrows represent situations where an interaction, response or effect was hypothesised to occur or be linked to another stage of the framework by at least one study, but where evidence was limited. Grey arrows depict the underlying framework that has not yet been studied, and thus highlights key knowledge gaps in the understanding of the ecological effects of LGDs.

reported an effect on reproduction via reduced offspring survival. A reduction in lethal control by farmers following LGD introduction, such as a reduction in shooting, trapping or poisoning of predators, was reported in six studies. Only one of these six studies explicitly monitored survival rates for species before and after LGD introduction. Overall, there were no studies monitoring LGD-induced changes at the population level, even as a result of reduced lethal control (Fig. 2).

In addition, few studies have attempted to link ecological responses or effects to the underlying interaction mechanism. Only one study investigated how an olfactory cue affects spatial responses by a target predator, and another study investigated survival rates of predators as a result of mortality induced by both LGDs and human behaviour. The remaining responses and effects featuring in the publications simply reported changes relating to LGD presence (Fig. 2).

Interactions, responses and effects

Chasing and killing wildlife

There were 43 publications reporting LGDs chasing and killing wildlife and two reporting the occurrence of wildlife remains in LGD scat. Over half of the 43 publications reporting LGDs chasing and killing wildlife provided observational or anecdotal accounts of these behaviours, with only 21 providing quantitative data. Two of these 21 publications provided information on the percentages of farmers or households that report their LGDs to interact with wildlife, although both studied mixed-breed dogs as opposed to traditional breeds of LGDs (Black & Green 1984, Sepúlveda et al. 2014). Another two of the 20 publications gave an indication as to the frequency of LGD interactions with grey wolves (*Canis lupus*). The first reported that LGDs chased away wolves in more than 90% of encounters (Rigg et al. 2017). The second used infrared video observations to monitor LGD-wolf interactions on sheep pastures in France, finding that agonistic interactions accounted for 65.7% of the interactions and were significantly more frequent than any other type of interaction (Landry et al. 2020). The remaining 17 publications, consisting of peer-reviewed journal articles (n = 6), magazine articles from Carnivore Damage Prevention News (n = 5), student theses (n = 3), conference proceedings (n = 2), and project reports (n = 1), provided enough data to extract or calculate the percentages of LGDs involved in lethal and non-lethal interactions.

On average, a third of LGDs in each study were reported to have non-lethal interactions with wildlife, and this reduced to less than 10% of LGDs for lethal interactions (Table 1). The term "non-lethal" is used to represent cases where LGDs were not known to directly kill the animals involved. Nevertheless, "non-lethal" interactions can still be harmful to wildlife and both lethal and non-lethal LGD-wildlife interactions pose welfare concerns for the animals involved. Whilst these percentages help gauge how many LGDs directly interact with wildlife, only one study that provided the percentages of LGDs involved in interactions with wildlife used video cameras to monitor LGD behaviour (Landry et al. 2014). The remaining estimates originated from direct researcher observations and farmer reports, so are subject to human error and biases. For example, LGDs might behave differently whilst being observed or accompanied by humans (Drouilly et al. 2020) and are often out of sight of farmers, meaning farmer reports may underestimate the occurrence of these behaviours (Whitehouse-Tedd et al. 2020). Furthermore, the percentage of LGDs involved does not provide insight into the frequency of the interactions per dog over a defined time period.

Adding to the uncertainty over the extent to which LGDs chase or kill wildlife is the high variability in the percentages of LGDs that engage in these behaviours (Table 1); some of which could be explained by factors related to the LGDs, such as the number and breed of LGDs used. The numbers of LGDs per farm were reported in 32 of the 56 publications. In 78% of these 32 publications, 1 or 2 LGDs per farm/livestock herd were used, but the numbers reached as high as 25 in France where up to 20 LGDs were reported to be involved in LGD-wolf interactions at any one time (Landry et al. 2020). There were not enough data to draw any conclusions from the number of LGDs used and the occurrence of LGDs chasing and killing wildlife, but using multiple LGDs per farm increases the chance that at least one of these dogs will engage in these behaviours. Similarly, some breeds may be more likely to exhibit behaviours such as chasing and killing wildlife (Green & Woodruff 1988, Sedefchev 2005). For example, one study reported that 23% of the studied Komondor LGDs had killed at least one predator, compared to none of the Great Pyrenees LGDs in the same study (Green & Woodruff 1980).

There are also human factors that likely influence whether LGDs chase or kill wildlife. First, studies

Table 1. Summary of reported percentages of livestock guarding dogs (LGDs) having lethal and non-lethal interactions with target and non-target species. Target species are predators responsible for livestock depredation, non-target species are any other co-occurring species in the study area. Percentages of LGDs were extracted or calculated from 17 of the 43 publications that reported LGDs chasing, killing or directly interacting with wildlife.

LGD-wildlife interaction category	Mean %	SE	Min %	Max %
All species				
Non-lethal interactions	33.5	6.9	0.0	100.0
Lethal interactions	9.5	2.2	0.0	47.0
Target species				
Non-lethal interactions	25.6	13.7	1.0	89.0
Lethal interactions	9.2	3.3	0.0	47.0
Non-target species				
Non-lethal interactions	37.2	8.1	0.0	100.0
Lethal interactions	9.7	3.0	0.0	47.0

have suggested that LGDs that are not treated or fed as well as others are more likely to chase and predate wildlife (Schumann 2004, Sepúlveda et al. 2014). Second, these behaviours can often be corrected with appropriate training, but their occurrence likely depends on human perceptions of desirable and undesirable behaviours (Whitehouse-Tedd et al. 2020). For example, sheep flocks in Turkey that were guarded by LGDs that actively chased wolves suffered lower rates of predation compared to those guarded by LGDs that did not chase wolves (Tuğ 2005). Thus, the chasing and killing of target, and even non-target species, may be desirable if it reduces agricultural damage so may be encouraged (Potgieter et al. 2013, Horgan 2015, Drouilly et al. 2020). As with any strategy working towards human-wildlife coexistence, the human dimensions of this research must be considered, and more empirical studies conducted to understand the drivers of LGD-wildlife interactions and how to mitigate undesirable interactions or outcomes.

Any negative ecological outcomes of LGD use must also be considered against potential positive effects. As has been hypothesised for red foxes (*Vulpes vulpes*) in Australia, wild predators might be more cautious around LGDs that chase and kill wildlife, thus increasing their vigilance at the expense of hunting (van Bommel & Johnson 2016). As such, LGDs could provide indirect protection to wild prey species (van Bommel & Johnson 2016). Gehring et al. (2010) counted more ground-nesting bird nests on pastures with LGDs, possibly due to the LGDs killing and suppressing mesopredators that would normally predate these nests. Similarly, the use of LGDs in the western USA has been suggested to reduce the impacts of predators on sage grouse (*Centrocercus urophasianus*), a species listed as Near Threatened on the IUCN Red List (VerCauteren et al. 2013). The chasing and killing of wildlife by LGDs might therefore be beneficial for some species. However, all of these effects have only been hypothesised and not statistically tested, thus highlighting the need to empirically determine the net ecological effect of LGD use.

In addition to the 43 publications reporting LGDs to chase and kill wildlife, we found two publications investigating LGD diet via morphological identification of prey remains in LGD scats. One revealed the consumption of ten wild mammal species by LGDs, as well as small quantities of invertebrates, reptiles and birds (Drouilly et al. 2020), and the other reported the rare occurrence of scrub hare (*Lepus saxatilis*), common duiker (*Sylvicapra grimmia*) and rodent remains in LGD scats (van Vliet 2011). However, it is not possible to confidently distinguish between remains in the scats that were actively hunted or scavenged by LGDs. Furthermore, although simple and inexpensive, morphological scat analysis has important shortcomings including uncertainty over identification of closely related species and variability in digestibility of species (Mumma et al. 2016). Methods that determine the ratios of consumed food originating from hunting versus scavenging, or use molecular techniques such as metabarcoding (Mumma et al. 2016, Gosselin et al. 2017), could therefore further enhance our understanding of LGD diet and the ecological effects of LGDs.

Visual, olfactory and auditory cues

Only one study investigated how indirect interactions such as visual, olfactory or auditory cues of LGDs affect wildlife. This study recorded the spatial responses of captive dingoes (*Canis lupus dingo*) to LGD urine, finding that LGD urine alone does not repel dingoes (van Bommel & Johnson 2017). Although many dingoes were tested (n = 28), the experiment took place in captivity so it is unclear whether this result would translate to the wild. As LGDs primarily bark to deter predators, and possibly scent-mark along territorial boundaries (Bidder et al. 2020), it is likely that co-occurring wildlife are exposed to these auditory and olfactory cues. Playback experiments of domestic dog vocalisations have been shown to dramatically reduce mesopredator foraging and increase vigilance, in turn benefitting the prey species of mesopredators (Suraci et al. 2016). The potential cascading ecological effects of indirect interactions between LGDs and wildlife likely have differing outcomes for species at different trophic levels and require much further investigation.

Disease transmission and hybridisation

There were no publications explicitly studying disease transmission from LGDs to wildlife. However, LGDs have been shown to carry intestinal diseases (Frey et al. 2010) and in one case were possibly responsible for transmission of a parasitic tapeworm to domestic sheep in Denmark (Petersen et al. 2018). It is widely acknowledged that free-ranging domestic dogs can transmit some diseases to wildlife (Knobel et al. 2013). As such, many LGDs are vaccinated against common diseases but vaccination rates can vary greatly. For example, in one report monitoring 129 LGDs in Italy, 87.5% farmers never vaccinated their dogs (Salvatori et al. 2017). Thus, the possibility of disease transmission from LGDs to wildlife should not be overlooked, especially in areas where vaccination rates are low.

On the contrary, LGDs might be beneficial in controlling the transmission of diseases between livestock and wildlife. Two of the included studies showed that LGDs deter white-tailed deer (*Odocoileus virginianus*) from entering pastures and consuming cattle feed, in turn possibly reducing disease transmission from deer to cattle (VerCauteren et al. 2008, Gehring et al. 2010). Disease transmission at the wildlife-livestock interface is bi-directional (Cleaveland et al. 2001). Thus, deterrence of wildlife by LGDs could be beneficial for wildlife by also preventing the spread of disease from livestock to wildlife, as has been suggested for wild bighorn sheep (*Ovis canadensis*) in the USA (VerCauteren et al. 2013). More research is needed to elucidate the role that LGDs may play in regulating multi-directional disease transmission between LGDs, livestock and wildlife.

Of the two publications reporting hybridisation between LGDs and wild canids, one simply stated that LGDs breed with grey wolves in Europe without any supporting detail (Linnell & Lescureux 2015). The second studied the genotypes of 102 grey wolves, 57 LGDs and 9 mongrel dogs from Georgia (Kopaliani et al. 2014). Recent wolf ancestry was found in more than 10% of the LGDs, and recent dog ancestry in 13% of the wolves. In addition, 2-3% of the sampled wolves and dogs were identified, with high probability, as first-generation hybrids. However, it was not differentiated whether these hybrids were a product of mongrel or LGD hybridisation with wolves. As such, although this study provides some suggestive evidence for LGD-wolf hybridisation, we have used a dashed arrow from LGDs to hybridisation in Fig. 2 to represent the uncertainty. In general, hybridisation between domestic dogs and wild canids is of growing conservation concern internationally (Leonard et al. 2013). Future research on this topic should target regions where sterilisation of LGDs is less common, LGDs are wide-ranging or unaccompanied, and where there are small or fragmented populations of threatened canids (Gómez-Sánchez et al. 2018).

Physiological and behavioural responses

We found 10 publications investigating LGD-mediated behavioural effects on wildlife (Fig. 2). Eight of these 10 studies provided quantitative data on behavioural responses through a variety of methods, including direct observations, camera traps and GPS tracking. From the eight quantitative studies, there were 18 reports of spatial responses by both target and non-target species, 11 of which were negative (implied spatial avoidance), four neutral, and three positive.

Spatial avoidance by target predators could be deemed desirable by farmers if it prevents livestock depredation and was noted for coyotes (*Canis latrans*), grey wolves and bobcats (*Lynx rufus*) in the USA (Gehring et al. 2010, Bromen et al. 2019), and red foxes in Australia (van Bommel & Johnson 2016). Spatial avoidance by non-target wildlife could also be deemed desirable by farmers if it prevents agricultural damage. For example, spatial avoidance of LGDs by several large herbivores in Australia, including Eastern grey kangaroos (*Macropus giganteus*), is viewed as a positive outcome by some farmers due to these animals competing with livestock for feed and grazing opportunities (van Bommel & Johnson 2016). On the contrary, some game species, such as kudu in southern Africa, are highly valuable to farmers (Potgieter et al. 2016); their exclusion from farmland would likely be perceived as a negative outcome of LGD use. Generally, excluding wildlife from areas guarded by LGDs could restrict access to resources and fragment the available habitat for wildlife. Furthermore, spatial exclusion of target predators could exacerbate livestock depredation on neighbouring farms, thereby simply shifting the problem elsewhere (Gehring et al. 2010, Santiago-Avila et al. 2018).

To meet the expectations of facilitating human-wildlife coexistence, LGDs need to reduce agricultural damage, such as livestock losses, without excluding target species from agricultural land. The four neutral spatial responses were reported for three target species: dingoes in Australia that had overlapping territories with LGDs (Allen et al. 2017b) and did not avoid LGD urine (van Bommel & Johnson 2017), and leopards (*Panthera pardus*) and black-jacked jackals (*Canis mesomelas*) that occupied LGD-guarded and unguarded farmland equally in South Africa (Spencer et al. 2020). Whilst neutral spatial responses could be indicative of coexistence, they need to occur at the same time as a reduction in livestock losses to prove the LGDs are effective. Spencer et al. (2020) reported that there were no livestock fatalities on the guarded farms during their study, thus suggesting LGD-mediated coexistence between farmers and predatory wildlife on South African farms. However, these relationships need further examination due to a small sample size of farms and more studies are needed that combine studying the ecological effects of LGDs with the effectiveness of LGDs at reducing livestock losses.

The three positive spatial associations with LGDs were reported for brown hyaena (*Hyaena brunnea*) in South Africa (Spencer et al. 2020), and raccoons (*Procyon lotor*) and ringtails (*Bassariscus astutus*) in the USA (Bromen et al. 2019). Positive spatial associations with LGDs might not be directly related to LGD presence, but to a perceived reduction in risk where LGDs have facilitated a reduction in lethal predator control. However, this hypothesis is untested and there remains the possibility that some species might be directly attracted to LGDs. For instance, LGDs might provide a refuge for some wildlife by deterring the competitors and predators of these species. Attraction to LGDs by target predators could be curiosity-driven, alternatively predators might be seeking out LGDs as prey or trespassing conspecifics (Bangs et al. 2005). Whether these spatial responses are considered as detrimental or beneficial is dependent on the context, the species, and the attitudes of the people involved. For example, although rarely reported, LGD fatalities do sometimes occur as a result of confrontations with predators whilst defending livestock and this can worsen tolerance of predators by LGD owners (Bangs et al. 2005, Mertens & Schneider 2005). Furthermore, exposing LGDs to harm in this way raises ethical considerations for their use (Allen & Hampton 2020).

In addition to spatial responses, five temporal responses were reported, all of which were negative or neutral. Negative temporal effects suggest a shift in activity to avoid LGDs and were reported for white-tailed deer that significantly reduced the time they spent in pastures guarded by LGDs (Gehring et al. 2010), and red foxes and Eastern grey kangaroos in Australia (van Bommel & Johnson 2016). This same study in Australia found that swamp wallabies (*Wallabia bicolor*) and sambar deer (*Rusa unicolor*) did not show a temporal response to LGD presence, suggesting again that behavioural responses are likely to be highly species-specific. In general, more studies on temporal responses by wildlife are needed to complement the studies on spatial responses as animals not responding spatially to LGDs might be compensating temporally (Sévêque et al. 2020). Similarly, animals might compensate with increased stress levels or by adjusting other anti-predator behaviours such as vigilance and grouping (Say-Sallaz et al. 2019). Yet, there were no studies on physiological responses and only one study reporting LGDs to affect the activity levels of a non-target species (Gingold et al. 2009). The complex behavioural, physiological and ecological impacts of the fear of predation are only just beginning to be understood (Say-Sallaz et al. 2019) and warrant much further investigation with regards to the use of LGDs.

Lethal control, survival, reproduction and population dynamics

There is a paucity of studies investigating the ecological outcomes of LGD-wildlife interactions

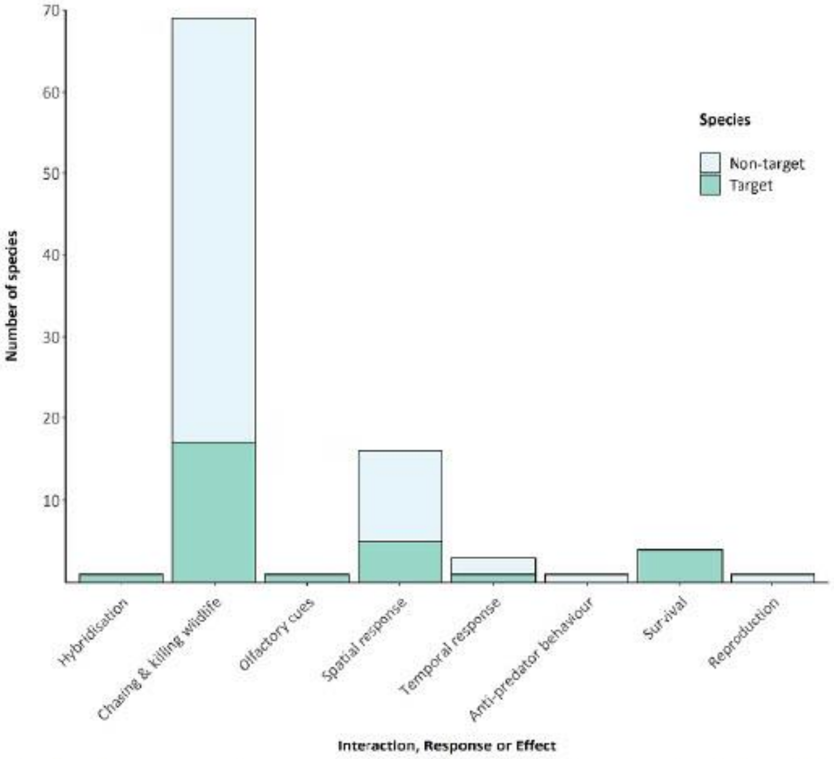

Fig. 3. Number of named species reported to interact with, respond to, or be affected by livestock guarding dogs (LGDs) as determined from a literature search (1970-July 2020). Bars are stacked by the number of target species (responsible for livestock depredation) and non-target species.

with regards to reproduction, survival and overall population-level effects. Only one study investigated the reproductive output of a species, finding a lower survival rate of mountain gazelle (*Gazella gazella*) fawns when kept in enclosures with LGDs compared to without (Gingold et al. 2009). The authors suggest this reduction in offspring survival could be due to direct predation by LGDs or be physiologically-mediated but could not determine the exact cause (hence the dashed arrows in Fig. 2). Despite the seemingly widespread occurrence of LGDs chasing and killing wildlife, only one study measured adult survival rates of wildlife before and after LGD introduction. This study found a net decrease in leopard and cheetah (*Acinonyx jubatus*) deaths, but a net increase in black-backed jackal and caracal (*Caracal caracal*) deaths due to combined killing from farmers and LGDs (Potgieter et al. 2016). The effects of LGDs are therefore dependent upon the abundance and type of species, and importantly, farmer behaviours towards specific predators.

Six publications reported changes in farmer behaviour in the form of a reduction in the use of lethal control, such as shooting, trapping and poisoning, in association with LGD use. Two of these publications simply stated a decrease in the use of lethal control (Ribeiro & Petrucci-Fonseca 2005, Infante & Azorin 2017), whereas the other four provided more quantitative data on the percentages of farmers that employed lethal control methods before and after LGD introduction (González et al. 2012, Horgan 2015, Potgieter et al. 2016, Binge 2017). These studies found that as many as 88% of farmers reported that they no longer killed predators after using LGDs. However, all of the studies use farmer-reported data, which must be interpreted with caution. Furthermore, with the exception of Potgieter et al. (2016), none of these studies report on predator survival rates or the impact at the population level. Whilst actually measuring lethal control is extremely difficult, monitoring the effects on survival and populations of target predators is necessary

Table 2. Species found to interact with, respond to, or be affected by, livestock guarding dogs (LGDs) that are listed as Endangered (EN), Vulnerable (VU) or Near Threatened (NT) on the IUCN Red List. Species marked with an asterisk (*) were classed as target species in the study region. A description of the reported interactions and studied responses/effects are provided. The sambar deer is included here as a globally vulnerable species, though note that it was studied in Australia where it is a non-native species.

Species	IUCN Red List Status	Interactions & Effects
Mountain gazelle (*Gazella gazella*)	EN	Increase in anti-predator behaviour (running instead of resting), negative spatial response to LGD presence and reduced reproductive output via reduced offspring survival (Gingold et al. 2009)
Marine otter (*Lontra felina*)	EN	"Direct interactions" with LGDs (Sepúlveda et al. 2014)
European rabbit (*Oryctolagus cuniculus*)	EN	Chased and killed by LGDs (Ribeiro & Petrucci-Fonseca 2005, Ribeiro et al. 2017)
Cheetah (*Acinonyx jubatus*)*	VU	"Direct interactions" with LGDs (Whitehouse-Tedd et al. 2020) and killed by LGDs (Potgieter et al. 2016)
Wolverine (*Gulo gulo*)*	VU	Chased by LGDs (Hansen et al. 2002)
Kodkod (*Leopardus guigna*)*	VU	"Direct interactions" with LGDs (Sepúlveda et al. 2014)
Lion (*Panthera leo*)*	VU	"Direct interactions" with LGDs (Whitehouse-Tedd et al. 2020)
Leopard (*Panthera pardus*)*	VU	"Direct interactions" with LGDs (Whitehouse-Tedd et al. 2020), killed by LGDs (Marker et al. 2005b). Neutral spatial response to LGD presence (Spencer et al. 2020)
Sambar deer (*Rusa unicolor*)	VU	Negative spatial response to LGD presence, no temporal response to LGD presence (van Bommel & Johnson 2016)
Brown hyaena (*Hyaena brunnea*)*	NT	Killed by LGDs (Whitehouse-Tedd et al. 2020). Positive spatial response to LGD presence (Spencer et al. 2020)
Southern pudu (*Pudu puda*)	NT	"Direct interactions" with LGDs (Sepúlveda et al. 2014)

to determine if LGDs are indeed beneficial for predator conservation.

Wildlife species

A total of 80 species were reported in the literature as being affected by LGDs (Table S2). These species were predominantly mammals (n = 75), with the exception of five species of bird: Western capercaillie (*Tetrao urogallus*), wild turkey (*Meleagris gallopavo*), helmeted guineafowl (*Numida meleagris*), ostrich (*Struthio camelus*) and little penguin. There were six publications that reported LGDs chasing, killing or consuming birds, reptiles, or invertebrates, but the species were not named. Whilst LGDs likely affect many mammal species, future studies should ensure monitoring of a diverse range of taxa.

Although LGDs are used to deter target predators, 62 of the 80 affected species were non-target species ranging from small rodents and lagomorphs to non-target mesopredators and large ungulates. The proportion of non-target species involved was most often greater than target species for each interaction, response, or effect type with relevant data; exceptions to this were hybridisation, olfactory cues and survival (Fig. 3). In addition, we found that the percentage of LGDs involved in non-lethal interactions with wildlife were higher for non-target species, although the percentages of LGDs involved in lethal interactions with wildlife were similar for target and non-target species (Table 1).

Interacting more with non-target than target species could simply be caused by a typically higher species diversity and abundance of herbivores than predators. It could also be due to a lack of instinctive fear in non-target species in areas where LGDs have only recently been introduced. Regardless of the underlying cause, our results still highlight that LGDs interact with and affect many non-target species and therefore likely have unintended ecological effects. Interacting with non-target species could be deemed in defence of livestock if the animal is in close proximity to the herd, but a recent study from South Africa found that only 28% of cases of LGD-herbivore interactions were classed as defensive of livestock, compared to 100% of LGD-predator interactions (Whitehouse-Tedd et al. 2020). Future studies should therefore focus on quantifying and characterising the interactions between LGDs and non-target species, as well as target species, in order to better understand the nature and outcome of LGD-wildlife interactions.

Of the 80 named species in the publications, only one – the dingo – does not feature on the IUCN Red List. Although the conservation status of the dingo is debated, a recent study concluded that it does not meet the criteria for listing as a threatened species in Australia (Allen et al. 2017a), thus we have not included it. Most of the listed species (n = 68) are classified as Least Concern, with the remaining species (n = 11) listed as Near Threatened (NT), Vulnerable (VU) or Endangered (EN) (Table 2). Although a large proportion of the species reported in the papers were of Least Concern, it is possible that observers are biased towards reporting LGD interactions with rare or threatened species. Thus, interactions with common species might be even more frequent and widespread than suggested by the literature. The 11 threatened species consist of 33% of the target species and 8% of the non-target species affected by LGDs. A greater proportion of threatened target than non-target species is to be expected as LGDs are often used as a conservation tool to protect threatened predators from lethal control. However, if these interactions have negative outcomes, for either target or non-target species, then they are of immediate conservation concern. Before LGDs can be considered beneficial for predator conservation, empirical studies need to assess if and how LGD-wildlife interactions affect both target and non-target species, especially those of conservation concern.

Future Research

Our review has highlighted an overall paucity of studies investigating whether interactions with LGDs induce behavioural or physiological responses by wildlife, or affect wildlife populations. Before LGDs can be considered beneficial for conservation, their net effect on both target predator and non-target species populations must be empirically assessed. This is particularly important where species of conservation concern are involved in LGD-wildlife interactions.

For a comprehensive understanding of the ecological effects of LGDs, future studies should focus on: i) Quantifying and characterising LGD-wildlife interactions and their outcomes for both target and non-target species of a diverse range of taxa. As the direct outcome of lethal interactions are known, more research should investigate the outcomes of non-lethal interactions for affected wildlife. Assessment of factors influencing interaction parameters (e.g. breed, number, age, and sex of LGDs), as well as the effectiveness of corrective training, should also be investigated. Mitigation of any unintended ecological effects must follow accordingly. ii) Differentiating between scavenged and hunted prey items in LGD diet, and complementing morphological scat analysis with molecular techniques. iii) Assessing the risk of hybridisation between LGDs and wild canids, and the role LGDs may play in multi-directional disease transmission between LGDs, livestock, wildlife, and humans. iv) Investigating how wildlife respond behaviourally and physiologically to direct and indirect LGD-wildlife interactions. v) Determining if and how LGDs affect the survival, reproduction, or population dynamics of co-occurring species, particularly target predators and non-target species that frequently interact with LGDs. vi) Combining studies on the ecological effects of LGDs with monitoring the effectiveness of LGDs at reducing livestock depredation.

Conclusion

Incidences of LGDs chasing and killing wildlife were widely reported in the literature. However, the frequency of these interactions and the outcome for the species involved has rarely been quantified. Although chasing and killing wildlife might be deemed desirable by farmers if it protects them from agricultural damage, LGD-induced behavioural and physiological responses by co-occurring species warrant concern from an ecological and conservation perspective. Some studies have begun to address spatial responses by wildlife to LGD presence, finding that whilst some species avoid, or are even attracted to LGDs, some show no spatial response at all. Similarly, the few studies reporting temporal responses by wildlife show mixed results for different species. In addition, through trophic knock-on effects, LGD-mediated effects on one species could benefit others. Therefore, the ecological effects of LGDs are likely to be context and species-specific, benefitting some species whilst adversely affecting others.

For LGDs to truly facilitate human-predator coexistence, they need to increase farmer tolerance and reduce lethal control of predators without adversely affecting these predators or other non-target species. We found that LGDs affect a multitude of both target and non-target species, several of which are classified as Near Threatened, Vulnerable or Endangered on the IUCN Red List. By interacting with non-target as well as target species, LGDs likely incur unintended ecological costs. To date, there have been few quantitative studies examining the impacts of LGDs on wildlife, and no studies have explicitly monitored whether LGDs affect population sizes of co-occurring species. The wider ecological implications, whether detrimental or beneficial for wildlife, remain unclear. A more empirical and holistic approach needs to be taken to study the net ecological outcome of LGD use to ensure that any negative impacts on target or non-target species are mitigated and benefits maximised for both wildlife and farmers.

Acknowledgements

We thank A. Sévêque for constructive feedback on an earlier draft. We would also like to thank three anonymous reviewers for providing constructive feedback that greatly improved the flow and clarity of the manuscript. Author contributions: All authors conceived the study. B.R. Smith performed the literature search and led the writing of the manuscript with input from K. Whitehouse-Tedd, R.W. Yarnell and A. Uzal.

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Appendix B

Table B.1. Summary of the 56 publications found in the literature search that investigated or reported an ecological effect associated with the use of LGDs. The publication type is denoted as J (peer-reviewed journal article), CP (conference proceedings summary or abstract), R (project report), T (student thesis), CDPN (article from Carnivore Damage Prevention News) or B (book chapter).

ID	Study	Type	Ecological effect	Method	Description
1	(Green and Woodruff 1980)	J	Killing wildlife	Farmer reports	23% of Komondor and 0% of Great Pyrenees LGDs killed predators
2	(Black 1981)	J	Chasing and killing wildlife	Farmer reports and direct observations	LGDs regularly killed coyotes, porcupines, rodents, and rabbits and chased rabbits, ground squirrels and lizards
3	(McGrew and Blakesley 1982)	J	Chasing wildlife	Direct observations	Komondor LGDs chased coyotes away in an enclosure experiment
4	(Pfeifer and Goos 1982)	CP	Chasing wildlife	Farmer reports	LGDs regularly chased red foxes and coyotes away from pastures
5	(Green and Woodruff 1983)	J	Chasing wildlife	Direct observations	LGDs chased coyotes and hares
6	(Black and Green 1985)	J	Chasing and killing wildlife	Farmer reports	91% of respondents said their LGDs chased coyotes, and 8% knew of LGDs that had killed coyotes
7	(Coppinger *et al.* 1988)	CP	Chasing and killing wildlife	Farmer reports	In 1983: 3% of LGDs chased birds 0.6% of LGDs killed birds 19% of LGDs chased mammals 5% of LGDs killed mammals In 1984: 5% of LGDs chased birds 0% of LGDs killed birds 22% of LGDs chased mammals 4% of LGDs killed mammals
8	(Green 1989)	CP	Killing wildlife	Direct observations	1 LGD (1%) killed a coyote
9	(Timm and Schmidt 1989)	J	Chasing and killing wildlife	Direct observations	LGDs chased and killed jackrabbits and Columbian black-tailed deer Sightings of wild turkeys also decreased on LGD-guarded pastures
10	(Hansen and Bakken 1999)	J	Chasing wildlife	Direct observations	91% of LGDs chased reindeer Some LGDs chased brown bears

11	(Hansen and Smith 1999)	J	Chasing and killing wildlife	Direct observations	LGDs chased moose, roe deer, woodland birds, brown bears, and Norway lemmings 50% of lemming chases resulted in the death of the lemming
12	(Hansen *et al.* 2002)	J	Chasing and killing wildlife	Direct observations	1 capercaillie and 1 hare killed by LGDs Red foxes chased by LGDs on 3 occasions and a wolverine chased once
13	(Lapeyronie and Moret 2003)	R	Chasing and killing wildlife	Direct observations	100% of LGDs chased Alpine marmots Of 174 reported chases of marmots by LGDs, the marmot escaped unharmed from 168 3 chases resulted in the death of a marmot, and in the remaining 3 chases the outcome for the marmot was not known 24% of LGDs chased ungulates (mainly chamois) LGDs also chased small mammals, birds, wild boar, and red foxes
14	(Rigg 2004)	T	Chasing and killing wildlife	Farmer reports	1 LGD (7%) chased hares and small birds 1 LGD (7%) chased a brown bear 1 LGD (7%) killed a wild boar
15	(Caporioni *et al.* 2005)	J	Chasing wildlife	Farmer reports	Some LGDs chased wild boar and other wildlife
16	(Landry *et al.* 2005)	CDPN	Chasing and killing wildlife	Direct observations	1 LGD (1.5%) observed chasing wildlife Dead badgers and red foxes found near sheep and assumed to have been killed by LGDs
17	(Marker *et al.* 2005a)	J	Chasing wildlife	Farmer reports	Almost 50% of LGDs reported to chase game
18	(Marker *et al.* 2005c)	CDPN	Chasing and killing wildlife	Direct observations	LGDs chased game species e.g. kudu and sometimes killed then ate these species LGDs killed black-backed jackals, leopards and chacma baboons that were threatening livestock
19	(Ribeiro and Petrucci-Fonseca 2005)	CDPN	Chasing and killing wildlife Reduction in lethal predator control	Direct observations	83% of LGDs chased red foxes, wild boar and rabbits On 3 occasions, a fox or rabbit was killed LGD use associated with a reduction in lethal control
20	(Sedefchev 2005)	CDPN	Chasing wildlife	Direct observations	LGDs chase predators as far as 2 km away from livestock
21	(Tedesco and Ciucci 2005)	J	Chasing and killing wildlife	Farmer reports	LGDs chased wildlife and seen killing then eating roe deer and Alpine marmots
22	(Tuğ 2005)	T	Chasing wildlife	Farmer reports	LGDs chased wolves away from livestock
23	(Yılmaz 2007)	B	Chasing and killing wildlife	NA	Statement that Kangal LGDs are known for chasing and killing wolves
24	(VerCauteren *et al.* 2008)	J	Spatial response	Direct observations,	LGDs reduced the rates of white-tailed deer entering pastures and using cattle feed

				Motion-activated cameras	
25	(Gingold *et al.* 2009)	J	Spatial response Anti-predator behaviour Reproduction	Direct observations	Mountain gazelles avoided LGDs in enclosures Also spent more time running instead of resting in enclosures with LGDs Fawn survival decreased in enclosures with LGDs
26	(Gehring *et al.* 2011b)	J	Killing wildlife Spatial response Temporal response	Direct observations, Farmer reports, Track swaths	LGDs killed mesopredators (Virgina opossums, striped skunks, northern raccoons, and red foxes) LGDs excluded coyotes, wolves, and non-target mesopredators from pastures White-tailed deer changed activity spending less time in pastures with LGDs
27	(Gehring *et al.* 2011a)	J	Chasing wildlife	Direct observations	LGDs chased white-tailed deer, predators, and other wildlife from pastures
28	(Marucco 2011)	R	Killing wildlife	Direct observations	One issue stated to be a problem for LGDs is that they can disturb and kill wildlife
29	(Rigg *et al.* 2011)	J	Chasing wildlife	Farmer reports	LGDs chased predators away
30	(van Vliet 2011)	T	Chasing and consumption of wildlife	Scat analysis	Scrub hare, rodents and common duiker found in the scats of LGDs (common duiker remains likely from the killing of one by an LGD when it approached livestock)
31	(González *et al.* 2012)	J	Reduction in lethal predator control	Farmer reports	88% of farmers with LGDs reported they no longer kill carnivores
32	(VerCauteren *et al.* 2012)	J	Chasing wildlife Spatial response	Direct observations	LGDs chased grey wolves, deer, and wildlife away from pastures Red deer avoided pastures protected by LGDs
33	(Potgieter *et al.* 2013)	J	Chasing wildlife	Farmer reports	15% of LGDs chased wildlife
34	(VerCauteren *et al.* 2013)	B	Chasing and killing wildlife Spatial response	Direct observations	LGDs observed preying on small mammals in pastures. Overall fewer small mammals in pastures guarded by LGDs. These small mammals are named in Gehring et al. (2010a), but this is not included as a separate study due to being the same effect reported. LGDs killed ≥ 10 Virginia opossums per year on one farm LGDs useful for deterring bighorn sheep from domestic sheep LGDs possibly beneficial for sage grouse conservation by reducing predation

35	(Kopaliani *et al.* 2014)	J	Hybridisation	Genetics	Recent wolf ancestry in 10% of the dogs and recent dog ancestry in 13% of the wolves, with 3% of the dogs and 2% of the wolves likely being first-generation hybrids
36	(Landry *et al.* 2014)	CDPN	Chasing wildlife	Video observations, GPS tracking of LGDs	0% of LGDs chased red deer, European hares or mountain hares Unknown percentage of LGDs chased chamois, red foxes and grey wolves
37	(Sepúlveda *et al.* 2014)	J	Direct interactions with wildlife	Farmer/household reports	Percentage of households reporting interactions between their LGDs and the following species: 0% (river otter, lesser grison) 1% (marine otter, coypu) 6% (southern pudu, American mink) 8% (Molina's hog-nosed skunk) 8.1% (kodkod) 10.6% (pumas) 17.9% (chilla's fox) 59.3% (European hare)
38	(Chynoweth *et al.* 2015)	J	Killing wildlife	NA	Statement that Caucasian lynx are regularly killed and threatened by LGDs
39	(Horgan 2015)	T	Chasing and killing wildlife Reduction in lethal predator control	Farmer reports	Approx. 50% of LGDs chased game 21% of LGDs killed non-target game species 51% of farmers reduced and 38% stopped lethal control after using LGDs
40	(King *et al.* 2015)	J	Killing wildlife	Direct observations	LGDs thought to have injured and killed some of the Little penguins they are protecting through playful behaviour
41	(Linnell and Lescureux 2015)	R	Hybridisation	NA	Statement that LGDs breed with wolves in Europe
42	(Ali *et al.* 2016)	J	Killing wildlife	Farmer reports	1 LGD killed a grey wolf
43	(Potgieter *et al.* 2016)	J	Killing wildlife	Farmer reports	15 LGDs (18%) killed prey species e.g. gemsbok, eland, and kudu 8 LGDs (10%) killed baboons 1 LGD (1%) killed 1 bat-eared fox 1 LGD (1%) killed 1 cheetah 1 LGD (1%) killed an unknown number of African wildcats 0 LGDs (0%) killed leopards 37 LGDs (47%) killed black-backed jackals

					3 LGDs (4%) killed caracals Net mortality after LGD introduction was lower for cheetahs and leopards, but higher for black-backed jackals and caracals Numbers of target predators killed per farm per year (by farmers alone before LGD introduction → by farmers and LGDs combined): Cheetah: 0.11 ± SE 0.06 → 0.02 ± SE 0.02 (not significant) Leopard: 0.02 ± SE 0.02 → 0.00 ± SE 0.00 (not significant) Black-backed jackal: 1.7 ± SE 0.68 → 3.4 ± SE 0.77 (significant) Caracal: 0.10 ± SE 0.06 → 0.19 ± SE 0.10 (not significant)
			Reduction in lethal predator control		Fewer predators killed by farmers
44	(van Bommel and Johnson 2016)	J	Spatial response	Camera traps, Pellet counts, GPS tracking of LGDs	Spatial avoidance of LGDs noted for Eastern grey kangaroo, common wombat, swamp wallaby, sambar deer and red foxes
			Temporal response		Temporal avoidance of LGDs noted for Eastern grey kangaroo, red fox No temporal change noted for sambar deer and swamp wallaby
45	(Allen *et al.* 2017b)	J	Spatial response	GPS tracking of LGDs and dingoes	Dingo territory overlapped with Maremma LGD territory suggesting no spatial avoidance of LGDs by dingoes
46	(Binge 2017)	T	Chasing and killing wildlife	Farmer reports	LGDs chased black-backed jackals away from livestock 1 LGD (4%) killed a hare 1 LGD (4%) killed an unknown number of hyraxes 1 LGD (4%) killed a skunk (assumed African skunk AKA striped polecat) 36% of farmers reported their LGDs killed target predators. 6 LGDs (24%) killed black-backed jackals 3 LGDs (12%) killed caracals 5 respondents said their LGDs killed 1-2 caracals or black-backed jackals a year 1 respondent said their LGD killed approximately 5 caracals per year
			Reduction in lethal control		79% (n = 19) of farmers killed predators before LGD use compared to only 21% after (n = 5) 3/5 farmers said they killed fewer predators than before

47	(Infante and Azorin 2017)	CDPN	Reduction in lethal predator control	Direct observations	Reduction in illegal poisoning noted after LGD use
48	(Ribeiro *et al.* 2017)	CDPN	Chasing and killing wildlife	Direct observations	42% of LGDs chased rabbits/hares 72% of LGDs chased wild boar or roe deer 89% of LGDs chased red foxes 13% of LGDs killed rabbits/hares 15% of LGDs killed red foxes 17% of LGDs killed wild boar or roe deer
49	(Rigg *et al.* 2017)	CDPN	Chasing and killing wildlife	Farmer reports	LGDs barked at and chased grey wolves away in > 90% of encounters LGDs killed 2 grey wolves
50	(Salvatori *et al.* 2017)	CDPN	Chasing and killing wildlife	Farmer reports	7 LGDs (47%) regularly killed wildlife including hares, roe deer and red foxes, and were observed consuming these kills too 13 LGDs (87%) chased wolves and bears
51	(van Bommel and Johnson 2017)	J	Olfactory cue Spatial response	Direct observations	Dingoes actively investigated LGD urine Dingoes showed no spatial avoidance of LGD urine
52	(Bromen *et al.* 2019)	J	Spatial response	Camera traps, GPS tracking of LGDs	Spatial avoidance of LGDs noted for bobcats, gray foxes, and skunk species Positive spatial response noted for ringtails and northern raccoons, suggesting these species could be attracted to LGDs
53	(Drouilly *et al.* 2020)	J	Consumption of wildlife	Scat analysis	Relative frequency of occurrence of animal remains in LGDs scats as follows: Wild ungulates (springbok, klipspringer, steenbok, common duiker) – 4.8% Rock hyrax – 3.8% Micromammals (bush vlei rat, Namaqua rock mouse & unknowns) – 3.2% Invertebrates – 2.3% (mainly beetles but 1 scat comprised entirely of termites) Cape porcupine – 2.2% Scrub hare – 2.6% Small carnivores (meerkats) – 0.5% Reptiles – 0.8% Birds – 0.2% (only in 1 scat)
54	(Landry *et al.* 2020)	J	Chasing and killing wildlife	Video observations	175 LGD-wolf interactions observed through infrared video: 65.7% of interactions were agonistic including chasing, pursuing, and fighting 25.1% of interactions were LGDs searching for wolves 5.9% of interactions were LGDs barking 3.3% of interactions were non-belligerent, including tolerance of wolves and play behaviour

					1 wolf reported to have been killed by LGDs
55	(Spencer *et al.* 2020)	J	Spatial response	Camera traps	No spatial response to LGDs noted for leopards or black-backed jackals as equal occupancy of farmland guarded by LGDs than farmland without LGDs Increase in occupancy for brown hyaena on LGD-guarded farms
56	(Whitehouse-Tedd *et al.* 2020)	J	'Non-lethal interactions' with and killing wildlife	Farmer reports	48% of LGDs involved in non-lethal interactions and 9% of LGDs involved in lethal interactions with herbivores (impala, springbok, blesbok, waterbuck, helmeted guineafowl, warthog, bush pig, steenbok, ostrich, nyala, kudu, bushbuck) 22 LGDs (10%) had non-lethal interactions, and 23 LGDs (10%) had lethal interactions with civets, African wildcats, honey badgers and chacma baboons 0 LGDs (0%) killed cheetahs 5 LGDs (2%) had non-lethal interactions with cheetahs 1 LGD (0.5%) killed brown hyaena 8 LGDs (3.5%) had non-lethal interactions with brown hyaena 0 LGDs (0%) killed lions 3 LGDs (1%) had non-lethal interactions with lions 0 LGDs (0%) killed leopards 12 LGDs (5%) had non-lethal interactions with leopards

Table B.2. Species investigated with regards to interacting with LGDs, responding to LGDs, or being affected by LGDs, and the direction of any reported effects. Each species is listed along with their status as a target or non-target species and their IUCN Red List status. Where interactions were present, or responses and effects negative or positive, these species were categorised as having been affected by LGDs (Y = yes in "Affected"). In total, there were 83 named species in the 56 publications from the literature search (1970-July 2020), 80 of which were categorised as having been affected by LGDs in at least one publication. The three species that were monitored but categorised as not having been affected by LGDs are highlighted with blue text.

Common name	**Scientific name**	**IUCN Status**	**Interactions**	**Responses**	**Effects**	**Affected**
Target species						
Cheetah	*Acinonyx jubatus*	VU	**Killed** (Potgieter *et al.* 2016) **Not killed** (Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)		**Survival (+ve)** (Potgieter *et al.* 2016)	Y
Coyote	*Canis latrans*	LC	**Killed** (Black 1981; Black and Green 1985; Green 1989) **Chased** (Pfeifer and Goos 1982; McGrew and Blakesley 1982; Green and Woodruff 1983; Black and Green 1985)	**Spatial (–ve)** (Gehring *et al.* 2011b)		Y
Grey wolf	*Canis lupus*	LC	**Chased** (Tuğ 2005; Sedefchev 2005; VerCauteren *et al.* 2012; Landry *et al.* 2014; Rigg *et al.* 2017; Salvatori *et al.* 2017; Landry *et al.* 2020) **Killed** (Yılmaz 2007; Ali *et al.* 2016; Rigg *et al.* 2017; Landry *et al.* 2020) **Hybridised** (Kopaliani *et al.* 2014; Linnell and Lescureux 2015)	**Spatial (–ve)** (Gehring *et al.* 2011b)		Y
Dingo	*Canis lupus dingo*	Not listed	**Olfactory cues** (van Bommel and Johnson 2017)	**Spatial (N)** (van Bommel and Johnson 2017; Allen *et al.* 2017b)		Y
Black-backed jackal	*Lupulella mesomelas*	LC	**Chased** (Binge 2017) **Killed** (Marker *et al.* 2005c; Potgieter *et al.* 2016; Binge 2017; Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)	**Spatial (N)** (Spencer *et al.* 2020)	**Survival (–ve)** (Potgieter *et al.* 2016)	Y
Caracal	*Caracal caracal*	LC	**Killed** (Potgieter *et al.* 2016; Binge 2017; Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)		**Survival (–ve)** (Potgieter *et al.* 2016)	Y
Wolverine	*Gulo gulo*	VU	**Chased** (Hansen *et al.* 2002)			Y
Brown hyena	*Hyaena brunnea*	NT	**Killed** (Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)	**Spatial (+ve)** (Spencer *et al.* 2020)		Y
Kodkod	*Leopardus guigna*	VU	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Lessor grison	*Lycalopex griseus*	LC	**Not interacted with** (Sepúlveda *et al.* 2014)			N

Caucasian lynx	*Lynx lynx dinniki*	LC	**Killed** (Chynoweth *et al.* 2015)			Y
Bobcat	*Lynx rufus*	LC		**Spatial (–ve)** (Bromen *et al.* 2019)		Y
American mink	*Neovison vison*	LC	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Lion	*Panthera leo*	VU	**Not killed** (Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)			Y
Leopard	*Panthera pardus*	VU	**Killed** (Marker *et al.* 2005c) **Not killed** (Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)	**Spatial (N)** (Spencer *et al.* 2020)	**Survival (+ve)** (Potgieter *et al.* 2016)	Y
Chacma baboon	*Papio ursinus*	LC	**Killed** (Marker *et al.* 2005c; Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)			Y
Mountain lion	*Puma concolor*	LC	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Brown bear	*Ursus arctos*	LC	**Chased** (Hansen and Smith 1999; Hansen and Bakken 1999; Rigg 2004; Sedefchev 2005; Salvatori *et al.* 2017)			Y
Red fox	*Vulpes vulpes*	LC	**Chased** (Pfeifer and Goos 1982; Hansen *et al.* 2002; Lapeyronie and Moret 2003; Ribeiro and Petrucci-Fonseca 2005; Landry *et al.* 2014; Ribeiro *et al.* 2017) **Killed** (Landry *et al.* 2005; Ribeiro and Petrucci-Fonseca 2005; Gehring *et al.* 2011b; Ribeiro *et al.* 2017; Salvatori *et al.* 2017)	**Spatial (–ve)** (van Bommel and Johnson 2016) **Temporal (–ve)** (van Bommel and Johnson 2016)		Y
Non-target species						
Impala	*Aepyceros melampus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Moose	*Alces alces*	LC	**Chased** (Hansen and Smith 1999)			Y
Springbok	*Antidorcas marsupialis*	LC	**Consumed** (Drouilly *et al.* 2020) **Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Ringtail	*Bassariscus astutus*	LC		**Spatial (+ve)** (Bromen *et al.* 2019)		Y
Roe deer	*Capreolus capreolus*	LC	**Chased** (Hansen and Smith 1999; Ribeiro *et al.* 2017) **Killed** (Tedesco and Ciucci 2005; Ribeiro *et al.* 2017; Salvatori *et al.* 2017)			Y
Red deer	*Cervus elaphus*	LC	**Not chased** (Landry *et al.* 2014)	**Spatial (–ve)** (VerCauteren *et al.* 2012)		Y
Civet	*Civettictis civetta*	LC	**Killed** (Whitehouse-Tedd *et al.* 2020)			Y

			Non-lethal interactions (Whitehouse-Tedd *et al.* 2020)			
Molina's hog-nosed skunk	*Conepatus chinga*	LC	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Blesbok	*Damaliscus pygargus phillipsi*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Virginia opossum	*Didelphis virginiana*	LC	**Killed** (Gehring *et al.* 2011b)			Y
North American porcupine	*Erethizon dorsatum*	LC	**Killed** (Black 1981)			Y
Little penguin	*Eudyptula minor*	LC	**Killed** (King *et al.* 2015)			Y
African wildcat	*Felis silvestris*	LC	**Killed** (Potgieter *et al.* 2016; Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)			Y
Mountain gazelle	*Gazella gazella*	EN		**Spatial (–ve)** (Gingold *et al.* 2009) **Anti-predator (+ve)** (Gingold *et al.* 2009)	**Reproduction (–ve)** (Gingold *et al.* 2009)	Y
Cape porcupine	*Hystrix africaeaustralis*	LC	**Consumed** (Drouilly *et al.* 2020)			Y
Striped polecat	*Ictonyx striatus*	LC	**Killed** (Binge 2017)			Y
Waterbuck	*Kobus ellipsiprymnus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Norway lemming	*Lemmus lemmus*	LC	**Chased** (Hansen and Smith 1999) **Killed** (Hansen and Smith 1999)			Y
Black-tailed jackrabbit	*Lepus californicus*	LC	**Chased** (Timm and Schmidt 1989) **Killed** (Timm and Schmidt 1989)			Y
European hare	*Lepus europaeus*	LC	**Chased** (Rigg 2004; Ribeiro *et al.* 2017) **Not chased** (Landry *et al.* 2014) **Killed** (Hansen *et al.* 2002; Ribeiro *et al.* 2017; Salvatori *et al.* 2017)			Y

			Interacted with (Sepúlveda *et al.* 2014)			
Mountain hare	*Lepus timidus*	LC	**Not chased** (Landry *et al.* 2014)			N
Scrubhare	*Lepus saxatilis*	LC	**Consumed** (van Vliet 2011; Drouilly *et al.* 2020)			Y
Marine otter	*Lontra felina*	EN	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Southern river otter	*Lontra provocax*	EN	**Not interacted with** (Sepúlveda *et al.* 2014)			N
Eastern grey kangaroo	*Macropus giganteus*	LC		**Spatial (–ve)** (van Bommel and Johnson 2016) **Temporal (–ve)** (van Bommel and Johnson 2016)		Y
Alpine marmot	*Marmota marmota*	LC	**Chased** (Lapeyronie and Moret 2003) **Killed** (Lapeyronie and Moret 2003; Tedesco and Ciucci 2005)			Y
Wild turkey	*Meleagris gallopavo*	LC		**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Timm and Schmidt 1989)	**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Timm and Schmidt 1989)	Y
European badger	*Meles meles*	LC	**Killed** (Landry *et al.* 2005)			Y
Honey badger	*Mellivora capensis*	LC	**Killed** (Whitehouse-Tedd *et al.* 2020) **Non-lethal interactions** (Whitehouse-Tedd *et al.* 2020)			Y
Striped skunk	*Mephitis mephitis*	LC	**Killed** (Gehring *et al.* 2011b)			Y
Namaqua rock mouse	*Micaelamys namaquensis*	LC	**Consumed** (Drouilly *et al.* 2020)			Y
Meadow vole	*Microtus pennsylvanicus*	LC	**Killed** (VerCauteren *et al.* 2013) *(stated small mammals killed in* (VerCauteren *et al.* 2013)*, only named in a review by same authors* (Gehring *et al.* 2010)*)*	**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Gehring *et al.* 2010)	**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Gehring *et al.* 2010)	Y
Coypu	*Myocastor coypus*	LC	**Interacted with** (Sepúlveda *et al.* 2014)			Y

Helmeted guineafowl	*Numida meleagris*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Columbian black-tailed deer	*Odocoileus hemionus columbianus*	LC	**Chased** (Timm and Schmidt 1989) **Killed** (Timm and Schmidt 1989)			Y
White-tailed deer	*Odocoileus virginianus*	LC	**Chased** (Gehring *et al.* 2011a)	**Spatial (–ve)** (VerCauteren *et al.* 2008) **Temporal (–ve)** (Gehring *et al.* 2011b)		Y
Klipspringer	*Oreotragus oreotragus*	LC	**Consumed** (Drouilly *et al.* 2020)			Y
European rabbit	*Oryctolagus cuniculus*	EN	**Chased** (Ribeiro and Petrucci-Fonseca 2005; Ribeiro *et al.* 2017) **Killed** (Ribeiro and Petrucci-Fonseca 2005; Ribeiro *et al.* 2017)			Y
Gemsbok	*Oryx gazella*	LC	**Killed** (Potgieter *et al.* 2016)			Y
Bat-eared fox	*Otocyon megalotis*	LC	**Killed** (Potgieter *et al.* 2016)			Y
Bush vlei rat	*Otomys unisulcatus*	LC	**Consumed** (Drouilly *et al.* 2020)			Y
Bighorn sheep	*Ovis Canadensis*	LC		**Spatial (–ve)** (VerCauteren *et al.* 2013)		Y
North American deer mouse	*Peromyscus maniculatus*	LC	**Killed** (VerCauteren *et al.* 2013) *(stated small mammals killed in*(VerCauteren *et al.* 2013)*, only named in a review by same authors*(Gehring *et al.* 2010)*)*	**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Gehring *et al.* 2010; VerCauteren *et al.* 2013)	**Unknown if anecdotal reduction in sightings is a spatial response or abundance effect** (Gehring *et al.* 2010; VerCauteren *et al.* 2013)	Y
Common warthog	*Phacochoerus africanus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Bush pig	*Potamochoerus larvatus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Rock hyrax	*Procavia capensis*	LC	**Killed** (Binge 2017) **Consumed** (Drouilly *et al.* 2020)			Y
Northern raccoon	*Procyon lotor*	LC	**Killed** (Gehring *et al.* 2011b)	**Spatial (+ve)** (Bromen *et al.* 2019)		Y

Southern pudu	*Pudu puda*	NT	**Interacted with** (Sepúlveda *et al.* 2014)			Y
Reindeer	*Rangifer tarandus*	LC	**Chased** (Hansen and Bakken 1999)			Y
Steenbok	*Raphicerus campestris*	LC	**Consumed** (Drouilly *et al.* 2020) **Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Chamois	*Rupicapra rupicapra*	LC	**Chased** (Lapeyronie and Moret 2003; Landry *et al.* 2014)			Y
Sambar deer	*Rusa unicolor*	VU		**Spatial (–ve)** (van Bommel and Johnson 2016) **Temporal (N)** (van Bommel and Johnson 2016)		Y
Common ostrich	*Struthio camelus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Meerkat	*Suricata suricatta*	LC	**Consumed** (Drouilly *et al.* 2020)			Y
Wild boar	*Sus scrofa*	LC	**Chased** (Lapeyronie and Moret 2003; Caporioni *et al.* 2005; Ribeiro and Petrucci-Fonseca 2005; Ribeiro *et al.* 2017) **Killed** (Rigg 2004; Ribeiro *et al.* 2017)			Y
Common duiker	*Sylvicapra grimmia*	LC	**Killed & consumed** (van Vliet 2011; Drouilly *et al.* 2020)			Y
Western capercaillie	*Tetrao urogallus*	LC	**Killed** (Hansen *et al.* 2002)			Y
Nyala	*Tragelaphus angasii*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Common eland	*Tragelaphus oryx*	LC	**Killed** (Potgieter *et al.* 2016)			Y
Greater kudu	*Tragelaphus strepsiceros*	LC	**Killed** (Potgieter *et al.* 2016) **Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Bushbuck	*Tragelaphus sylvaticus*	LC	**Interacted with** (Whitehouse-Tedd *et al.* 2020)			Y
Gray fox	*Urocyon cinereoargenteus*	LC		**Spatial (–ve)** (Bromen *et al.* 2019)		Y

Common wombat	*Vombatus ursinus*	LC		**Spatial (–ve)** (van Bommel and Johnson 2016)		Y
Swamp wallaby	*Wallabia bicolor*	LC		**Spatial (–ve)** (van Bommel and Johnson 2016) **Temporal (N)** (van Bommel and Johnson 2016)		Y

Interactions, responses, and effects:
chased – species is chased by LGDs
not chased – species is actively reported not to be chased by LGDs
killed – species is reported to be killed by LGDs
not killed – species is actively reported not to be killed by LGDs
consumed – species remains found in scat of LGDs
interacted – species reported to directly interact with LGDs, but the nature of the interaction (e.g. chasing or killing) not specified
not interacted with – species reported not to directly interact with LGDs
visual, auditory, or olfactory cues – species interacts with LGD cues, e.g. barks, scent-marks
hybridised – species bred with LGDs
spatial – no change (N), or species moved away (–ve) or towards (+ve) LGDs
temporal – no change (N), or species changed active time to when LGDs active (+ve) or when LGDs not active (–ve)
anti-predator – no change (N), or species increased (+ve) or decreased (–ve) anti-predator behaviour such as increase in vigilance
survival – no change (N), reduction (–ve) or increase (+ve) in survival
reproduction – no change (N), reduction (–ve) or increase (+ve) in reproductive output

Appendix C

Personal reference collection for microscopic hair patterns of several wild species.

Insectivora

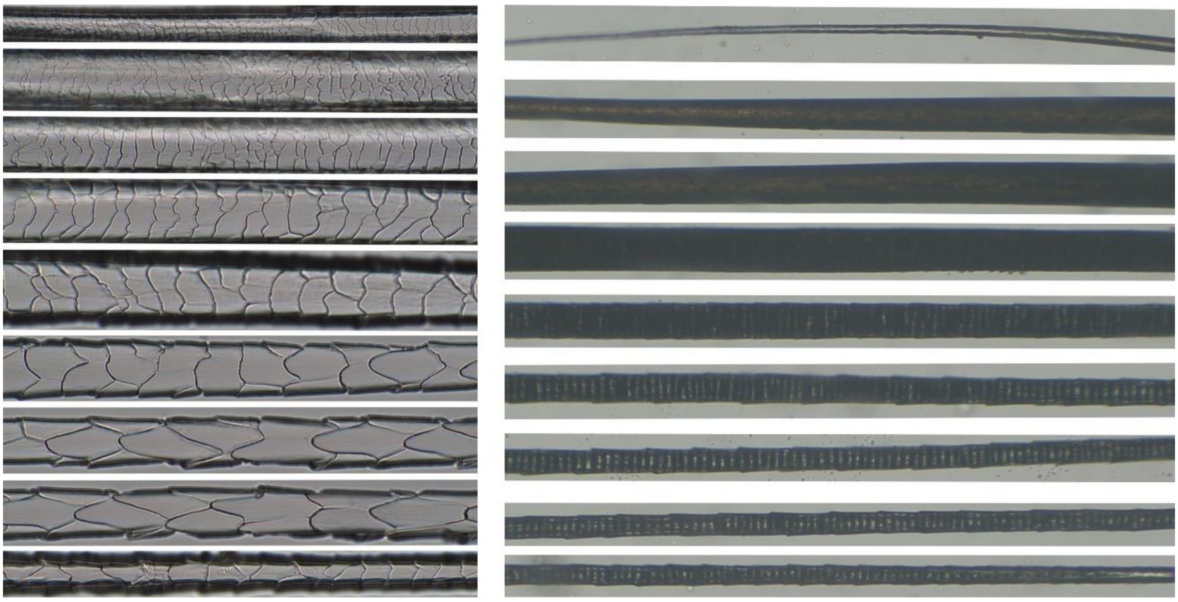

Figure C.1. Water shrew (Neomys fodiens) – left: cuticle; right: medulla.

Rodentia

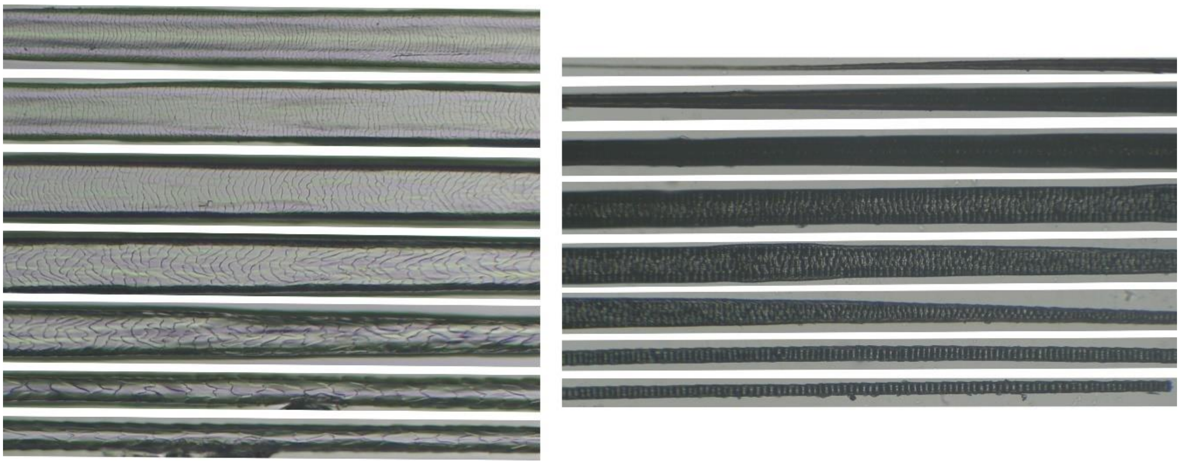

Figure C.2. Bank vole (Myodes glareolus) – left: cuticle; right: medulla.

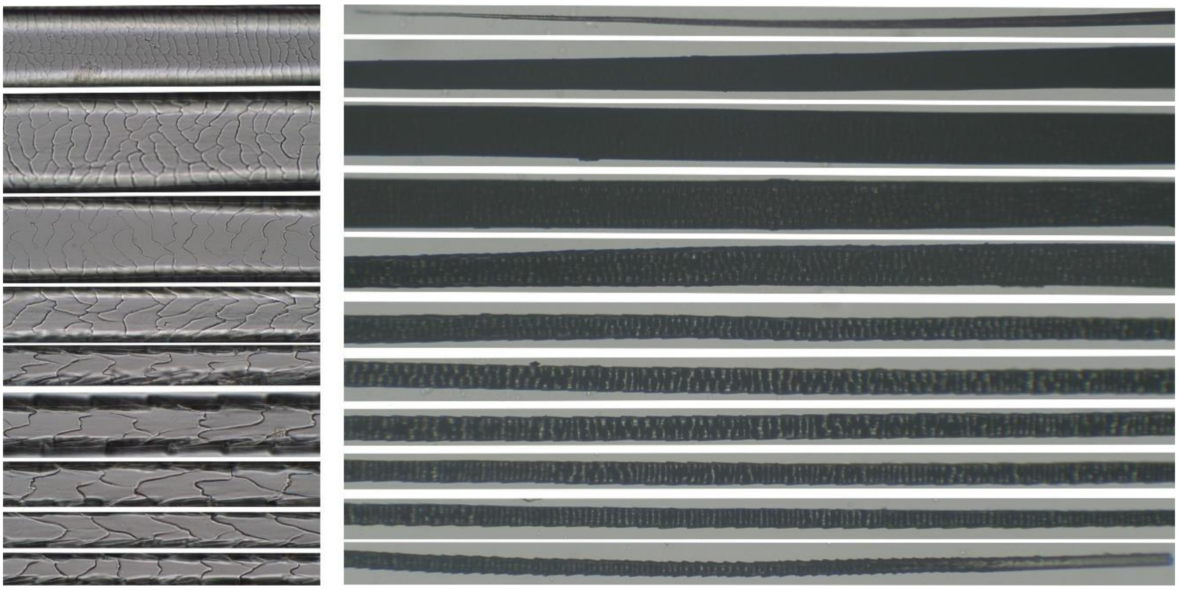

Figure C 3. Water vole (Arvicola amphibius) – left: cuticle; right: medulla.

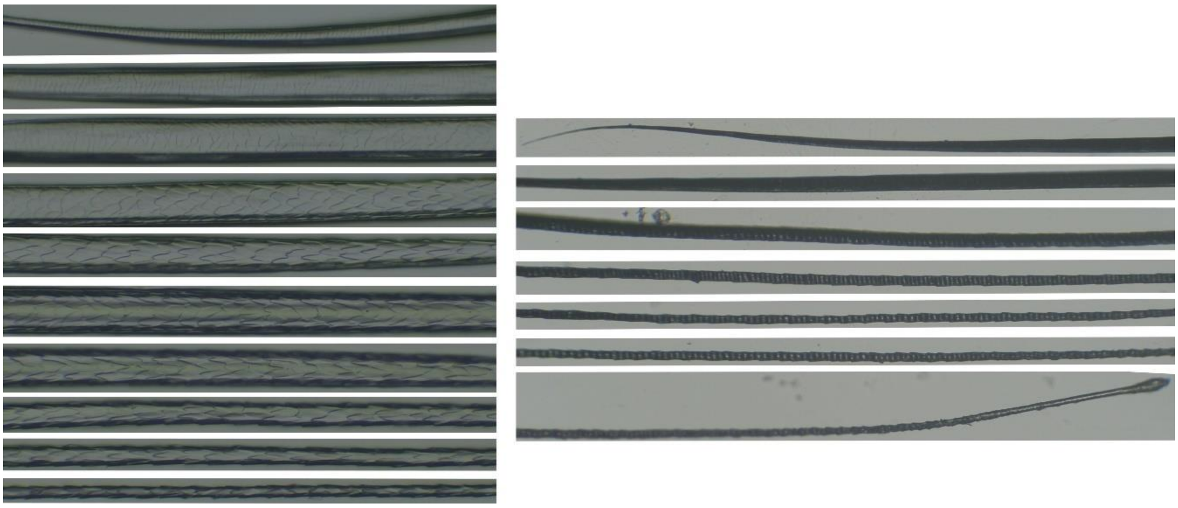

Figure C.4. Wood mouse (Apodemus sylvaticus) – left: cuticle; right: medulla.

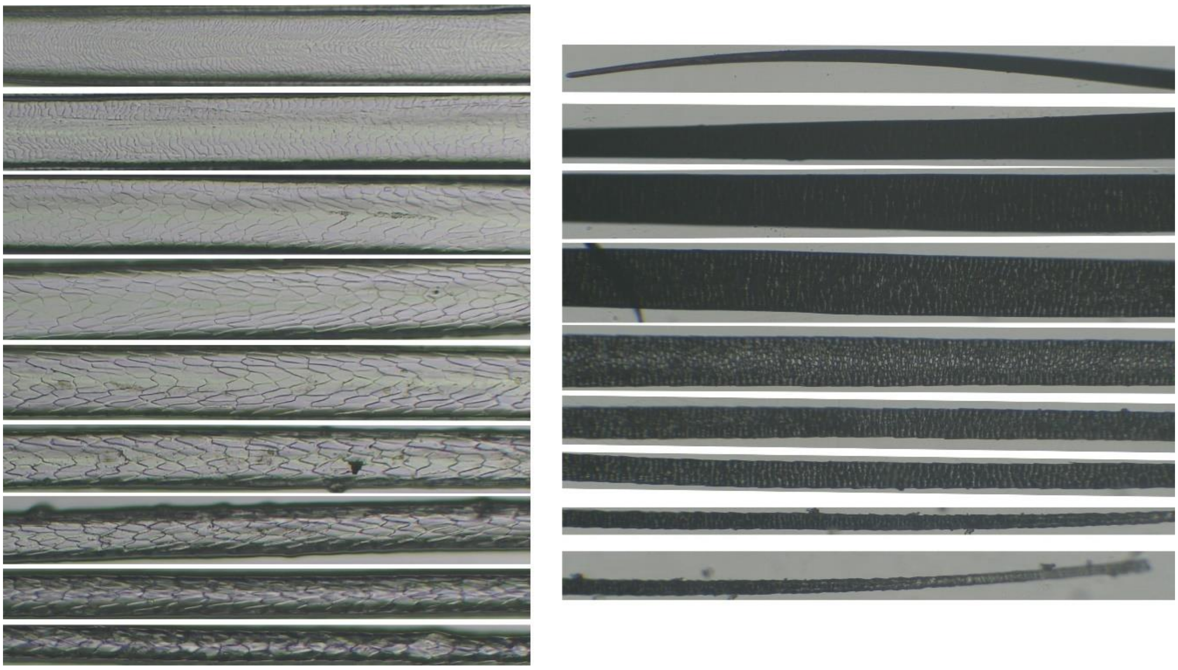

Figure C.5. Brown rat (Rattus norvegicus) – left: cuticle; right: medulla.

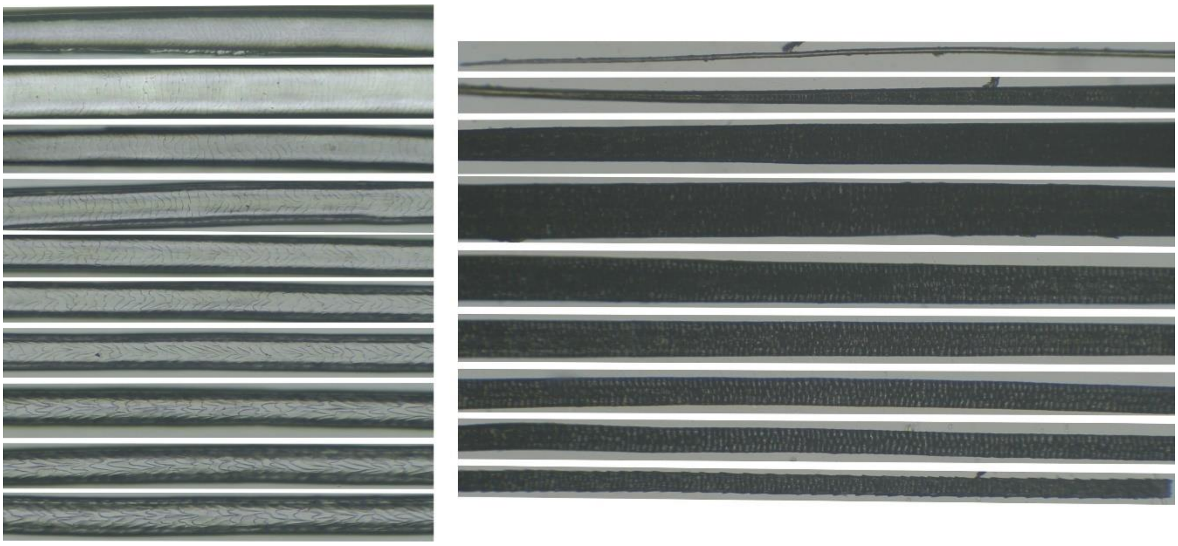

Figure C.6. Red squirrel (Sciurus vulgaris) – left: cuticle; right: medulla.

Lagomorpha

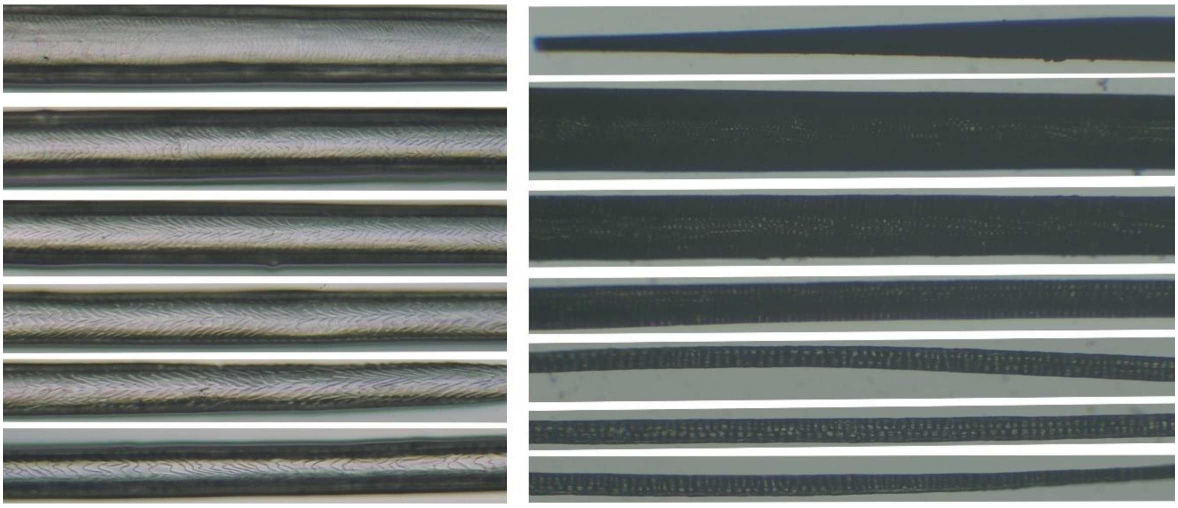

Figure C.7. European hare (Lepus europaeus) – left: cuticle; right: medulla.

Carnivora

Figure C.8. Brown bear (Ursus arctos) cuticle pattern.

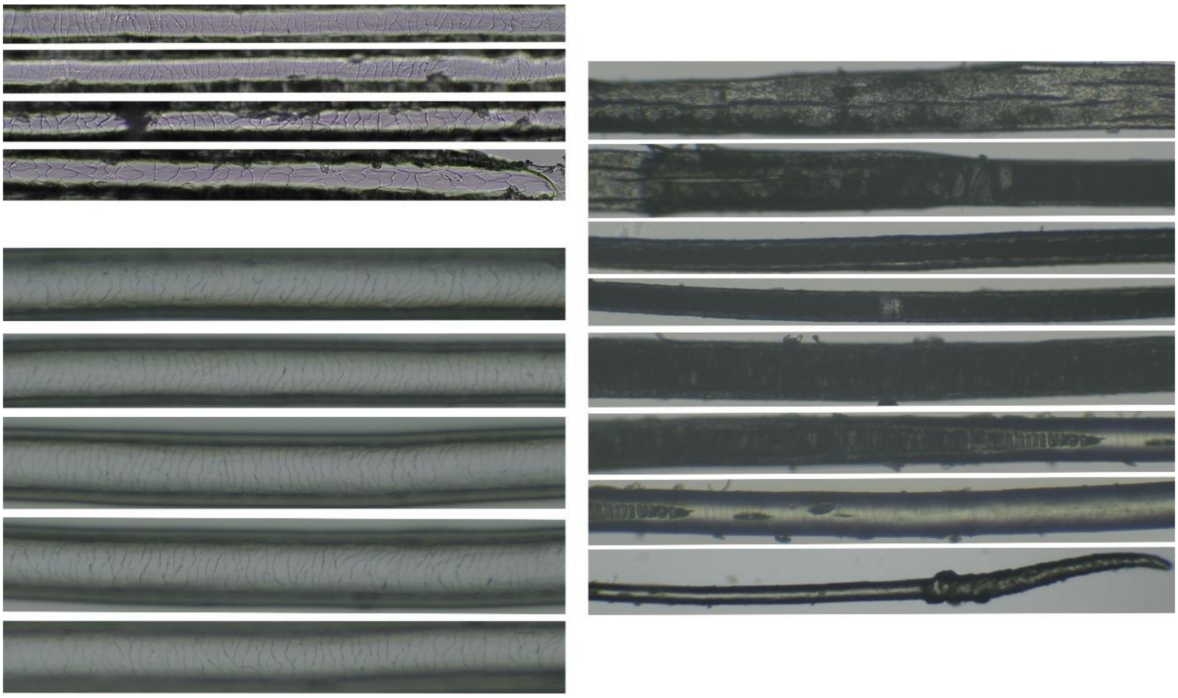

Figure C.9. Grey wolf (Canis lupus) cuticle patterns (top left and bottom left) and medulla pattern (right).

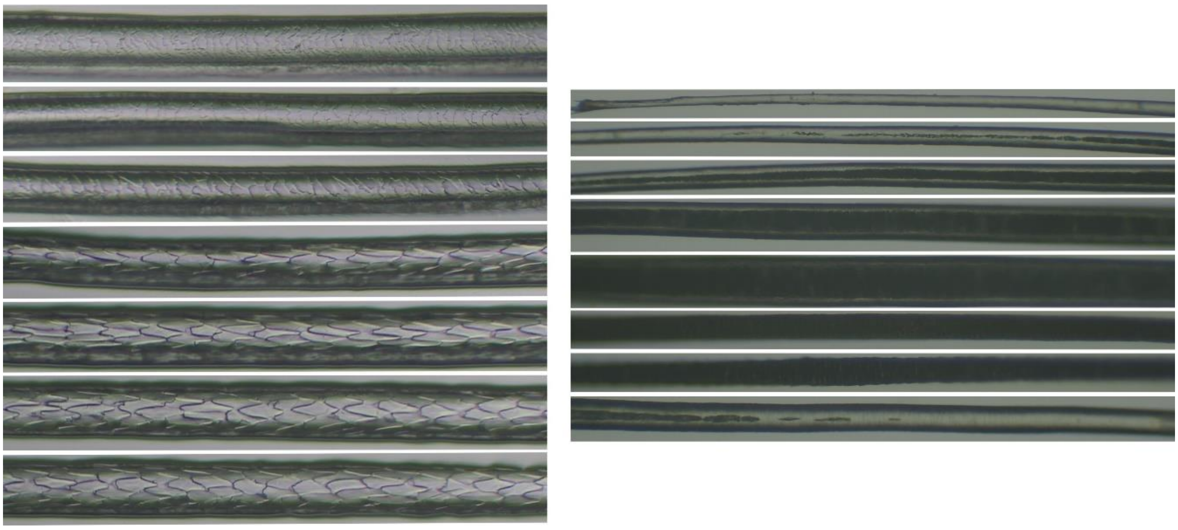

Figure C.10. Red fox (Vulpes vulpes) – left: cuticle; right: medulla.

Figure C.11. Domestic dog (Canis familiaris), specifically Carpathian Shepherd dog breed – left: cuticle; right: medulla.

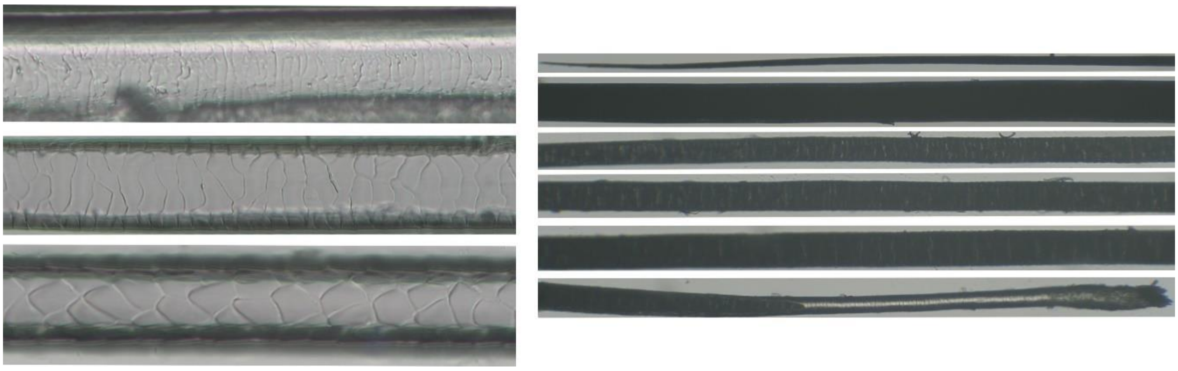

Figure C.12. Domestic cat (Felis catus) – left: cuticle; right: medulla.

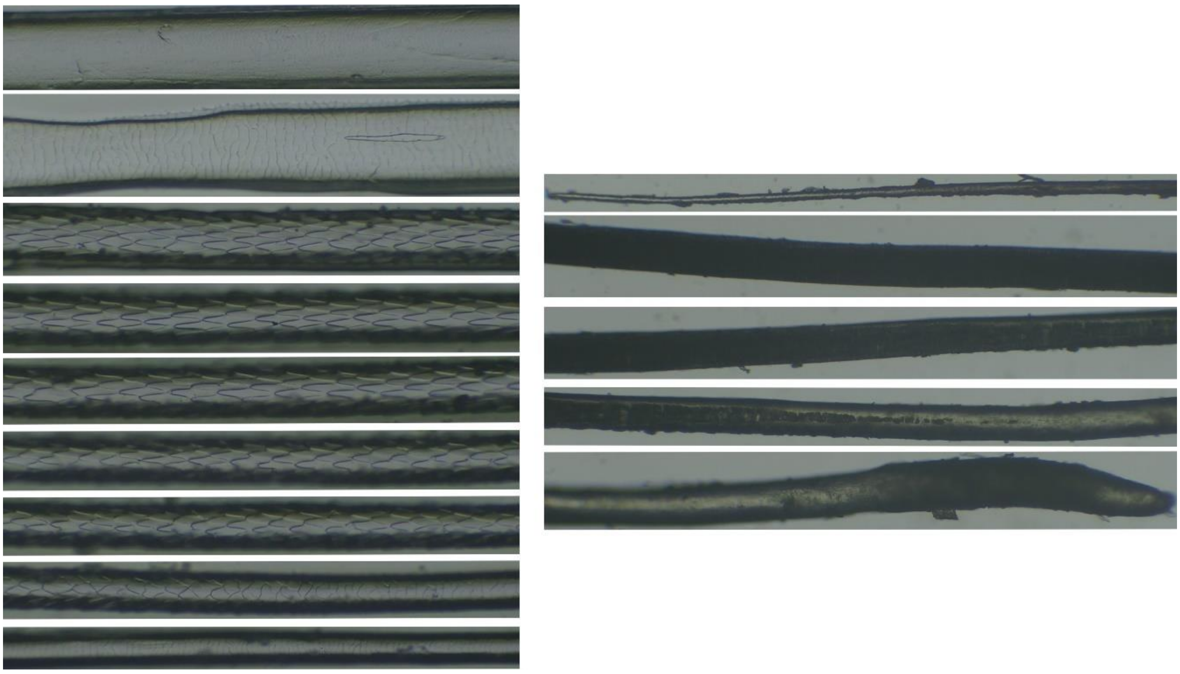

Figure C.13. Pine marten (Martes martes) – left: cuticle; right: medulla.

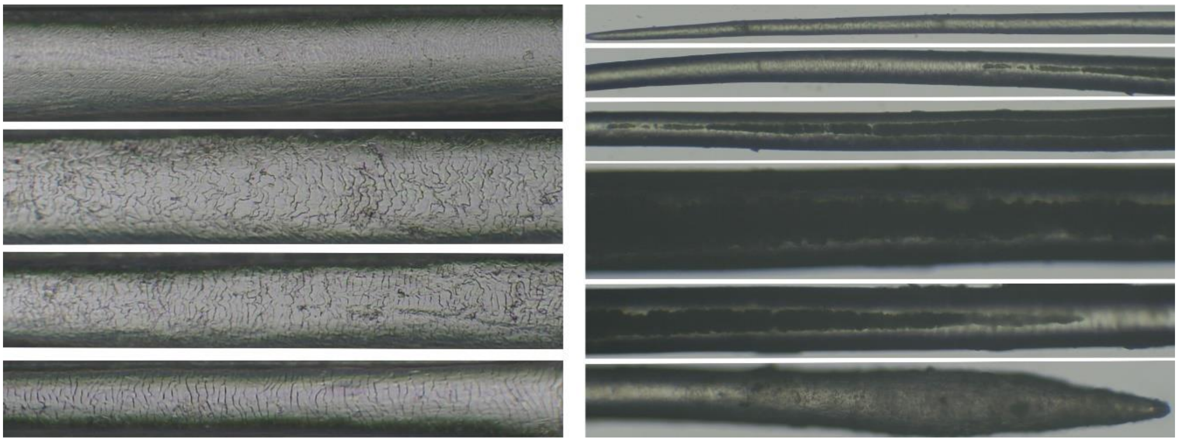

Figure C.14. European badger (Meles meles) – left: cuticle; right: medulla.

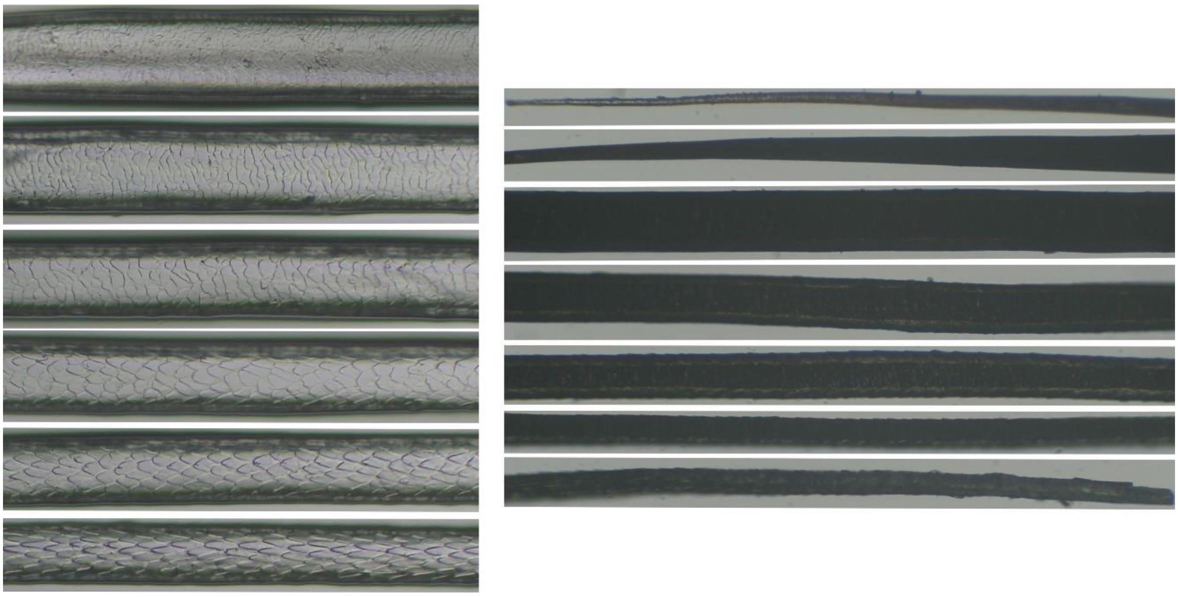

Figure C.15. European polecat (Mustela putorius) – left: cuticle; right: medulla.

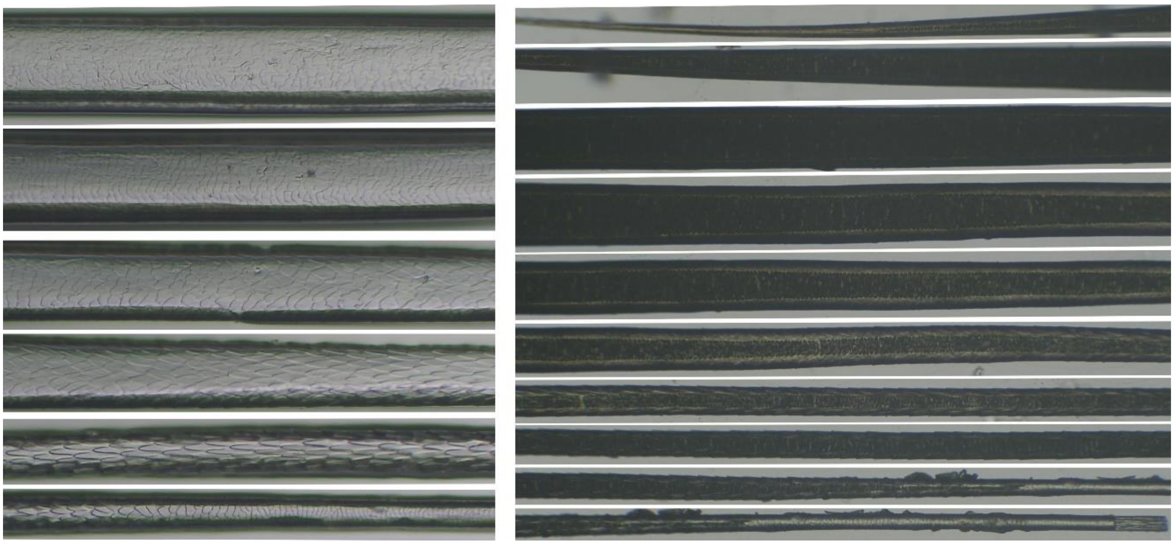

Figure C.16. American mink (Neovison vison) – left: cuticle; right: medulla.

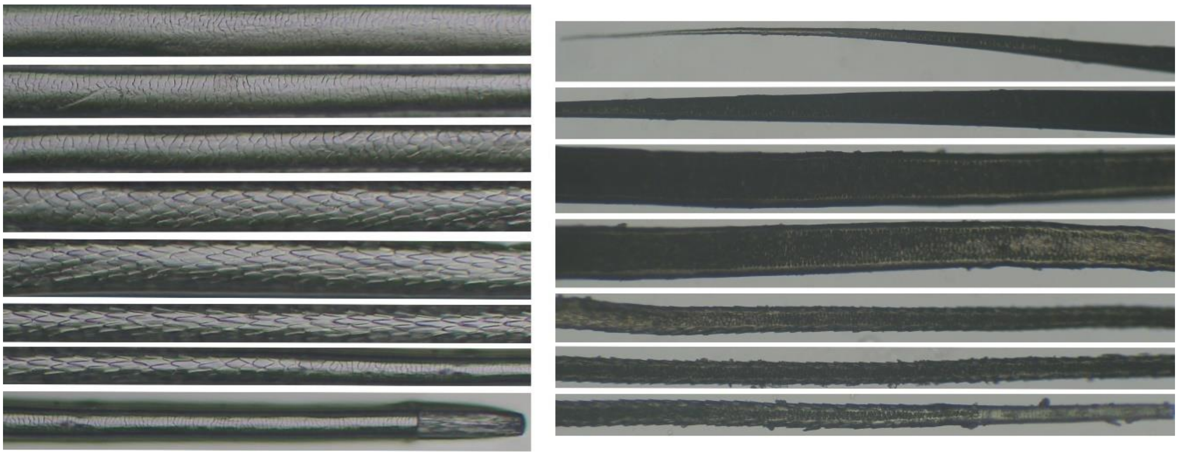

Figure C.17. Stoat (Mustela erminea) – left: cuticle; right: medulla.

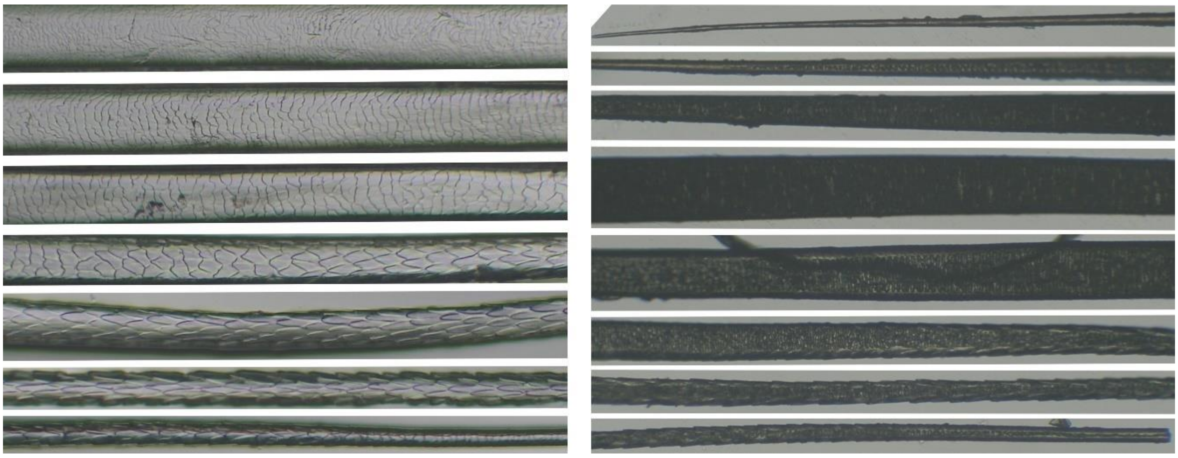

Figure C.18. Weasel (Mustela nivalis) – left: cuticle; right: medulla.

Artiodactyla

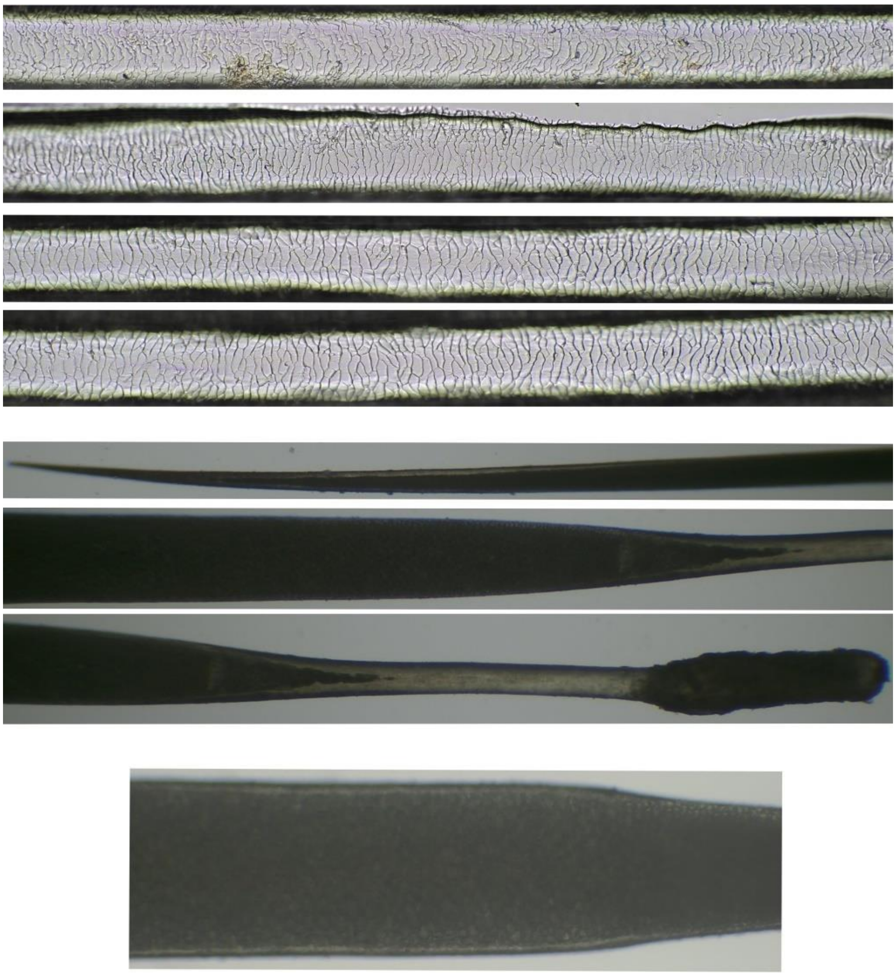

Figure C.19. Red deer (Cervus elaphus) – top: cuticle; middle: medulla; bottom: close-up of medulla.

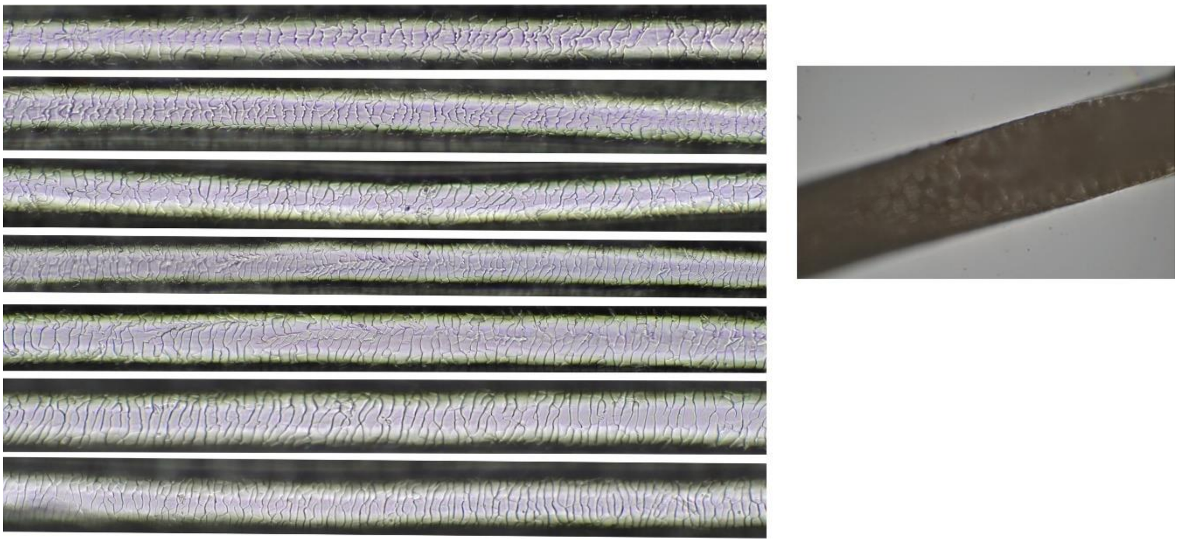

Figure C.20. Roe deer (Capreolus capreolus) – left: cuticle; right: close-up of medulla.

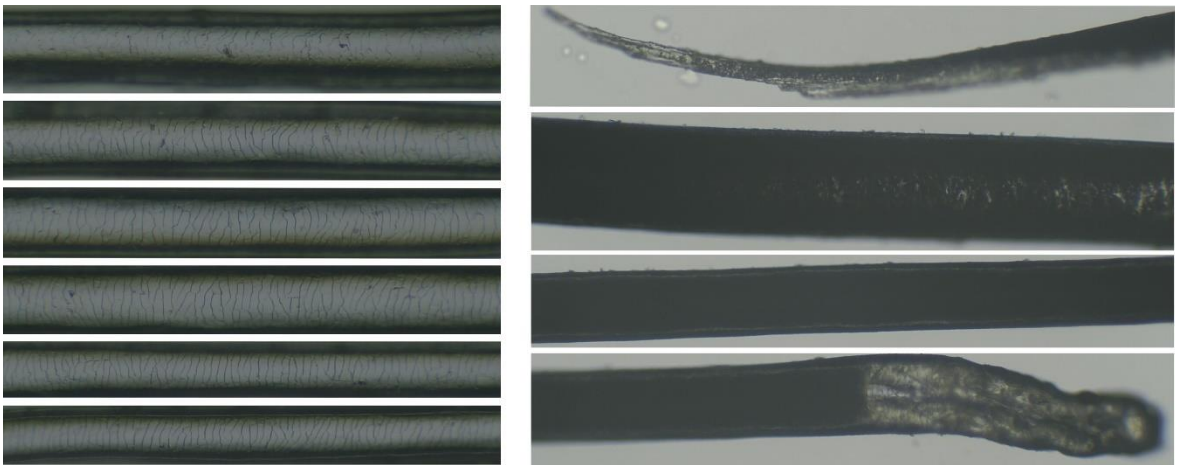

Figure C.21. Domestic goat (Capra capra) – left: cuticle; right: medulla.

Figure C.22. Domestic sheep (Ovis aries) – top: cuticle; bottom: medulla.

Appendix D

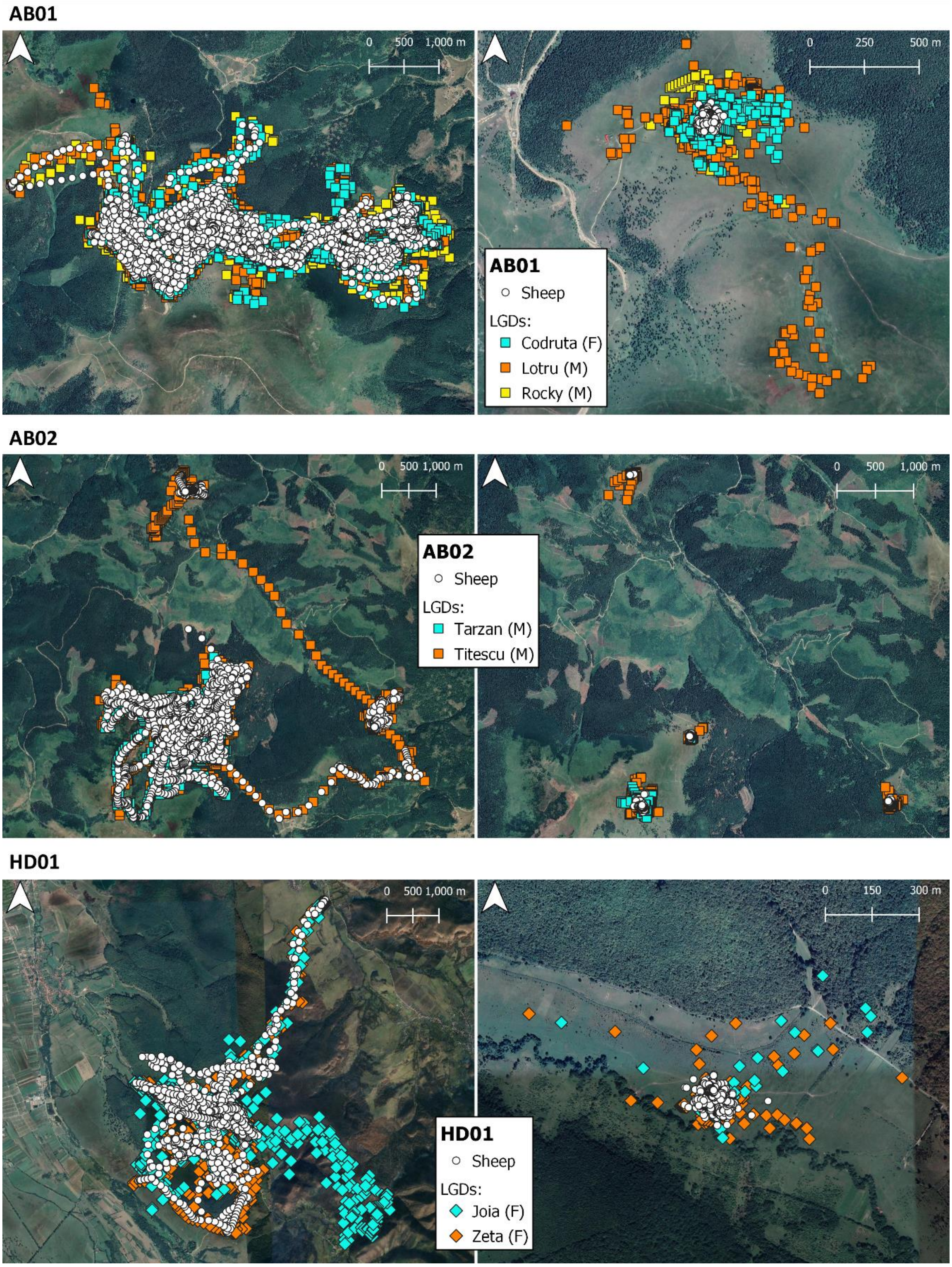

Figure D.1. Locations of sheep (white circles) and LGDs at sites AB01, AB02, and HD01 for the entire GPS tracking duration split between when the sheep were in the sheepfold (right) and out of the sheepfold on the pastures (left). These data are regularised to a 5-minute sampling interval. Each LGD is shown with a coloured diamond for Carpathian Shepherd dogs or square for mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). Maps produced in QGIS using Google Satellite imagery.

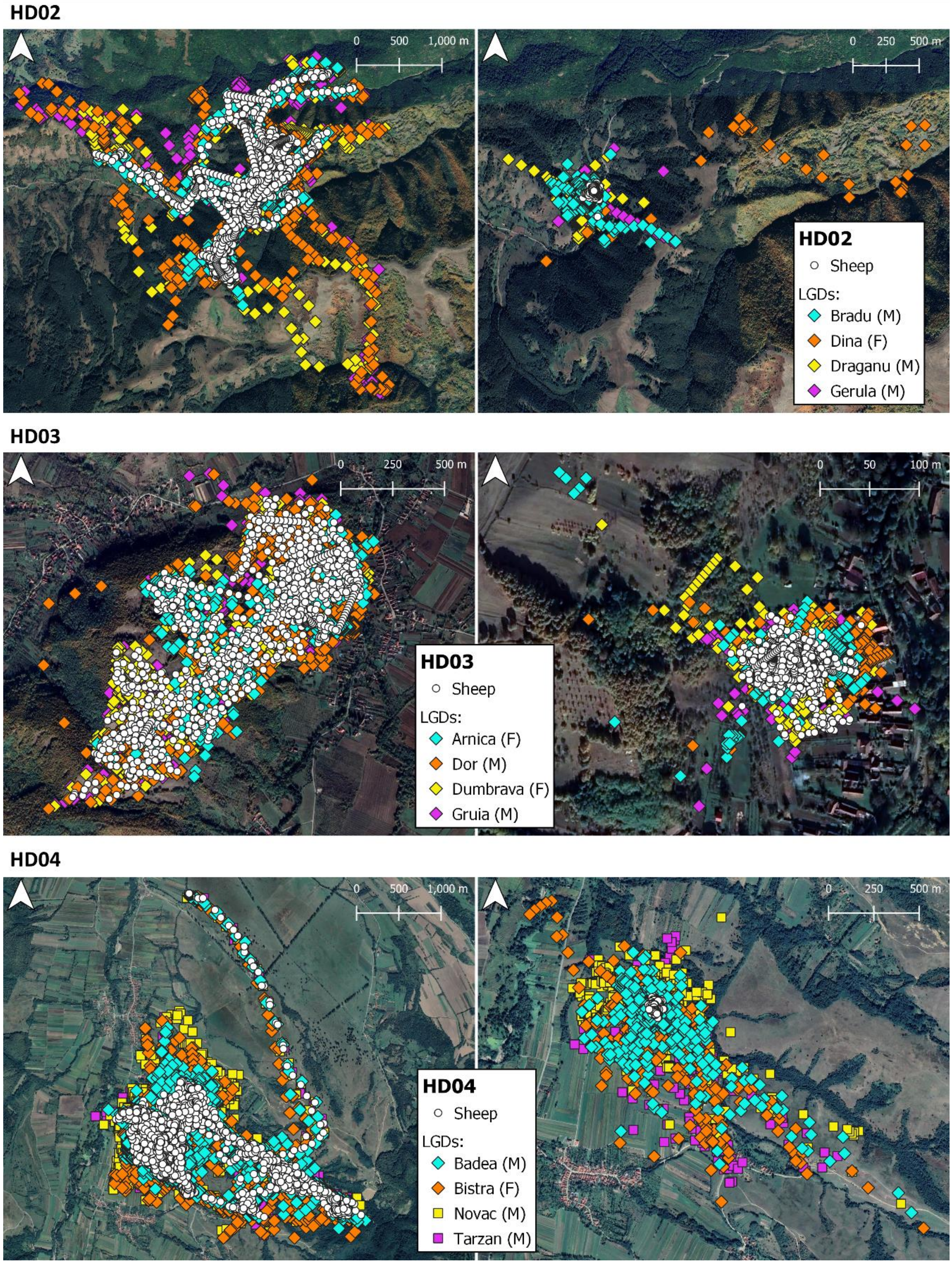

Figure D.2. Locations of sheep (white circles) and LGDs at sites HD02, HD03, and HD04 for the entire GPS tracking duration split between when the sheep were in the sheepfold (right) and out of the sheepfold on the pastures (left). These data are regularised to a 5-minute sampling interval. Each LGD is shown with a coloured diamond for Carpathian Shepherd dogs or square for mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). Maps produced in QGIS using Google Satellite imagery.

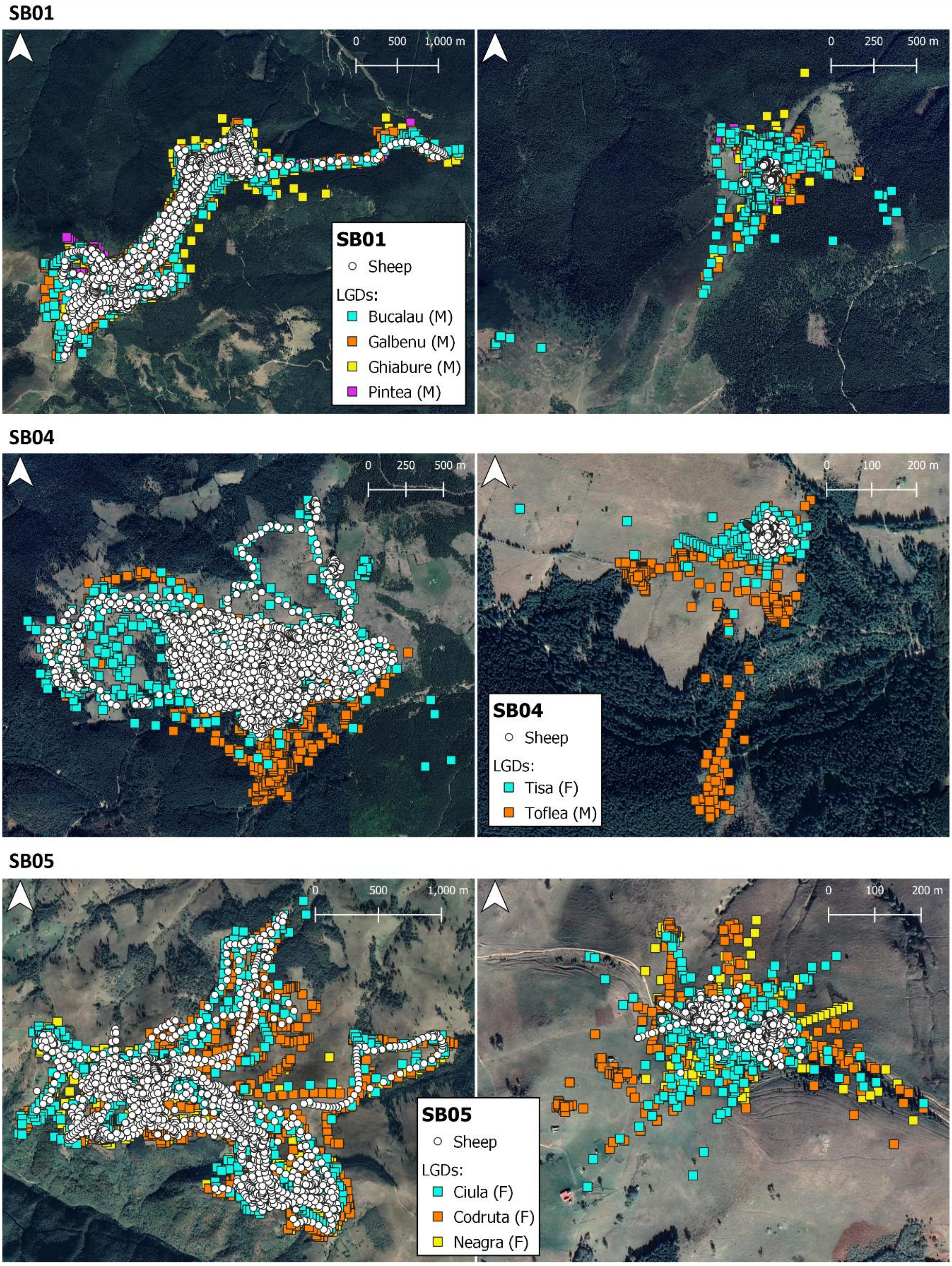

Figure D.3. Locations of sheep (white circles) and LGDs at sites SB01, SB04, and SB05 for the entire GPS tracking duration split between when the sheep were in the sheepfold (right) and out of the sheepfold on the pastures (left). These data are regularised to a 5-minute sampling interval. Each LGD is shown with a coloured diamond for Carpathian Shepherd dogs or square for mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). Maps produced in QGIS using Google Satellite imagery.

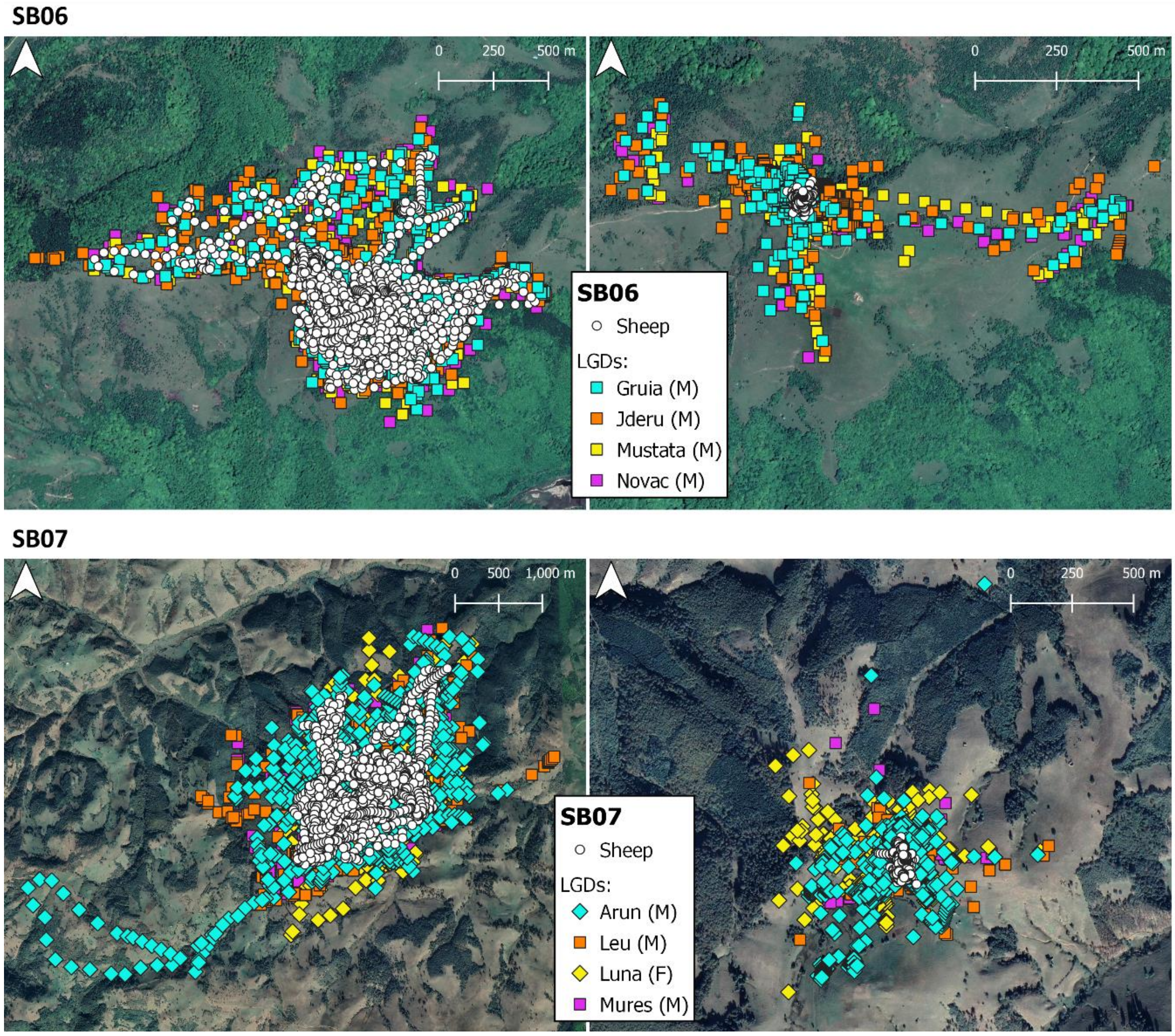

Figure D.4. Locations of sheep (white circles) and LGDs at sites SB06 and SB07 for the entire GPS tracking duration split between when the sheep were in the sheepfold (right) and out of the sheepfold on the pastures (left). These data are regularised to a 5-minute sampling interval. Each LGD is shown with a coloured diamond for Carpathian Shepherd dogs or square for mixed-breed dogs. The sex of each LGD is given in brackets in the legend (M – male; F – female). Maps produced in QGIS using Google Satellite imagery.

Appendix E

Table E.1. Duration in seconds of independent observations of each species grouping. Observations were considered independent when images of the same species at the same site were separated by at least 5 minutes, thus the duration is the time difference between the time of the first and last image of each species grouping per independent observation.

Species common name	**Minimum (s)**	**Maximum (s)**	**Mean (s)**	**SD of the mean**
Human	0	2038	32	96
Herding dog	0	508	42	87
Livestock guarding dog	0	958	72	144
Pet dog	0	205	31	61
Unknown dog type	0	232	12	41
Brown bear	0	494	16	41
Domestic sheep	0	804	181	150
Eurasian badger	0	26	1	4
Eurasian lynx	0	264	14	43
Eurasian red squirrel	0	285	9	42
European hare	0	68	5	12
Grey wolf	0	340	28	51
Martes species	0	150	5	22
Northern chamois	0	999	151	243
Red deer	0	930	68	126
Red fox	0	308	4	22
Roe deer	0	488	26	68
Wild boar	0	1545	39	156
Wildcat	0	64	4	11

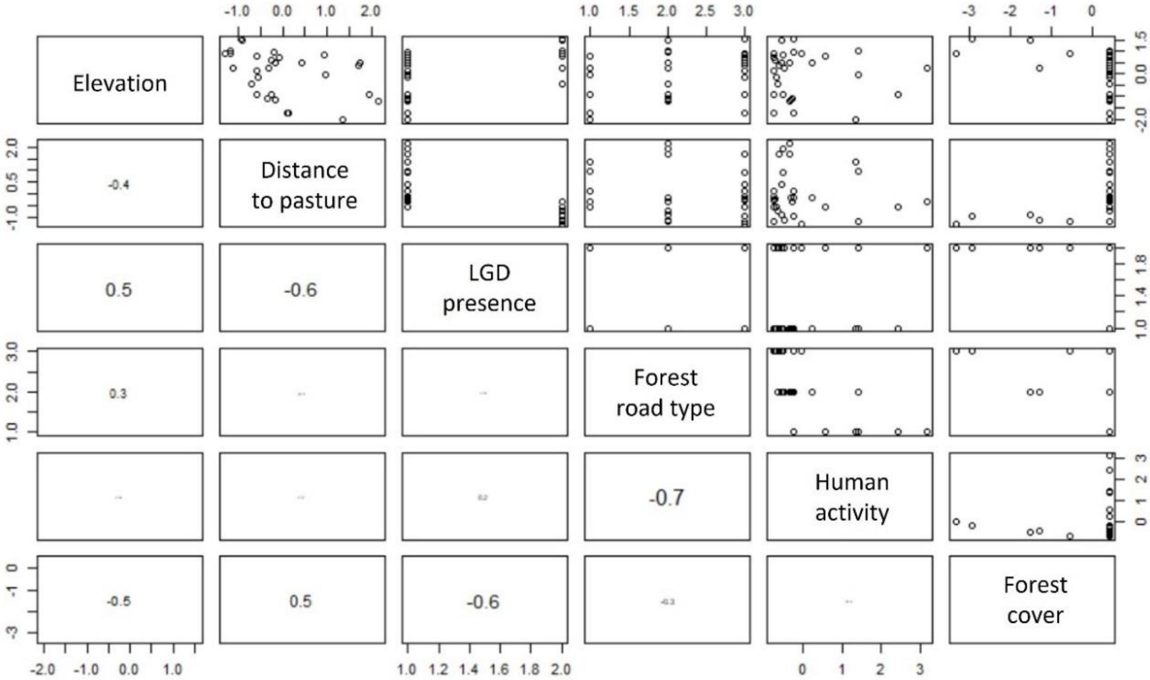

Figure E.1. Correlation plots of the variables considered to influence species occupancy.

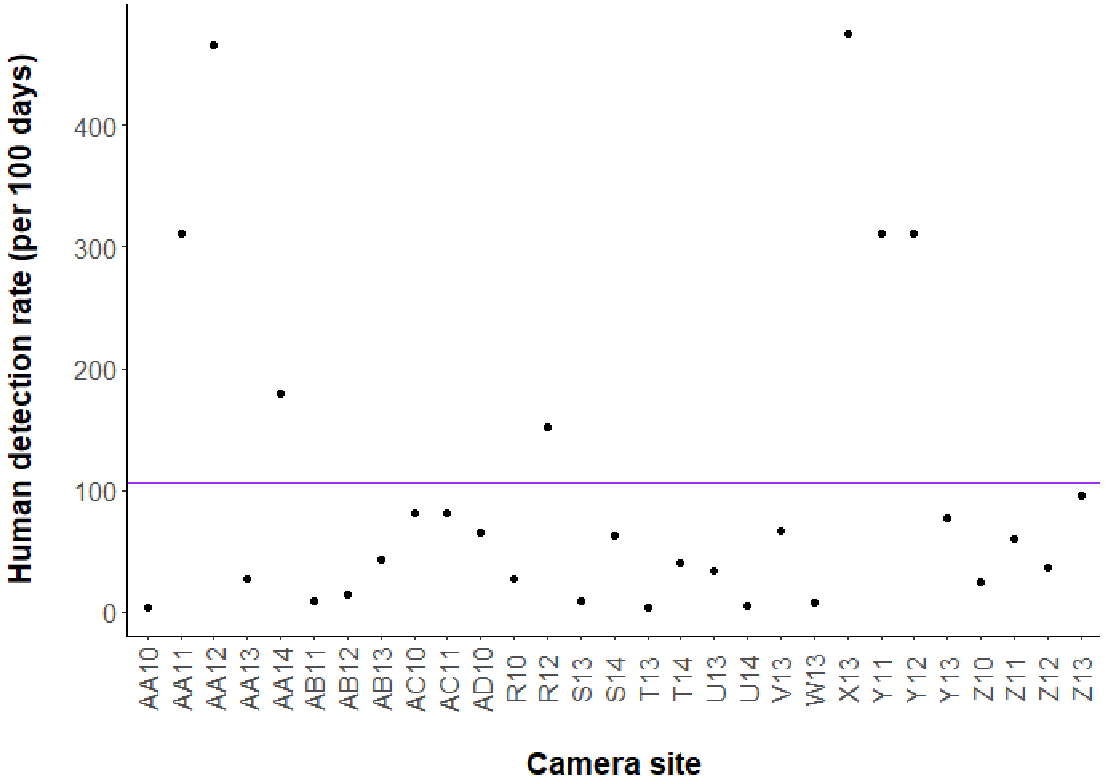

Figure E. 2. Detection rates of humans at each camera site. The purple horizontal line represents the mean detection rates used to split camera sites into high (n = 7) and low (n = 22) human activity sites.

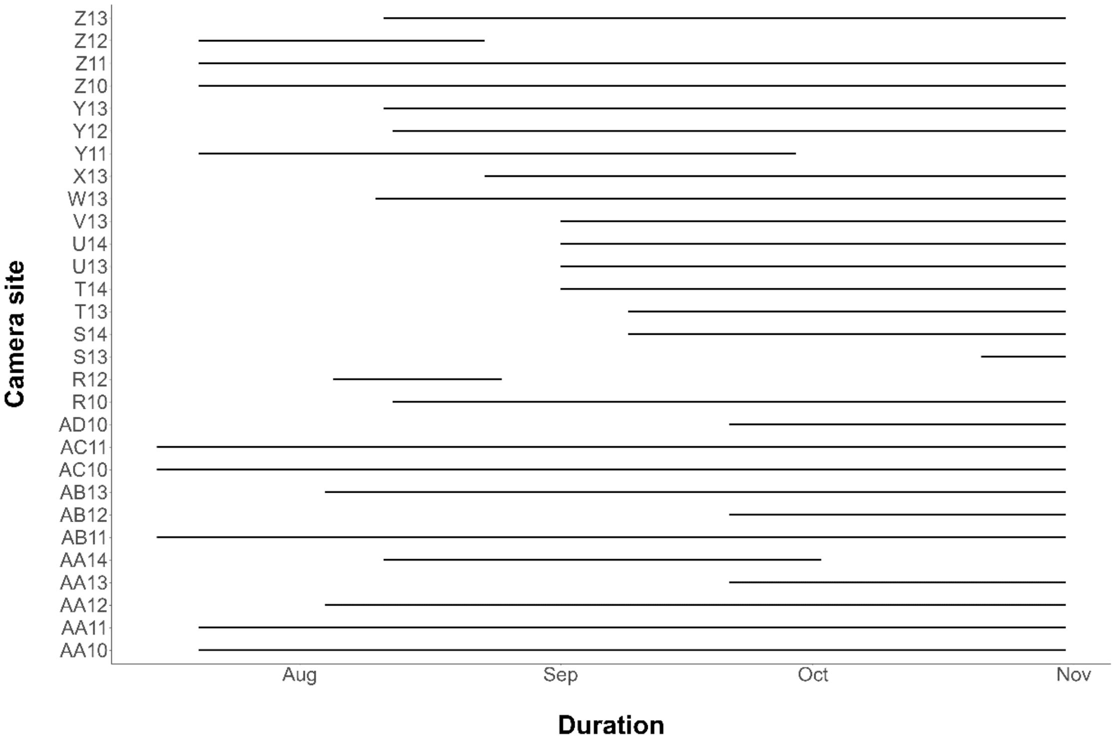

Figure E.3. Active periods of the 29 cameras included in the analyses during the 2021 transhumance grazing season.

Table E.2. Candidate model sets for single species, single season occupancy models ranked by AICc weights. All combinations of candidate models were fitted (eight in total), then those with delta AICc ≤ 10 were subset and the weights recalculated. Final model selection is highlighted in bold, blue text and was based on consideration of the delta AICc, model weights, and per-variable sum of model weights (Table E.3).

Species	**Variables**	**df**	**AICc**	**delta AICc**	**weight**
LGD	**~ Distance to pasture + Human activity**	**4**	**147.50**	**0.00**	**0.62**
	~ Distance to pasture + Human activity + Elevation	5	149.20	1.76	0.26
	~ Elevation + Human activity	4	151.10	3.66	0.10
	~ Human activity	3	156.00	8.47	0.01
	~ Distance to pasture	3	157.20	9.71	0.01
Bear	**~ Elevation + Human activity**	**4**	**280.70**	**0.00**	**0.50**
	~ Elevation	3	282.30	1.59	0.22
	~ Elevation + LGD presence + Human activity	5	283.60	2.83	0.12
	~ Elevation + LGD presence	4	284.00	3.29	0.10
	~ LGD presence	3	286.00	5.30	0.04
	~ LGD presence + Human activity	4	286.90	6.22	0.02
	~ 1	2	289.70	8.94	0.01
Wolf	**~ Elevation**	**3**	**232.80**	**0.00**	**0.59**
	~ Elevation + LGD presence	4	235.40	2.59	0.16
	~ Elevation + Human activity	4	235.40	2.66	0.16
	~ 1	2	238.10	5.32	0.04
	~ Elevation + LGD presence + Human activity	5	238.30	5.48	0.04
	~ Human activity	3	240.60	7.82	0.01
	~ LGD presence	3	242.60	9.86	0.00
Fox	**~ 1**	**2**	**362.00**	**0.00**	**0.43**
	~ LGD presence	3	364.00	2.03	0.16
	~ Human activity	3	364.00	2.06	0.15
	~ Elevation	3	364.50	2.50	0.12
	~ LGD presence + Human activity	4	366.40	4.45	0.05
	~ Elevation + LGD presence	4	366.50	4.54	0.04
	~ Elevation + Human activity	4	366.70	4.74	0.04
	~ Elevation + LGD presence + Human activity	5	369.30	7.38	0.01
Red deer	**~ LGD presence**	**3**	**346.00**	**0.00**	**0.51**
	~ Elevation + LGD presence	4	348.10	2.05	0.18
	~ LGD presence + Human activity	4	348.70	2.68	0.13
	~ 1	2	350.30	4.28	0.06
	~ Elevation + LGD presence + Human activity	5	351.00	4.98	0.04

	~ Elevation	3	351.30	5.24	0.04
	~ Human activity	3	352.50	6.45	0.02
	~ Elevation + Human activity	4	352.70	6.64	0.02
Wild boar	**~ 1**	**2**	**196.20**	**0.00**	**0.40**
	~ LGD presence	3	197.90	1.70	0.17
	~ Human activity	3	198.20	1.98	0.15
	~ Elevation	3	198.40	2.16	0.13
	~ LGD presence + Human activity	4	200.30	4.06	0.05
	~ Elevation + Human activity	4	200.40	4.25	0.05
	~ Elevation + LGD presence	4	200.60	4.39	0.04
	~ Elevation + LGD presence + Human activity	5	203.10	6.94	0.01

Table E.3. Per-variable sum of model weights to infer relative importance of each variable in the candidate model sets from Table E.2. The sum of the weights and number of models in the candidate set containing each variable are provided, with variables considered to have the greatest relative importance highlighted in bold, blue text.

Species	**Variables**	**Sum of weights**	**No. of models**
LGD	Elevation	0.36	2
	Human activity	**0.99**	**4**
	Distance to pasture	**0.89**	**3**
Bear	**Elevation**	**0.94**	**4**
	Human activity	0.64	3
	LGD presence	0.27	4
Wolf	**Elevation**	**0.94**	**4**
	Human activity	0.2	3
	LGD presence	0.2	3
Fox	Elevation	0.217	4
	Human activity	0.25	4
	LGD presence	0.256	4
Red deer	Elevation	0.28	4
	Human activity	0.21	4
	LGD presence	**0.86**	**4**
Wild boar	Elevation	0.237	4
	Human activity	0.258	4
	LGD presence	0.277	4

Table E.4. Number of images and independent detections of each species or species grouping across all of the sites, a subset of the sites (the 30 selected for inclusion in the analyses in this study) and lastly just for the 2021 grazing season. Values denoted with an asterisk (*) are data used in this study.

Species	**Common name**	**Images (all)**	**Independent observations (all)**	**Independent observations (site subset)**	**Independent observations (site subset, grazing season)**
Ursus arctos	Brown bear	2695	535	476	163 *
Canis lupus	Grey wolf	2040	293	292	91 *
Lynx lynx	Eurasian lynx	336	86	86	18
Canis aureus	Golden jackal	5	2	2	0
Vulpes vulpes	Red fox	1761	1037	1007	447 *
Felis silvestris	Wildcat	88	53	46	33
Meles meles	Eurasian badger	90	54	53	12
Martes spp.	Martes spp.	122	86	79	11
Cervus elaphus	Red deer	18190	955	783	378 *
Capreolus capreolus	Roe deer	648	115	98	45
Rupicapra rupicapra	Chamois	1190	93	93	25
Sus scrofa	Wild boar	1596	145	110	72 *
Sciurus vulgaris	Eurasian red squirrel	99	84	80	53
Lepus europaeus	European hare	67	43	38	8
Erinaceus roumanicus	Northern white-breasted hedgehog	9	6	6	0
Aves	Bird	180	89	78	38
Felis catus	Domestic cat	5	4	4	4
Canis familiaris	Dog - pet	201	41	36	15
Canis familiaris	Dog - herding	467	47	47	45
Canis familiaris	Dog - Livestock guarding dog	1833	164	159	155 *
Canis familiaris	Dog - unknown type	80	38	37	17
Bos taurus	Domestic cattle	433	3	2	2
Equus asinus	Domestic donkey	914	39	39	39
Equus ferus caballus	Domestic horse	806	99	98	86
Ovis ares	Domestic sheep	5695	54	53	50
Homo sapiens	Human	34061	4234	4162	2272 *
Unknown	Unknown animal	359	272	226	116
Blank	Blank	27810	4943	3460	1752

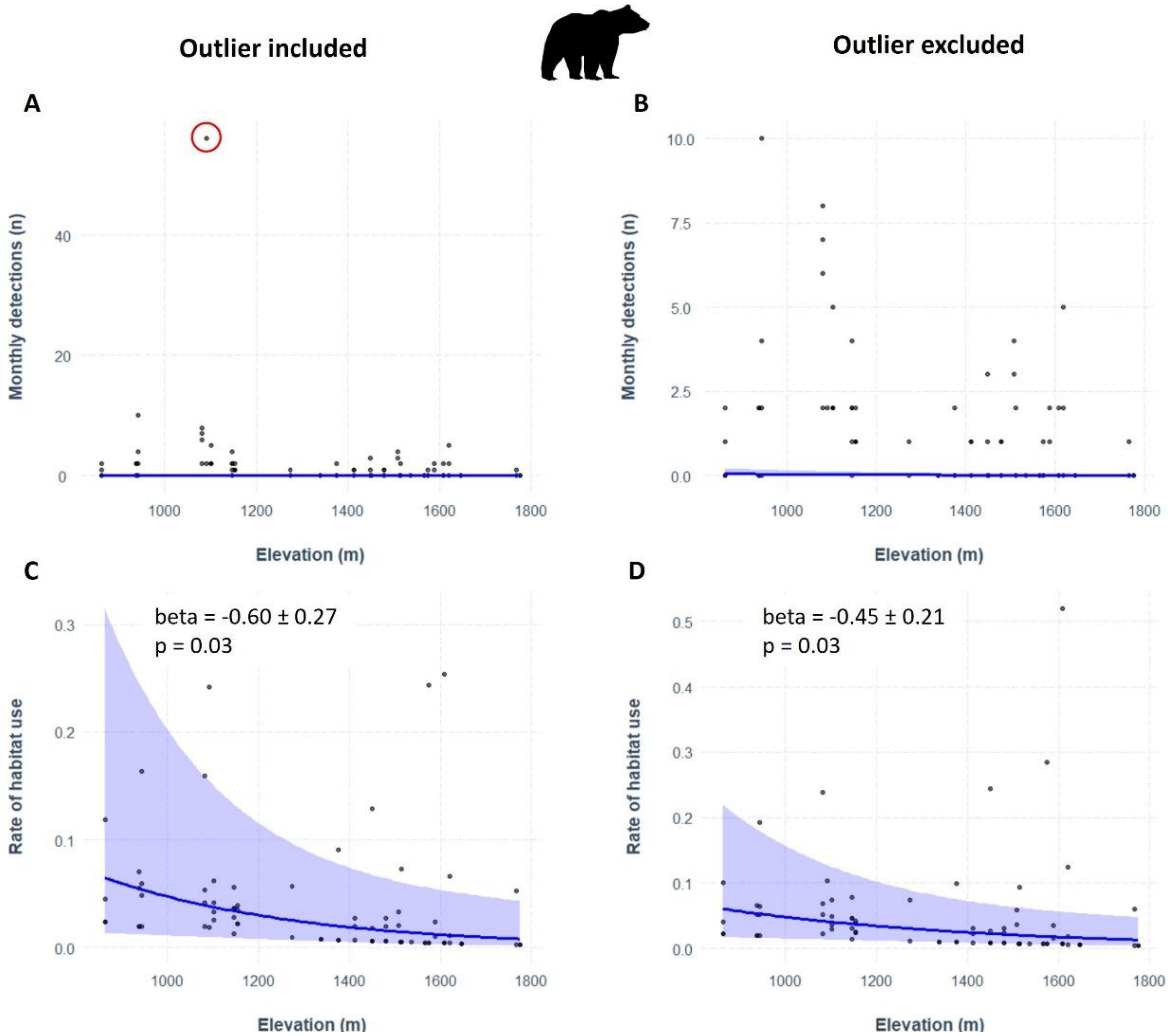

Figure E.4. Monthly detections of brown bears modelled with and without an outlier in the data. The outlier (A-red circle) was one site in October 2021 that captured 56 independent observations of brown bears. Both the raw counts (A-B) and the model predictions shown with the partial residuals (C-D) are shown. The y-axis in the model predictions represents a rate of detections as the number of active camera trapping days each month was included in the model as an offset. The model estimate (beta) and p-value of the effect of elevation on brown bear detections is given showing little difference in effect sizes and level of statistical significance between including and excluding the outlier.