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Authors: Smith, Bethany R., Yarnell, Richard W., Uzal, Antonio, and Whitehouse-Tedd, Katherine

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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

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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

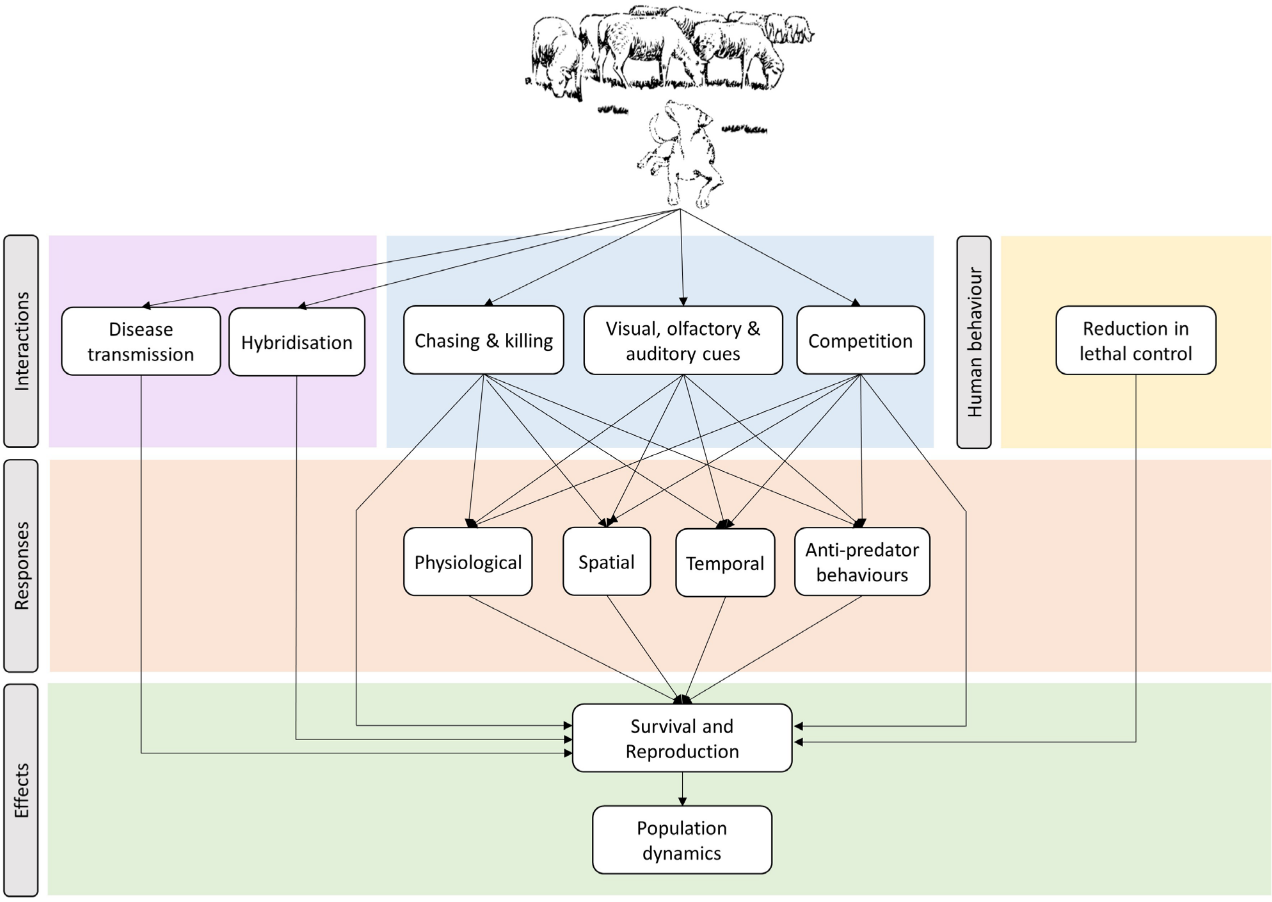

Fig. 1. Conceptual ecological framework of the pathways by which livestock guarding dogs (LGDs) could affect wildlife. As a form of free-ranging domestic dog, LGDs could interact with wildlife and affect species via disease transmission and hybridisation (purple), or by acting as predators or competitors 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

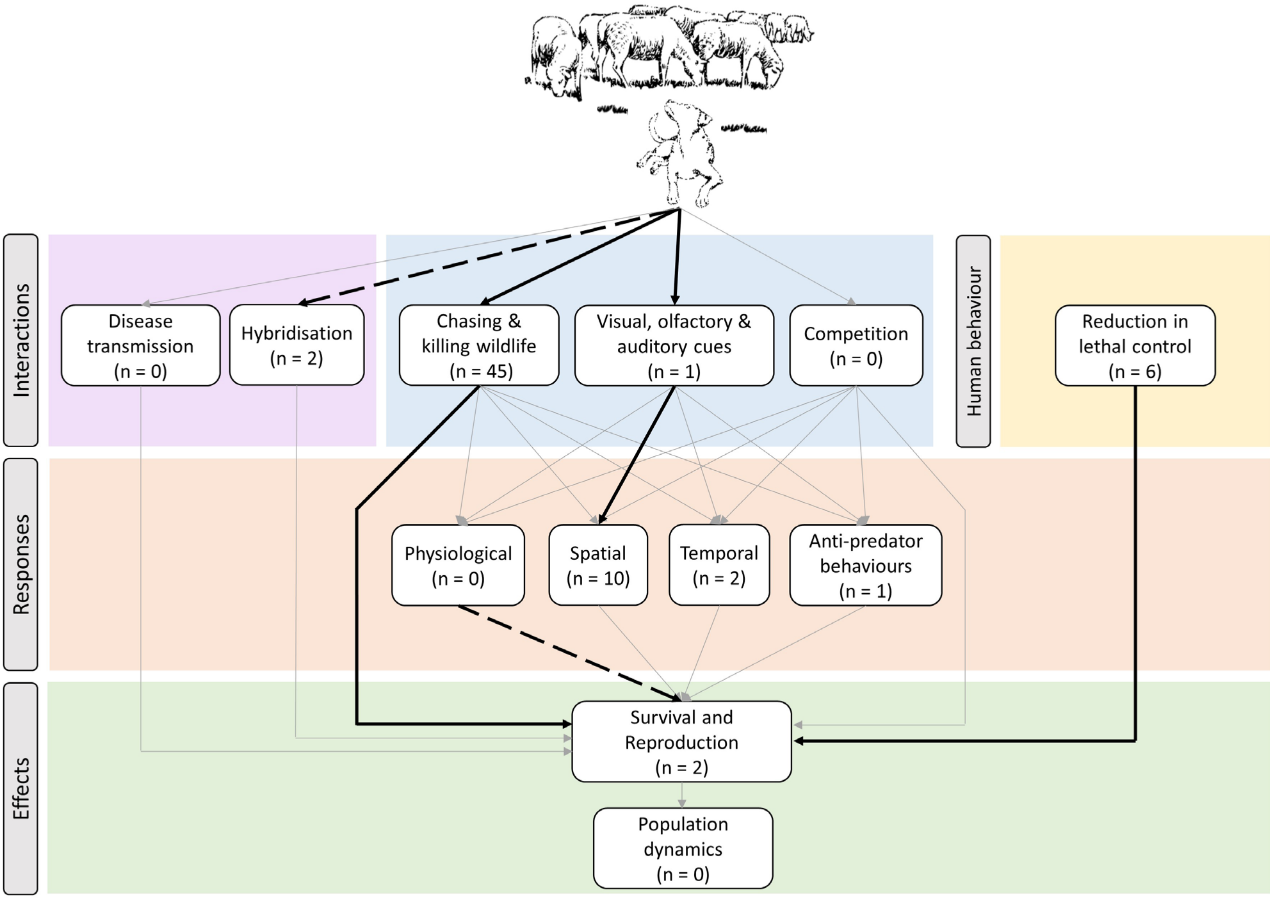

Fig. 2. Representation of the 56 studies found investigating each of the pathways by which livestock guarding dogs (LGDs) could theoretically affect wildlife. The number of publications (n) reporting each interaction, response or effect is given in each associated box. These publication numbers are not 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

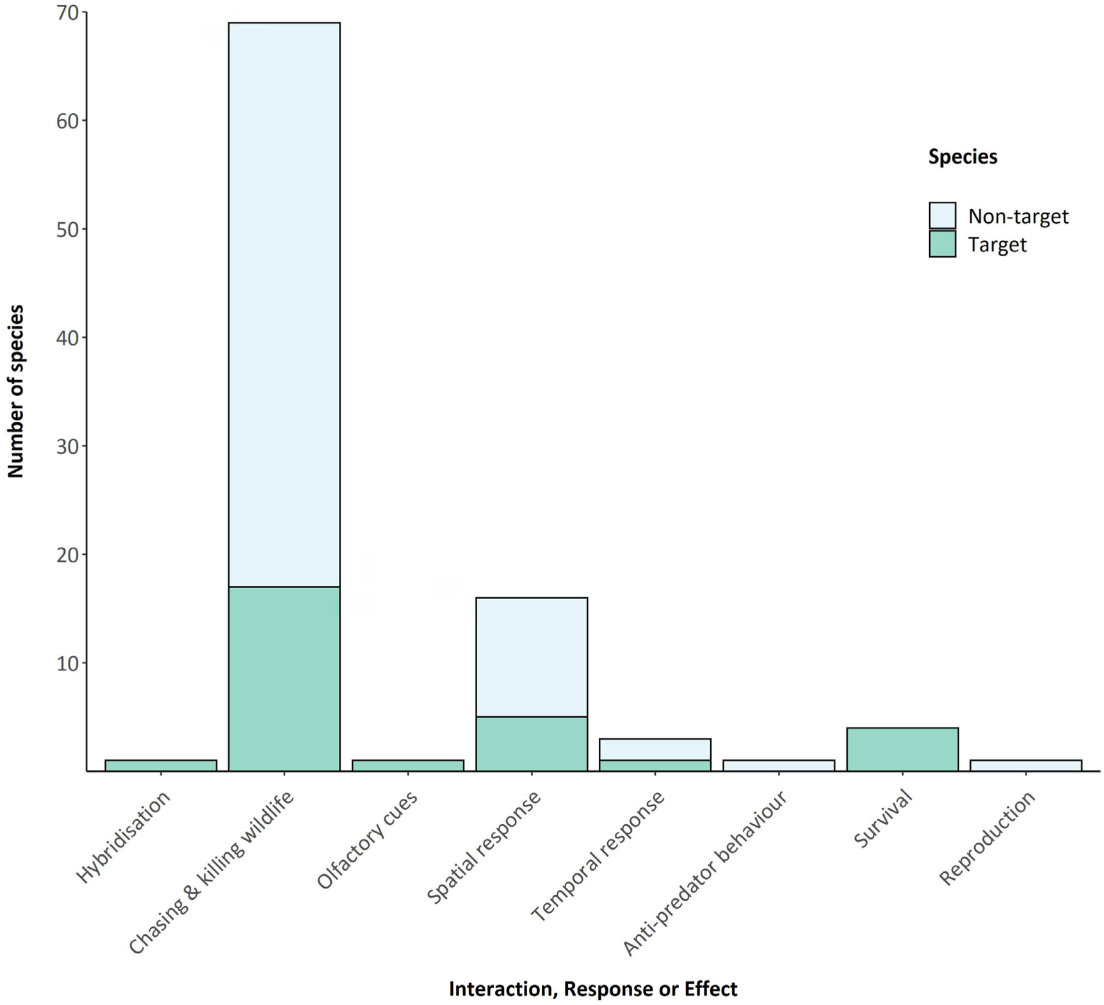

Fig. 3. Number of named species reported to interact with, respond to, or be affected by livestock guarding dogs (LGDs) as determined from a literature search (1970-July 2020). Bars are stacked by the number of target species (responsible for livestock depredation) and non-target species.

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.

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Supplementary online material

Table S1. Summary of the 56 publications found in the literature search that investigated or reported an ecological effect associated with the use of livestock guarding dogs (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) (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-3-2020-SmithB.R.-et-al.-Table-S1.docx).

Table S2. Species investigated with regards to interacting with livestock guarding dogs (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, we categorised the species as having been affected by LGDs (Y = yes in "Affected"). In total, we found 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 (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-3-2020-SmithB.R.-et-al.-Table-S2.docx).