



Predation of wildlife by free-ranging domestic dogs in Polish hunting grounds and potential competition with the grey wolf



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ABSTRACT

Although the domestic dog (*Canis familiaris*) is a ubiquitous exotic predator that can detrimentally affect natural environments, studies on their ecological impact are relatively scarce, particularly at a national scale. We exploited data derived from Polish Hunting Association reports to provide a national evaluation of rural free-ranging dogs in Poland. Our results demonstrate that free-ranging dogs are widespread and abundant, frequently killing wildlife and livestock in Poland and likely exerting intraguild competition with native carnivores such as grey wolves (*Canis lupus*). On average, hunting club records estimate that over 138,000 rural free-ranging dogs occurred annually in hunting grounds. In addition, nearly 3000 free-ranging greyhounds and their mixed breeds occurred annually on hunting grounds, although greyhound hunting has been banned in Poland and they are legally required to be restrained within fencing. On average, over 33,000 wild animals and 280 livestock were killed by free-ranging dogs on Polish hunting grounds annually. The number of both wild animals and livestock killed by dogs were strongly and positively correlated with the numbers of rural free-ranging dogs recorded on hunting grounds, reflective of their predation pressure. Also, the number of wild animals killed by dogs was positively correlated with estimates of population sizes and harvest levels of wildlife, reflective of prey availability. Dog predation, in conjunction with harvest by humans, may cause unsustainable off-take rates of some game species. Grey wolves, documented within 39 of the 49 Hunting Districts, ate similar prey as dogs, including ungulates and livestock, and killed dogs on hunting grounds, suggesting both resource and interference competition between these sympatric canids. This comprehensive analysis provides important information about the ecological impact of free-ranging dogs and recommendations for alternative legislative and management measures to control their impacts.

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1. Introduction

Domestic dogs (*Canis familiaris*) are among the most popular companion animals and one of the world's most common carnivores (Gompper, 2014b). Globally, dog ownership is widespread, ranging from 37% of US households (AVMA, 2012), 27% of European households (FEDIAF, 2010), 39% of Australian households (AHA, 2014), and up to 86% of households in Chile (Sepulveda et al., 2014; Silva-Rodríguez and Sieving, 2012). The worldwide dog population is estimated to be between 700 and 900 million (Gompper, 2014b; Hughes and Macdonald, 2013). Given their close association with and subsidies

from humans, dogs have access to most ecosystems globally (Gompper, 2014b; Hughes and Macdonald, 2013; Young et al., 2011).

A growing body of literature demonstrates that dogs can have significant detrimental effects on natural environments. For example, dogs act as predators of a variety of native fauna, primarily mammals but also birds, reptiles, amphibians, and invertebrates, and also prey on domestic livestock (Hughes and Macdonald, 2013; Ritchie et al., 2014; Vanak and Gompper, 2009; Young et al., 2011). Non-lethal interactions can also disturb wild animals, including disruption of physiology and normal behaviour such as foraging, vigilance, and bedding (Weston and Stankowich, 2014). Dogs carry pathogens transmissible to wildlife and humans, serving as reservoirs and vectors for disease such as rabies and canine distemper virus (Knobel et al., 2014; Macpherson et al., 2013). Intraguild interactions between domestic dogs and native carnivores can be particularly impactful. Dogs act as resource and interference competitors with sympatric carnivores, competing for prey and

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carion and excluding, and sometimes killing, predators in their guild (Butler and du Toit, 2002; Vanak et al., 2014; Vanak and Gompper, 2009). Conversely, dogs also serve as prey for other carnivores, exacerbating human-carnivore conflict (Butler et al., 2014; Kojola and Kuittinen, 2002; Young et al., 2011). Additionally, dogs hybridize with native canids, including wolves (*Canis lupus*, *Canis simensis*), jackals (e.g., *Canis aureus*), and coyotes (*Canis latrans*), resulting in loss of genetic integrity (Leonard et al., 2014).

Recent publications (e.g., Hughes and Macdonald, 2013; Lescureux and Linnell, 2014; Ritchie et al., 2014) stress the paucity of scientific studies on the ecological impact of domestic dogs. Research on the impacts of domestic dogs at a national rather than local scale are notably scarce. Legislation in Poland specific to dogs and wildlife provides an unusual opportunity to conduct such an analysis. The 1995 Hunting Act in Poland stipulates that hunting can be exercised only by members of the Polish Hunting Association (PHA), with Poland divided into hunting grounds managed by hunting clubs within 49 Hunting Districts. Recent data estimate 116,000 hunters in the 2550 PHA hunting clubs (CSO, 2014). Although members of hunting clubs can hunt free of charge, they are obliged to deliver the harvested animals to hunting club headquarters as all game belong to the Polish government. Hunting Districts must prepare annual hunting reports that include data on hunting ground management, annual harvest, and estimated population sizes of game species. In addition, reports include information on free-ranging dogs, both owned and stray, including greyhounds, which are still illegally used for hunting.

Poland contains an estimated 6–8 million dogs (Fiszdon and Boruta, 2012; Tasker, 2007), including between 75,000 and 650,000 strays (Kofłataj et al., 2011; Tasker, 2007). No study has evaluated the population status, management, and ecological impact of free-ranging dogs in Poland. Here, we exploit data derived from Polish Hunting Association reports to provide the first national evaluation of rural free-ranging (RFR) dogs, including their numbers and their prey recorded by hunting clubs between 2001 and 2011. We hypothesized that dog abundance would positively predict depredation of wildlife and livestock on hunting grounds. We also hypothesized that depredation events would be positively correlated with prey availability, as indexed both by estimated population sizes of wildlife as well as hunter harvest. In addition, we evaluated available data on the geographic distribution of free-ranging grey wolves in Poland between 2006 and 2011 to predict the degree of spatial overlap and hence potential intraguild interactions by dogs and wolves. This comprehensive analysis represents one of the first such studies of dogs and their impacts on a national scale and provides important guidance on alternative legislative and management measures to control their impacts.

2. Materials and methods

2.1. Study area

The study was conducted in Poland, a 322,575 km² country with an estimated 38.5 million people, including 23.3 million urban and 15.3 million rural residents (CSO, 2014). Poland contains 4696 hunting grounds encompassing 252,546 km². Each hunting ground is rented and managed by a hunting club for at least 10 years. Each hunting club contains at minimum 10 hunters. According to the Polish Hunting Act, each hunting club must employ at least one hunting guard who lives in close proximity to the hunting grounds and is responsible for continuously monitoring the area. There are approximately 7200 hunting guards distributed across the 4696 hunting clubs.

Until 1997, free-ranging domestic cats and dogs observed by hunters in hunting grounds were considered pests and had to be eliminated by shooting. Between 1981 and 1996, the average (SD) annual numbers of domestic dogs and domestic cats killed was 59,596 (10,069.5) and 58,427 (10,158.3), respectively (RS PHA, 1998). A 1997 Polish Animal Protection Act, however, mandated that dogs and cats could be killed

only in specific instances, such as humanitarian or health circumstances or excessive aggressiveness towards humans. The potential ecological impact of domestic dogs and cats was disregarded in Polish law until 2003, when a new regulation was amended to the Animal Protection Act permitting shooting of free-ranging cats and dogs at least 200 m from the nearest households within hunting grounds. Increasing public protest forced additional revisions to the Act in 2011 and 2013, which still allowed lethal control when animals presented a direct threat to humans or wildlife, but stipulated other management options for free-ranging dogs, including requiring restraint of owned dogs and trapping roaming dogs and placing them in animal shelters.

A separate regulation relates to greyhounds, which have a long traditional link to hunting in Poland. The Polish greyhound, originating in the 13th century, is officially registered as a dog breed by Federation Cynologique International (Davis, 1999). Until the mid-20th century, these dogs were bred and used for chasing game. In 1959, hunting with greyhounds was banned in Poland and breeding of greyhounds was allowed only with permission of local municipalities. Although greyhounds and their mixed breeds must be kept in fenced enclosures to prevent escape, they are still found in Polish villages and are used for illegal hunting, especially on brown hares (*Lepus europaeus*).

2.2. Data collection

We collected data from hunting reports submitted by the 49 Polish Hunting Districts between 2001 and 2011. We summarized data on estimates of the numbers of free-ranging dogs observed by hunters on hunting grounds. As illegal hunting with greyhounds is still a problem in some regions of Poland, hunting clubs are obliged to report such cases in their annual reports; villages are inspected by designated hunters and local municipality officers to verify if the owner has written permission to own a greyhound and if housing conditions are in accordance with the regulation mandating greyhound enclosures.

We classified dogs as RFR, which, following Vanak and Gompper (2009), are owned or peripherally associated with human habitations but not confined to prescribed outdoor areas. Such dogs include 'stray' dogs as well as owned farm or pastoral companion dogs whose ranging behaviour may bring them into contact with wildlife, especially when human habitations border natural habitat. Because hunting club members, including designated hunting guards, are often local villagers that live in the vicinity of hunting grounds, they communicate regularly with dog owners and typically know owned dogs and can recognize and identify unowned strays. The phenotypic diversity of dogs, including differences in size and pelt colour, enables hunting guards and club members to identify individual dogs and avoid double-counting. Nonetheless, the possibility remains that some double-counting does occur, resulting in an overestimation of the dog population. The procedure for counting dogs in hunting grounds is the same in all hunting clubs across Poland and is controlled and evaluated by the Polish Hunting Association, so any possible estimation bias is similar across Hunting Districts.

We also collected reported data on annual estimates of populations of game species on hunting grounds, estimated directly via visual observations of animals during line-transect distance sampling, drive counts, or plot sampling, or indirectly via track counts (Borkowski et al., 2011; Češko, 2011; Fonseca et al., 2007). Although survey methods differ among clubs and thus have limitations (Wawrzyniak et al., 2010), we assumed that they were reliable enough to provide comparable information on the relative abundance of game species, as have prior studies (e.g., Borkowski et al., 2011; Panek, 2006). In addition, we summarized data on harvest levels within each hunting ground. Because harvest management plans are based upon the estimated population of a game species, we assumed that harvest levels also reflected relative abundance of game and thus prey availability. Hunters cannot harvest more game than is permitted by the harvest management plan and cannot attribute their own harvest to dogs or wild predators. We focused

analyses of estimated population and hunter harvest of game species that are primary prey of dogs, including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*), and brown hare.

In addition to harvest, the cause of mortality of all game species must be reported in annual reports, including poaching, road kills, natural causes (e.g., disease, starvation), and predation by dogs or wild carnivores. The cause of death is verified and approved by hunting guards and hunting club members, who are obliged to participate in a two-year course and pass a final exam regarding the ecology of game species and identification of mortality causes. In contrast to native predators such as wolves, domestic dogs indiscriminately attack any part of the animal, but often tend to start to attack from the hindquarters and abdomen, typically injuring or killing them but seldom feeding on them (Gese et al., 2004; Green and Gipson, 1994; Kossak, 1998). If dogs do consume prey entirely, especially smaller animals such as brown hare, then such kills would not be available for identification, thus resulting in underestimates of predation by dogs. Similarly, if native carnivores remove carcasses of animals killed by dogs (Davis et al., 2015; Ritchie et al., 2014), then this would also result in the underestimation of dog kills.

We also summarized estimates of livestock depredated by dogs. Qualified officers of the Regional Directorate of Environmental Protection, in consultation with veterinarians and hunting club representatives, differentiate between those killed by dogs and by native species such as wolves, lynx (*Lynx lynx*), and brown bears (*Ursus arctos*). The Polish government provides monetary compensation for livestock killed by native carnivores but not by dogs.

Since 2006, the Poland Hunting Association also has collected data from each Hunting District on the presence of grey wolves and their extent of predation on livestock, domestic dogs, and ungulate species (i.e., red deer, roe deer, and wild boar). We summarized these data to estimate predation pressure by wolves in comparison to dogs, and to explore spatial overlap and hence potential for intraguild competition between these two sympatric canids. Data were unavailable for wolf predation on fallow deer, an introduced game species with a relatively restricted distribution in Poland, primarily where wolves are absent or sparse. Polish wolves rarely have brown hare remains in their diet (Jędrzejewski et al., 2012; Nowak et al., 2011). But, if wolves do predate on brown hare, unlike dogs, they typically eat them entirely, so hares predated by wolves would not be available for identification.

2.3. Statistical analyses

We calculated the estimated total and annual average (SD) numbers and density per 100 km² of RFR dogs and free-ranging greyhounds during 2001–2011 and the percentage of stray dogs based on Hunting District reports. We also calculated annual average (SD) numbers and density per 100 km² of RFR dogs in Hunting Districts with confirmed wolf presence compared to those without wolf detections during 2006–2011. Geographic distribution of wolves was recorded as a binary record (1 = presence; 0 = absence) using UTM (Universal Transverse Mercator) layers with grid cell size 100 km² (<http://www.iop.krakow.pl/ssaki/>). This UTM digital layer was combined with borders of Hunting Districts to display co-occurring wolves and RFR dogs.

For primary wildlife prey species, we also calculated total and annual average estimates of population, harvest, and predation by dogs (2002–2011) and wolves (2006–2011). In addition, we summarized total and annual averages of livestock killed by dogs (2002–2011) and wolves (2006–2011).

We used generalized linear models (GLM) to test for annual variation in numbers of RFR dogs, free-ranging greyhounds, and wildlife and livestock prey. We used a Spearman's rank correlation to test the prediction that the average numbers of dogs would be positively correlated with the number of wild animals and livestock killed annually by dogs on hunting grounds. For free-ranging greyhounds specifically, we

predicted that greyhound numbers would be positively correlated with depredation on brown hare, a primary prey (Cowan, 2004; Reid et al., 2007). We also used a Spearman's rank correlation to test the prediction that the average number of wild animals killed by dogs would be positively related to estimates of population and harvest of wildlife on hunting grounds. Statistical analyses were not conducted for livestock depredation events given low sample sizes. We also excluded data on prey from 2001, when it was not obligatory to include dog depredation of wildlife and livestock in hunting reports. For Hunting Districts with confirmed wolf presence between 2006 and 2011, we used Mann-Whitney U tests to compare the annual average numbers of roe deer, red deer, and wild boar and livestock depredations by RFR dogs versus wolves. All statistical analyses were performed with Statistica v.10. Spatial distribution of RFR dogs, greyhounds, wolves, and their prey were created from thematic digital maps in MapInfo 11.0.

3. Results

3.1. Rural free-ranging dogs and greyhounds

RFR dogs were recorded in all 49 Hunting Districts, primarily in central and eastern Poland (Fig. 1a). Between 2001 and 2011, the estimated average annual number of RFR dogs (excluding greyhounds) recorded in hunting grounds in Poland was 138,286 (SD: 8859.2; min-max: 126,157 in 2007 – 154,858 in 2001), of which 29.4% (SD: 0.84; min-max: 28.3% in 2006 – 31.1% in 2010) were stray dogs (Table 1). The estimated annual average number of observed free-ranging greyhounds in hunting grounds was 2990 (SD: 556.1; min-max: 2497 in 2011 – 4,335 in 2001). The estimated annual average density was 54.8 RFR dogs/100 km² (SD: 3.5; min-max: 50.0 in 2007 – 61.3 in 2001) and 1.2 free-ranging greyhounds/100 km² (SD: 0.2; min-max: 1.0 in 2009, 2008, and 2011 – 1.7 in 2001). The total numbers of RFR dogs ($F_{(1,10)} = 0.80, p = 0.67$) and greyhounds ($F_{(1,10)} = 0.64, p = 0.78$) did not vary among years.

In the 39 Hunting Districts with confirmed wolf presence (Fig. 2a), the annual average density of RFR dogs was 43.9 dogs/100 km² (SD: 3.0) compared to 44.6 dogs/100 km² (SD: 3.7) in the 10 Hunting Districts without recorded wolves. Annual average density of free-ranging greyhounds was 0.7 greyhounds/100 km² (SD: 0.02) in Hunting Districts with wolves and 1.1 greyhounds/100 km² (SD: 0.2) in Hunting Districts without wolves.

3.2. Prey of dogs

In total, 332,779 wild animals and 2835 livestock killed by free-ranging dogs were registered in hunting reports from 2002 to 2011 within all 49 Hunting Districts (Fig. 1b and c). Annually, dogs killed on average 3278 wild animals (SD: 3415.4; min-max: 27,137 in 2007 – 38,988 in 2002) and 284 livestock (SD: 64.8; min-max: 198 in 2004 – 385 in 2010). The annual number of animals killed by dogs did not vary annually between 2002 and 2011 for wildlife ($F_{(1,9)} = 1.59; p = 0.11$) and livestock ($F_{(1,9)} = 1.04; p = 0.41$).

Among wild animals, the most common prey were brown hare (50.2% of all wild prey) and roe deer (28.2%); wild boar (3.7%), red deer (0.9%), and fallow deer (0.4%) were less common (Fig. 3a). Other wild prey (16.6%) included game animals (e.g., European badger *Meles meles*, mallard *Anas platyrhynchos*, hazel grouse *Tetrastes bonasia*) and legally-protected, unharvested species (e.g., European hamster *Cricetus cricetus*, European otter *Lutra lutra*, black grouse *Tetrao tetrix*). Livestock most commonly killed by dogs were sheep (45.8%), goats (30.8%), and cattle (23.5%).

As predicted, the number of RFR dogs recorded on hunting grounds was strongly and positively correlated with the number of wild animals ($r = 0.65, p < 0.001$) and livestock ($r = 0.28, p < 0.001$) killed by dogs. For individual wildlife species, the number of RFR dogs was positively correlated with depredation events of roe deer ($r = 0.41, p < 0.001$)

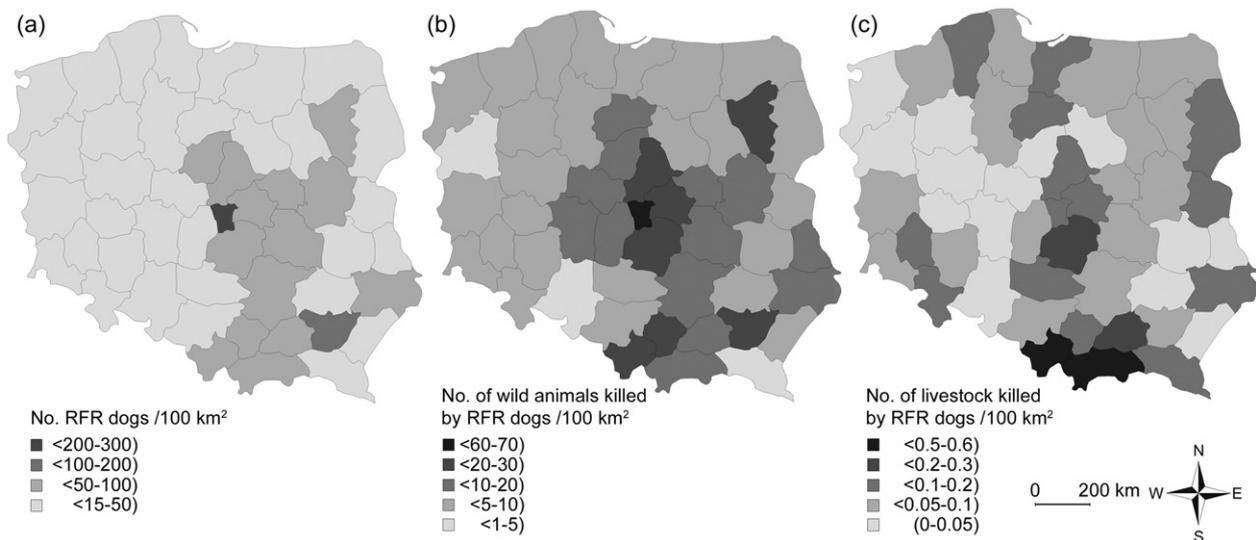


Fig. 1. Estimated annual average density [individuals/100 km²/year] of a) RFR dogs (excluding greyhounds), b) wild animals killed by RFR dogs, and c) livestock killed by RFR dogs within Polish Hunting Districts 2002–2011.

and brown hare ($r = 0.75, p < 0.001$), but not red deer ($r = 0.07, p = 0.480$) and wild boar ($r = -0.0006, p = 0.981$); sample sizes were insufficient for analyses of fallow deer. The number of free-ranging greyhounds was also positively correlated with their primary prey, brown hare ($r = 0.53, p < 0.001$).

As predicted, the number of wild animals killed by RFR dogs was strongly and positively correlated with the estimated population of red deer ($r = 0.56, p < 0.001$), roe deer ($r = 0.47, p < 0.001$), wild boar ($r = 0.61, p < 0.001$), and brown hare ($r = 0.74, p < 0.001$) on hunting grounds. Also consistent with predictions, predation rates were positively correlated with harvest estimates for red deer ($r = 0.51, p < 0.001$), roe deer ($r = 0.40, p < 0.001$), wild boar ($r = 0.57, p < 0.001$), and brown hare ($r = 0.69, p < 0.001$).

Overall, the number of wild animals killed by RFR dogs (Fig. 3a) represented approximately 9.4% of the annual harvest estimates (Fig. 3b) and 2.2% of the annual population estimates (Fig. 3c) of wildlife on hunting grounds. The percentage of the annual estimated population killed by dogs was highest for brown hare (mean: 3.4%; SD: 0.61), followed by roe deer (1.4%; 0.22), fallow deer (1.1%; 0.38), wild boar (0.7%; 0.19), and red deer (0.2%; 0.06). In comparison, the approximate percentage of the annual estimated population harvested by hunters was 5.6% (SD 3.87) for brown hare, 20.6% (1.52) for roe deer, 22.5%

(2.17) for fallow deer, 78.6% (1.75) for wild boar, and 28.0% (1.77) for red deer. Livestock killed by dogs accounted for approximately 0.005% of estimated annual livestock numbers in Poland.

Wild animals were most frequently preyed by dogs in central and northeastern Poland (Fig. 1b), whereas livestock prey were most frequently recorded in southern Poland (Fig. 1c). Specifically, roe deer, red deer, and wild boar were killed by RFR dogs throughout Poland (Fig. A1). Roe deer, the most common ungulate, were distributed and hence available to dogs throughout the entire country; in some hunting districts the number of killed roe deer exceeded 10 individuals per 100 km². Wild boar and red deer were available primarily in northern and western Poland. Both the number of free-ranging greyhounds and brown hares killed by dogs were highest in central and eastern Poland (Fig. 4).

3.3. Prey of wolves

In total, 14,140 wild animals and 2176 livestock killed by wolves were registered in hunting reports from 39 Polish Hunting grounds from 2006 to 2011 (Fig. 2c and d). Annually, wolves killed on average 2356 wild animals (SD: 182.8; min-max: 2090 in 2011 – 2580 in 2007) and 363 livestock (SD: 122.5; min-max: 238 in 2008 – 550 in 2009).

The most common wild ungulate species preyed by wolves was roe deer (55.4% of all ungulate prey); red deer (22.8%) and wild boar (16.6%) were less common prey items (Fig. 5). Cases of wild animals killed by wolves were most common in northeastern and southeastern Poland (Figs. 2b, A2). From 2006 to 2011, wolves killed red deer (annual average: 537; SD: 66.2) more often than RFR dogs (annual average 283; SD: 104.2) within the 39 Hunting Districts with wolves ($U = 0.0, p < 0.002$; Fig. 5). Conversely, dogs killed more roe deer (annual average 7979; SD: 1554.1) and wild boar (annual average: 1076; SD: 116.3) than wolves killed roe deer (annual average: 1305; SD: 119.31) and wild boar (annual average: 392; SD: 52.7; $U = 0.0, p < 0.002$). The estimated mortality of roe deer, red deer, and wild boar were dominated by hunter harvest (>90% of all mortality cases), followed by RFR dogs and wolf predation (Table A1).

Livestock most commonly killed by wolves were sheep (85.2%), cattle (10.0%), and goats (4.9%). Livestock killed by wolves accounted for approximately 0.006% of estimated annual livestock numbers in Poland. Cases of livestock killed by wolves were most common in southeastern and northeastern Poland (Fig. 2d). In comparison, in the Hunting Districts with confirmed wolf presence from 2006 to 2011, RFR dogs killed

Table 1

Estimates of free-ranging dogs recorded in hunting grounds in Poland between 2001 and 2011. RFR: rural free-ranging dogs; G: free-ranging greyhounds and their mixed breeds; RFR + G: total number of free-ranging dogs. % of stray dogs calculated from RFR.

Year	RFR	RFR/100 km ²	% stray dogs	G	G/100 km ²	RFR + G	
						RFR + G	G/100 km ²
2001	154,858	61.3	29.1	4335	1.7	159,193	63.0
2002	134,656	53.3	29.0	3453	1.4	138,109	54.7
2003	132,261	52.4	29.1	3256	1.3	135,517	53.7
2004	138,448	54.8	29.2	3216	1.3	141,664	56.1
2005	135,391	53.6	28.8	2974	1.2	138,365	54.8
2006	135,110	53.5	28.3	2640	1.1	137,750	54.5
2007	126,157	50.0	28.8	2685	1.1	128,842	51.0
2008	130,507	51.7	30.7	2597	1.0	133,104	52.7
2009	135,895	53.8	29.6	2452	1.0	138,347	54.8
2010	150,013	59.4	31.1	2779	1.1	152,792	60.5
2011	147,846	58.5	29.8	2497	1.0	150,343	59.5
Total	1,521,142			32,884		1,554,026	
Average	138,286	54.8	29.4	2990	1.2	141,275	55.9
(SD)	(8859.24)	(3.49)	(0.84)	(556.10)	(0.21)	(9110.79)	(3.60)

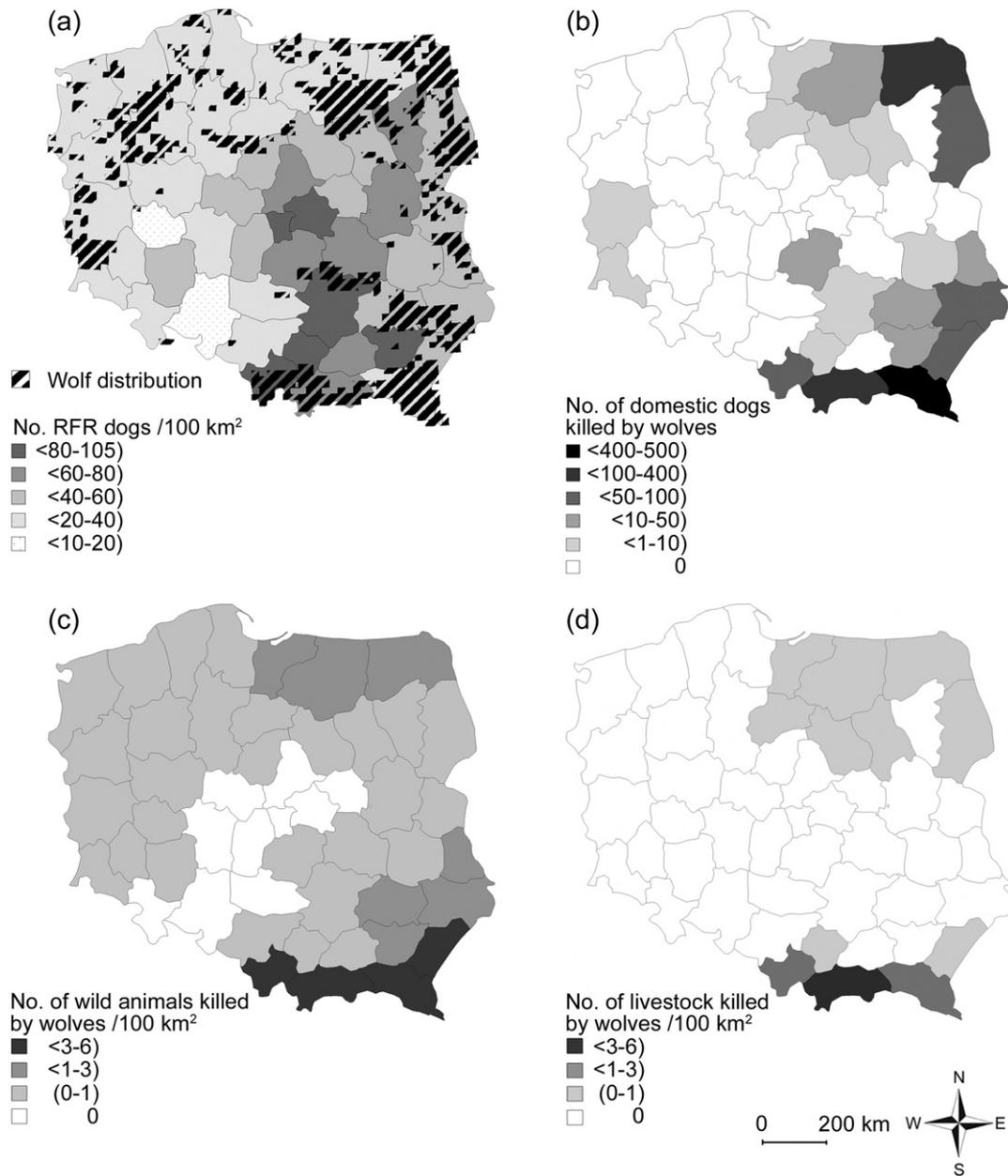


Fig. 2. Estimated a) annual average density [individuals/100 km²/year] of RFR dogs (excluding greyhounds) and recorded distribution of wolves, b) annual number of domestic dogs killed by wolves, c) annual average density [individuals/100 km²/year] of wild animals killed by wolves, and d) annual average density [individuals/100 km²/year] of livestock killed by wolves within Polish Hunting Districts 2006–2011.

1504 livestock from 2006 to 2011 (annual average: 206; SD: 56.5). Annual average number of livestock prey did not vary between wolves and dogs ($U = 7.0$, $p = 0.093$).

Additionally, wolves killed 1270 domestic dogs in Hunting Districts from 2006 to 2011, averaging 61 dogs annually (SD: 107.5; min–max: 163 dogs in 2011 – 289 in 2008). Depredation cases of dogs by wolves were most common in southeastern and northeastern Poland (Fig. 2b).

4. Discussion

Our results demonstrate that free-ranging dogs are widespread and abundant in Poland, frequently killing wildlife and livestock. On average, hunting club records estimate that over 138,000 RFR dogs, nearly 30% of which were unowned strays, occur annually across the 49 Polish Hunting Districts. In addition, estimates suggest that nearly 3000 free-ranging greyhounds and their mixed breeds occurred annually in hunting grounds, although greyhound hunting has been banned and they

are legally required to be restrained within fencing. Free-ranging dogs, including greyhounds, occurred at estimated densities of 55.9 dogs per 100 km² on hunting grounds. Due to subsidized food and shelter provided by humans, globally the densities of domestic dogs are typically higher than those of native predators and range from a few individuals to a few thousand per 100 km² (e.g., Atickem et al., 2010; Boitani, 1983; Gompper, 2014c; Paschoal et al., 2012; Silva-Rodríguez et al., 2010; Vanak et al., 2014; Vanak and Gompper, 2010).

Free-ranging dogs threaten various native fauna, primarily mammals (Hughes and Macdonald, 2013; Ritchie et al., 2014). On average, hunting reports documented over 33,000 wild animals killed by free-ranging dogs on Polish hunting grounds annually. However, these estimates are certainly conservative, in that it was impossible for hunters to record all wildlife killed by dogs; as such, these should be viewed as minimum estimates of the predation impact of dogs. Brown hares were the primary prey of dogs, accounting for 50% of their kills; free-ranging dogs killed on average over 16,500 brown hare annually, with

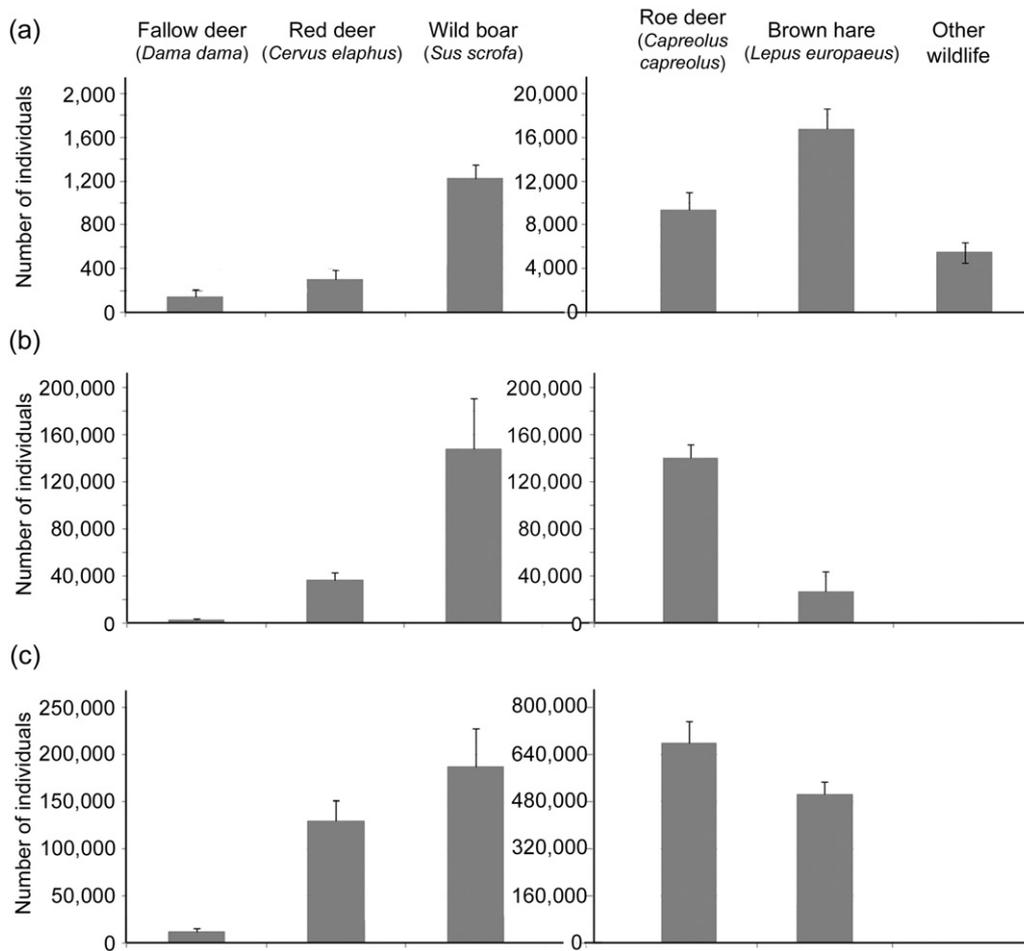


Fig. 3. Estimated a) number of wild animals killed by RFR dogs, b) number of wild animals harvested by hunters, c) wildlife population size within Polish Hunting Districts 2002–2011. Values displayed as average (SD) annual number of individuals.

a maximum of 20,540 hares killed in 2002. Annual kills represented 3.4% of the estimated population of brown hares on hunting grounds, close to the approximate 5.6% of the brown hare population harvested by hunters annually. In addition, ungulates, a primary prey of dogs elsewhere (Hughes and Macdonald, 2013; Ritchie et al., 2014; Young et al., 2011), were also targeted by free-ranging dogs in Poland. Roe deer were common prey, with dogs killing over 9000 roe deer annually on hunting grounds, representing 1.4% of the estimated population of roe deer, considerably less than the 20.6% of roe deer harvested annually by hunters. Although less common, dogs also preyed on a variety of other species, including 17 game animals and 9 legally-protected species. Domestic dogs might be particularly important apex predators where native large carnivores are absent or rare (Ritchie et al., 2014). Such is the case in Poland, where the grey wolf has become severely depleted from much of its historic range (Okarma, 2015) and has been replaced by dogs.

Dogs have been documented as an important predator of livestock globally, including in Europe (Boitani, 1983; Carding, 1969; Mattiello et al., 2012), the United States (Bergman et al., 2009; Boggess et al., 1978; Gese et al., 2004; USDA-APHIS, 2005), Australia (Mitchell and Banks, 2005), and Africa (Butler et al., 2004). Free-ranging dogs also killed livestock in Poland, primarily sheep, cattle and goats. In total, during 10 years, dogs killed 2835 head of livestock according to Polish hunting reports. However, these events only comprise 0.005% of annual total livestock population.

Greyhounds in particular have occupied an important role in Polish society for centuries. Greyhounds have been valued as hunting dogs owned exclusively by royal families and nobility, assisting hunters in

pursuit of a variety of game, often hares but also deer, red foxes, and wolves (Birrell, 2001; Lescureux and Linnell, 2014; White et al., 2003). Despite existing legislation, approximately 20,000 greyhounds were bred without permission and illegally used for hunting in the 1990s (Bilewicz, 2004). If owners do not want to pay for registration, greyhounds are provided to shelters or placed for adoption (Bilewicz, 2004). Nonetheless, free-ranging greyhounds were commonly detected in hunting grounds in our study, and we found a strong, positive correlation between estimated greyhound densities and brown hares killed by dogs. We assume this reflects ongoing breeding of greyhounds, likely for illegal hunting. Even if the dogs are not used for hunting, once free-ranging they instinctively will chase and attack prey. Reid et al. (2007) documented that greyhounds used for racing live hares frequently mauled the animals, ending with injuries and euthanasia of the hares.

Wolves and dogs are sympatric congeners globally, suggesting the potential for intense competitive interactions; surprisingly, however, research on competition between wolves and dogs is relatively limited (Lescureux and Linnell, 2014). Wolves in Poland have been legally-protected since 1988, and available data suggest that the Polish wolf population exceeds 1000 individuals and is increasing in number and range (Okarma, 2015). All hunting districts with a documented presence of wolves also had high densities of free-ranging dogs, possibility generating intraguild competition between these canids. Overlap in body size also suggests potential competition: adult wolves in Poland weigh 26–67 kg ($n = 152$ hunted individuals; Okarma, 1989), whereas RFR dogs range in size from 5 to 30 kg (pers. obs.). Wolves predominantly hunt ungulates in Poland (Jędrzejewski et al., 2012), and our data indicate that wolves eat similar ungulate prey as free-ranging

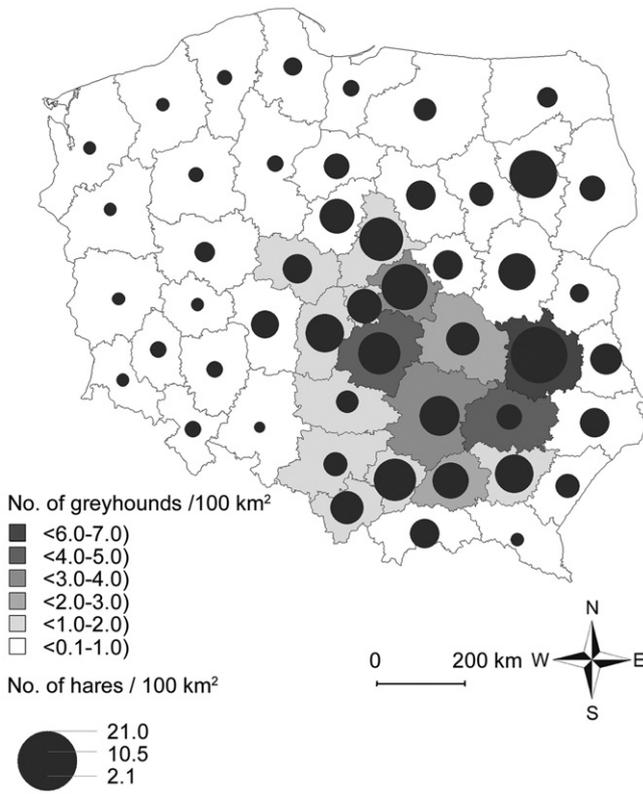


Fig. 4. Estimated annual average density [individuals/100 km²/year] of greyhounds and brown hares killed by RFR dogs within Polish Hunting Districts 2002–2011.

dogs on hunting grounds, including roe deer, red deer, and wild boar. Compared to dogs, wolves killed more red deer and fewer roe deer and wild boar. For wild boar, however, we note that wolves typically hunt piglets and frequently consume them whole (Jędrzejewski et al., 2012), possibly resulting in an underestimate of wolf predation on wild boar. Differing prey selection by wolves and dogs is likely due in part to habitat preferences and relative body size of ungulate species. Roe deer might be particularly susceptible to predation by free-ranging dogs because they are the most common ungulate and their medium size makes them easier to chase and kill compared to larger and stronger red deer or wild boar. Further, roe deer, as well as wild boar, are found in various landscapes, including agricultural and open habitat, which might be penetrated by RFR dogs more so than wolves (Krauze-Gryz and Gryz, 2014; Selva et al., 2005). In contrast, larger-bodied red deer are primarily a forest species and thus might be more

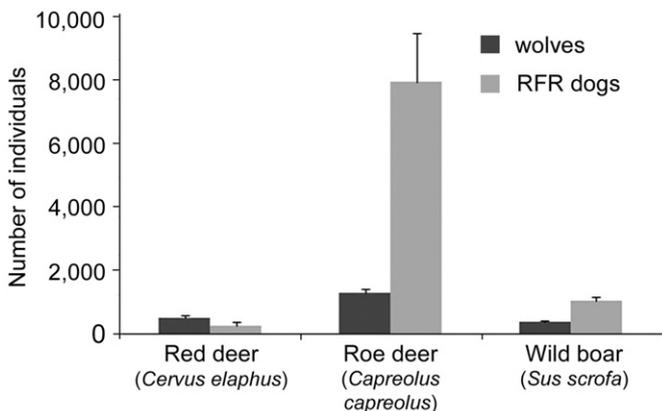


Fig. 5. Estimated number of wild ungulates killed by RFR dogs and wolves within 39 Polish Hunting Districts with confirmed wolf presence from 2006 to 2011.

accessible to wolves, which prefer forested habitat in Poland (Borowik et al., 2013; Huck et al., 2011). Brown hares, frequently killed by RFR dogs, are a small-bodied and typically agrarian prey and thus might be favored by dogs. Small animals such as brown hare are found in the diet of wolves in Poland, but not frequently (Jędrzejewski et al., 2012; Nowak et al., 2011).

Dogs and wolves may also compete for livestock. Rates of livestock depredation by wolves was similar to that by dogs; in the 39 Hunting Districts with confirmed wolf presence, dogs killed an average of 205.7 livestock annually on hunting grounds, compared to 362.7 livestock killed annually by wolves. Livestock owners in Poland are compensated for livestock killed by wolves but not dogs. Although there are special commissions comprised of experts to help distinguish wolf and dog depredations in Poland, the possibility remains that the cause of death is misidentified (Caniglia et al., 2013). Human persecution of wolves might be exacerbated if wolves are erroneously blamed for livestock depredation that was in reality caused by free-ranging dogs (Boitani, 1983; Cozza et al., 1996; Echegaray and Vilà, 2010). This can be viewed as a form of apparent competition, with wolves and dogs sharing humans as a common predator (Lescureux and Linnell, 2014).

In addition, domestic dogs supplement their diet by scavenging on carcasses and thus can also compete with wild scavengers, particularly given the high densities of dogs and their ability to forage both day and night (Butler and du Toit, 2002; Vanak et al., 2014). In Poland, although both wolves and dogs scavenge on ungulate carcasses, dogs tend to forage in open habitat close to human settlements and also tend to avoid wolf kills (Selva et al., 2005), thus potentially lessening intraguild competition. Given that dogs often do not consume their prey, they may also subsidize other scavengers, including other carnivores, small and medium-sized mammals, and birds (Newsome et al., 2015). The most frequent scavengers of ungulate carcasses in Poland were ravens (*Corvus corax*) and red foxes, followed by raccoon dog (*Nyctereutes procyonoides*), Eurasian jay (*Garrulus glandarius*), common buzzard (*Buteo buteo*), wild boars, wolves, European pine marten (*Martes martes*), white-tailed eagle (*Haliaeetus albicilla*), and great tit (*Parus major*; Selva et al., 2005). Such facultative scavengers may also benefit from prey left unconsumed by dogs.

It has been suggested that domestic dogs might be poor exploitative competitors of wild carnivores, particularly with larger-bodied predators, if dogs create unstable small groups that do not hunt cooperatively and instead rely primarily on scavenging (Butler et al., 2004; Vanak and Gompper, 2009; Lescureux and Linnell, 2014). However, dogs are social canids that can temporarily form packs consisting of 2–8 individuals (Causey and Cude, 1980; Galetti and Sazima, 2006; Manor and Saltz, 2004; Vanak and Gompper, 2010). These temporary packs, typically more common in rural than in urban areas (Lehner et al., 1983; Wandeler et al., 1993), do cooperatively hunt (Paschoal et al., 2012; Srbek-Araujo and Chiarello, 2008). In Poland, Krauze-Gryz and Gryz (2014) described cases of groups of RFR dogs that hunt collaboratively against roe deer and brown hare, deliberately chasing prey on fences and railway embankments. The ability of some dogs to hunt cooperatively likely increases their efficiency and thus the potential of resource competition with intraguild predators.

Dogs also act as interference competitors with native carnivores, resulting in spatial exclusion, harassment, and intraguild predation (Vanak and Gompper, 2009; Vanak et al., 2014). Most commonly, the larger-bodied wolf perceives dogs as both competitor and prey and will kill them (Butler et al., 2014; Lourenco et al., 2014; Lescureux and Linnell, 2014). In Poland, wolves killed an average of 61 domestic dogs annually on hunting grounds from 2006 to 2011, primarily in regions where wolves are residents and live in stable packs (Okarma, 2015). Anecdotal reports suggest that wolves sometimes kill dogs without being provoked, occasionally entering villages and attacking dogs that are chained to buildings. Such intraguild killing further exacerbates human-wolf conflict (Butler et al., 2014). Conversely, dogs have been known to kill other sympatric predators, including red fox (Vanak et

al., 2014), the most common mesocarnivore in Poland and also a nuisance urban species (Wierzbowska et al., 2011).

Further, high densities of free-ranging dogs increase the probability of interspecific contact and consequently disease transmission (Knobel et al., 2014). For example, dogs are a common vector of rabies, responsible for the transmission of the virus to wildlife and humans (Tenzin et al., 2015). In Poland, red fox is the main vector of rabies. Of the 2607 wild and domestic animals diagnosed with rabies between 2002 and 2012, red foxes comprised 69.5% of cases, followed by domestic dogs (3.6%) and wolves (0.2%; RBE, 2015). High densities of both red foxes and RFR dogs on hunting grounds increase the possibility of spreading the disease. Despite obligatory rabies vaccination programs for dogs, private owners in Poland often do not vaccinate their pets (Krzowska-Firych et al., 2012), increasing risk of disease transmission.

Finally, domestic dogs can hybridize with native canids (Leonard et al., 2014). In Poland, the first possible incidents of hybridization between domestic dogs and wolves have been described (Okarma, 2015). In addition, in 2015 golden jackals were for the first time recorded in Poland, attributed to natural range expansion (Kowalczyk et al., 2015); golden jackals thus represent another sympatric congeneric with which dogs might hybridize (Leonard et al., 2014).

5. Conclusions

Our results indicate the potential scope and impact of free-ranging dogs in Poland. A large number of unconfined dogs have access to natural areas, causing direct mortality of a variety of wildlife species and livestock, and consequently they may compete with the legally-protected grey wolf. In addition, it is conceivable that the additional animals killed by dogs, in conjunction with those harvested by humans, may result in an unsustainable off-take of some game species. This might be particularly the case for the primary prey of dogs, brown hares, which have been suffering considerable population decline since the 1960s (Misirowska and Wasilewski, 2012). This possibility warrants further investigation.

Although a variety of strategies have been suggested to mitigate the impact of free-ranging dogs (Gompper, 2014a), the effectiveness of such mitigation efforts have received relatively little attention. Legislation in Poland focused on control and management of free-ranging dogs, including greyhounds, is seemingly not effective. One potential solution is to capture and transport unsupervised free-ranging dogs to animal shelters for identification of ownership (via microchips) or for adoption or euthanasia. Indeed, between 1998 and 2011, 975,368 free-ranging abandoned or escaped dogs were captured and provided to 65 shelters in Poland. The number of dogs received at animal shelters has increased annually, from 71,921 in 2001 to 100,265 in 2011 (GVI, 2002, 2012). However, the most recent report on the quality of animal shelters, which are managed by local municipalities, highlighted poor conditions, including lack of space and overcrowding, resulting in high mortality of animals (NIK, 2013).

Consequently, there is an urgent need to implement alternative approaches to controlling domestic dogs in Poland, as well as in other regions globally with widespread and numerous RFR dogs (Gompper, 2014a). The most important initiative is education of the general public on issues concerning free-ranging dogs, including welfare of dogs as well as their impacts on wildlife and livestock. Effective communication programs regarding responsible dog ownership is critical, including limitation of dog numbers per household, obligatory identification by implanted microchips, and sterilisation of pets not used for breeding (ICAM, 2007; Kahn et al., 2008). Further, it might be reasonable to introduce legislation that requires muzzles for owned, unleashed dogs that pose a threat to wildlife in natural areas. Reid et al. (2007) found that the use of muzzles for coursing greyhounds decreased mortality of hares by 12%, although muzzled dogs can still chase and disturb wildlife.

Ultimately, if owners do not take responsibility for their pets, and dogs are allowed to roam freely in natural areas, fines could be

implemented and rigorously enforced. To be effective, educational and management efforts should be targeted and refined for different stakeholder groups, and should involve governmental agencies, non-governmental organization, and media. Such efforts would also be strengthened through consultation and collaboration with international organizations such as The World Organization for Animal Health (OIE), The World Society for the Protection of Animals (WSPA), or International Companion Animal Management Coalition. In our study area specifically, if Poland signed the European Convention for the Protection of Pets (ETS No. 125), this could also help promote the welfare of dogs in the country and help mitigate their impacts on wildlife.

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