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Review

Grey wolf (Canis lupus) predation on livestock in relation to prey availability

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ABSTRACT

1. Conflict between humans and large carnivores hinders carnivore conservation worldwide. Livestock depredations by large carnivores is the main cause of conflict, triggering poaching and retaliatory killings by humans. Resolving this conflict requires an understanding of the factors that cause large carnivores to select livestock over wild prey. Individual studies to date report contradictory results about whether wild prey density affects livestock depredation by large carnivores.
2. We carried out a systematic review of grey wolf (*Canis lupus*) dietary preferences. We reviewed and analysed 119 grey wolf dietary studies from 27 countries to determine whether wild prey or livestock density affects grey wolf dietary selection.
3. We also assessed whether there are traits that predispose species to be preyed upon (body size, group size, defence mechanisms, speed), and whether livestock management is a factor that affects selection of livestock by grey wolves.
4. Overall, wild prey (65% of the total frequency of occurrence in all reviewed grey wolf diet studies) was selected for even when livestock was abundant. The average proportion of biomass percentage in grey wolf diets was 13% for livestock and 19% for wild species.
5. Wild prey species in possession of defence mechanisms (horns, antlers, spikes, and fangs), with high body weight and present in high density were more likely to be depredated by grey wolves.
6. Even when prey abundance significantly affected selection of wild prey, livestock predation was much lower considering their substantially higher density. Areas where livestock were left to graze freely in small numbers (<20 individuals/km^2) were more vulnerable to grey wolf attacks.
7. Our results suggest that the adoption of attack prevention measures on pastures and the increase of wild prey abundance could reduce depredation on livestock by grey wolves, and in turn, provide better opportunities for coexistence between humans, grey wolves and livestock.

1. Introduction

Large carnivores have long been perceived as a threat to people's lives and livelihoods (Ripple et al., 2014). Changing attitudes towards large carnivores and their conservation have resulted in implementation of measures to protect them. At the same time increasing human expansion and subsequent destruction of (semi-)natural habitat has created widespread conflict (Behdarvand et al., 2014, Fall and Jackson, 1998; Messmer et al., 1997; Treves et al., 2004). Such conflict is increasing as large carnivores recolonise human-dominated landscapes (Chapron et al., 2014; Madhusudan and Mishra, 2003; Treves and Karanth, 2003), mainly because they sometimes prey on livestock and game species also valued by humans, incurring economic costs (Graham et al., 2005; Promberger et al., 1997; Treves and Karanth, 2003).

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Deeply held cultural views and hostility towards large carnivores can lead to their localised extermination (Jones, 2002; Kruuk, 2002), even if direct attacks on humans are rare (Brain, 1981; Karanth and Madhusudan, 2002; Linnell et al., 2002; Linnell et al., 2003). Public reports of attacks on livestock are somewhat unreliable, as exaggerating them is occasionally part of lobbying activities, even when evidence indicates that other factors, such as falling meat prices, threaten livestock farming to a greater extent (Chapron and López-Bao, 2014). Some administrations manage livestock-carnivore conflicts with compensation and carnivore relocation programs (Agarwala et al., 2010; Boitani et al., 2011, Nyhus et al., 2003; Treves and Karanth, 2003; Vos, 2000). Improvements in husbandry techniques appear to be the most effective means of preventing attacks (Ciucci and Boitani, 1998; Mishra, 1997), but uptake of such methods remains low at a global scale (van Eeden et al., 2018a, 2018b).

In human-dominated landscapes, balancing large carnivore conservation and farming interests is politically desirable. However, tensions run high when carnivores return to farming or hunting regions (Bangs et al., 1998; Jhala and Giles, 1991; Landa et al., 1999). Gamekeepers, farmers and ranchers typically oppose what they perceive to be cumbersome protective measures (Andersson, 1977; Bath and Buchanan, 1989) and may even support illegal killing and eradication programs (Blanco et al., 1992; Boitani and Ciucci, 1993; Huber et al., 1993; Jackson and Hunter, 1996). Social studies of human-large carnivore relationships have documented improving attitudes following a reduction of livestock killed (Gyorgy, 1984; Huber et al., 1993), suggesting that mitigating attacks on livestock is crucial for managing stakeholder attitudes to facilitate conservation. While several reviews have recently explored evidence of the effectiveness of different livestock protection measures (van Eeden et al., 2018b; Eklund et al., 2017; Miller et al., 2016; Treves et al., 2016), further research is needed to understand the broader context that shapes large carnivore attacks on livestock.

The grey wolf (*Canis lupus*) is considered an opportunist predator species (Carbyn, 1988; Salvador and Abad, 1987). As such, it usually consumes the food which occurs most abundantly, changing its diet depending on food availability (Glasser, 1982). Grey wolves are one of the most widely distributed large carnivores, and they frequently come into conflict with humans because they prey on livestock (Graham et al., 2005; Sillero-Zubiri and Laurenson, 2001). Because of legal protections, recolonisations, and reintroduction effects, grey wolves are now returning to parts of their former range, which will increase contact between grey wolves, humans and livestock (Ansorge et al., 2006; Lanszki et al., 2012; Wagner et al., 2012). Many studies have investigated grey wolf food habits in relation to wild prey availability (Meriggi and Lovari, 1996; Okarma, 1995), providing an ideal opportunity to analyse the extent to which they are opportunistic predators, and whether wild prey availability is linked to depredation rates on livestock at a global scale. Previous reviews suggest that grey wolves prefer large wild ungulates and medium-sized mammals in North America, domestic animals in Asia and medium-sized wild ungulates in Europe (Newsome et al., 2016), but a detailed review on the grey wolf's prey preferences in relation to prey availability remains lacking.

It is possible that a combination of prey size, prey defence strategies, and prey abundance affects grey wolf dietary preferences, because these factors determine the number of times a predator is likely to encounter prey, the risk of injury from attack, and the subsequent level of reward from a successful hunt. Multiple local studies have suggested that when wild prey is abundant and optimal in terms of size and catchability, large carnivores would be less likely to prey on livestock (Andersone and Ozolis, 2004; Gula, 2004; Jedrzejewski et al., 2000; Mech and Peterson, 2003). However, no study has tested this assumption at a global level under a meta-analysis framework using the necessary data including wild prey availability, livestock availability, defence traits of wild prey, and large carnivore dietary data from scat or stomach contents, which has limited our ability to draw firm conclusions.

Here we evaluate for the grey wolf (a) which ungulate species are the most preferred prey items, (b) whether prey consumption is determined by prey abundance at a given location, (c) whether there are traits that predispose species to be preyed upon (body size, group size, defence mechanisms, speed), and, (d) whether livestock management is a factor that affects the selection of livestock as wolf prey. We use the results to test the broad hypothesis that depredation on livestock by grey wolves would be lower under circumstances where abundant wild prey is available and where nonlethal livestock protection measures are in place.

2. Methods

2.1. Literature review and data collection

We conducted a systematic review of the available literature regarding grey wolf diet and prey densities. All studies used by a previous review (Newsome et al., 2016) were included when accessible. Additional studies were located by searches in JSTOR, Web of Science, Google Scholar, Wiley Online Library and Science Direct using the search terms ("diet" OR "food habits" OR "frequency of occurrence") AND ("wolf" OR "*Canis lupus*") without date or language restrictions (Appendices A and C). Bibliographies of relevant articles were searched for secondary studies. The last search was made in September 2018.

Studies usually included information about prey consumed by grey wolves and the other species occurring in the area. However, when this information was not available, we searched for studies undertaken at the same time period and location using articles from the same author or authors who conducted the grey wolf dietary study first, and then from other authors using the same search engines as above. We also searched for books, academic theses, conference presentations, national park and protected site reports, and official government sites.

Data regarding prey densities were collected the same way (Appendices A and D). From this search, we selected papers containing information about frequency of occurrence (FO) and biomass of prey species from scat contents, excluding studies where authors only analysed stomach contents. Then, we performed a bootstrap analysis in *R* (R Development Core Team, 2016) to evaluate whether the total number of papers screened was sufficient to represent the biomass frequencies of wolves. The bootstrap method is a resampling approach that enables estimation of the accuracy of an estimator by random sampling with replacement from the original dataset. Within the pool of reviewed papers, we based our bootstrap on 10,000 replications. The results show that our data were unbiased, as both sample frequency distributions were almost identical (Appendix B).

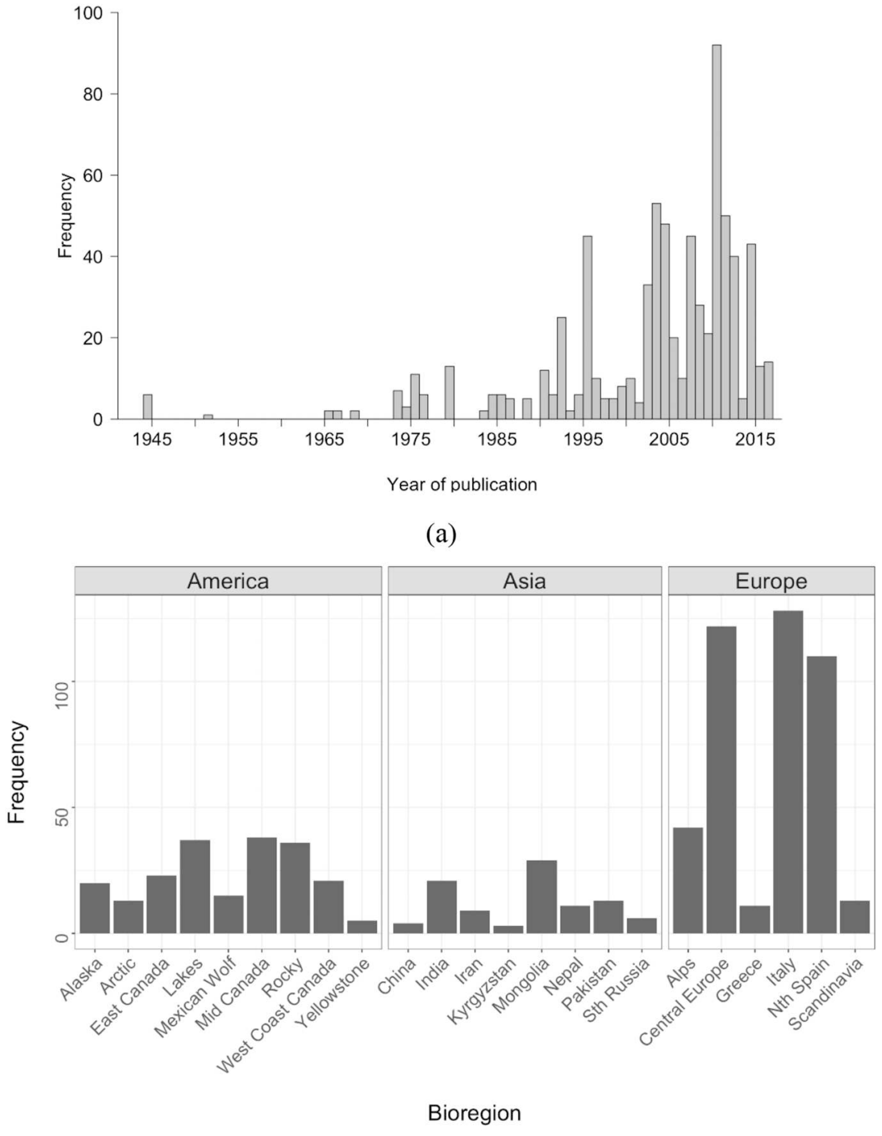
We classified the prey data obtained into three groups: wild ungulates, domestic ungulates and others. "Others" included small mammals (rodents, hares, hedgehogs, porcupines, etc.), garbage, fruits, birds, reptiles and other carnivores (cats, dogs, foxes, bears, etc.). The percentage-of-occurrence method enables relative comparison of the predator diet changing in time and space, but does not reflect the actual intake of particular prey (Klare et al., 2011; Trites and Joy, 2005). We therefore estimated biomass consumption in kg using the linear relationship established by Floyd et al. (1978) for wolves with modifications by Weaver (1993) that connects prey's presence in scats with the species body weight:

$$Y = 0.439 + 0.008\,X$$

where X is the average live mass of a prey species, obtained from the PanTHERIA database, and Y is the prey mass per scat. We then multiplied the values obtained in the above equation by the number of scats per prey to calculate the relative biomass per prey species:

$$\text{Relative biomass (kg)} = \text{Scats}_{\text{prey}} \times 0.439 + 0.008 \times \text{X}$$

Then we divided this value by the total relative biomass consumed in each study to obtain the percentage of biomass per prey species:



(a)

(b)

Fig. 1. Number of publications ($N = 119$) of grey wolf dietary preferences selected from the available literature and classified by (a) year of publication and (b) bioregion were the study took place.

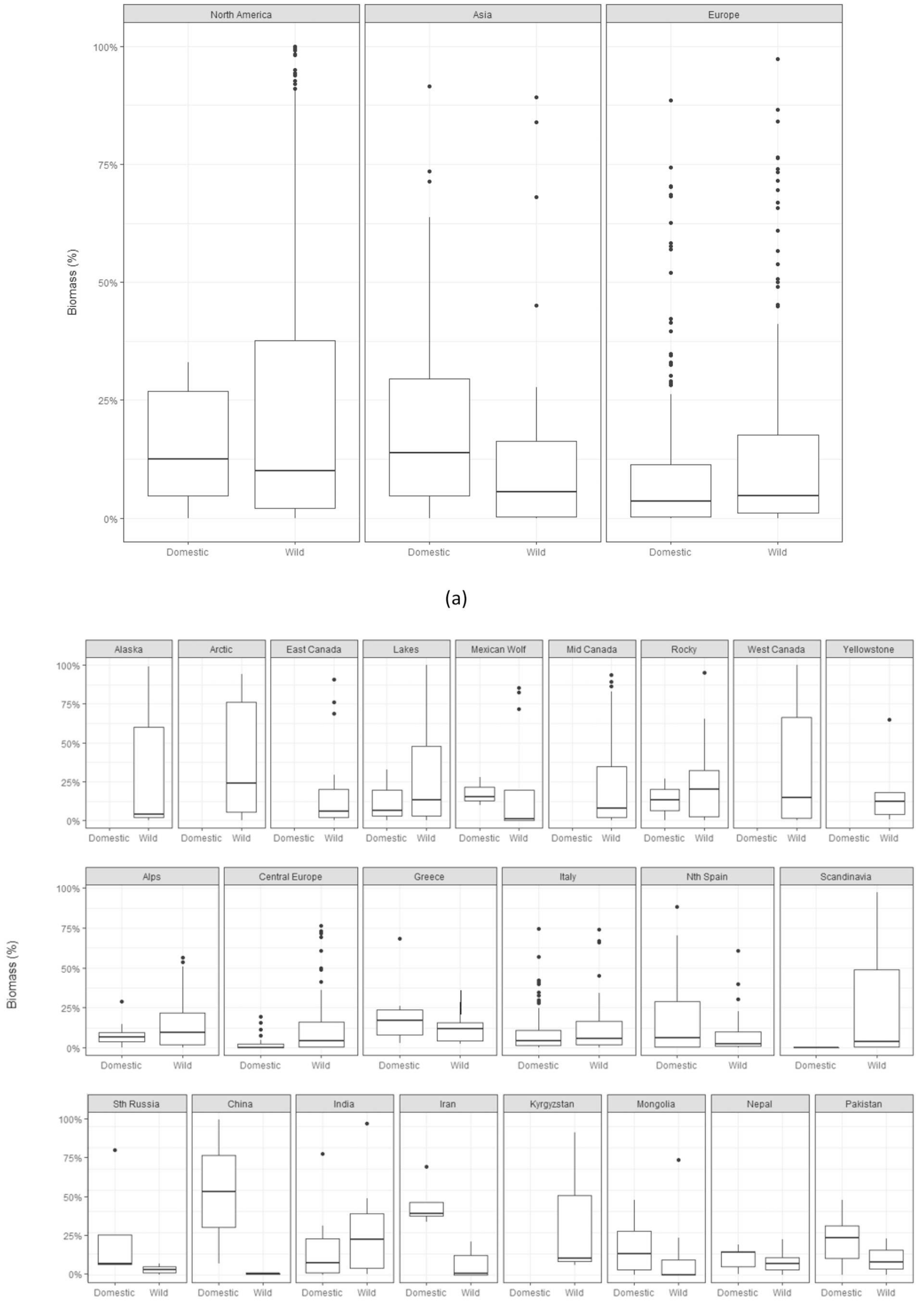
$$\%\text{biomass} = \frac{\sum \text{Relative biomass}}{\text{Total relative biomass}} \times 100$$

The approach above follows the methods used in other dietary studies (e.g. Bacon et al., 2011; Davis et al., 2012; Gable, 2017).

For each data point, we then extracted the year of publication, first author name, and sampling duration for classification purposes. We also recorded spatial data such as the country, biome and bioregions where the studies took place. Biome boundaries were based on mapping by Olson et al. (2001). Bioregions were used to separate studies occurring in the same biome but >100 km apart (Newsome et al., 2016). Some studies consisted of more than one study area, in which case each study area was recorded independently.

We extracted prey species abundance from the literature as density or counts. Density was calculated from the study area if only count data were given by dividing the total number of individuals by the study area size. All data points related to prey abundances were expressed in individuals/km^2. There were two limitations of this approach. First, prey abundances were usually not given in the original articles and had to be extracted from other sources (Appendix D) possibly leading to imprecise estimates of population density. More specifically, livestock densities were mostly obtained from governmental official statistics, which provided information at a municipal level, potentially underestimating or overestimating the species abundances in the mostly small study sites. Furthermore, the numbers of study site locations varied substantially across bioregions. We therefore reduced uncertainty by providing a large sample size and by analyzing the data at three different and broad spatial levels (global, bioregion, and country).

Prey species were recorded and grouped into domestic and wild prey for the analysis. Each livestock management method was classified according to descriptions in each study for at least one of the domestic species present there. We documented the type of management for each individual domestic species, making it possible to have more than one management measure per study area: presence of guard dogs protecting flocks and herds, enclosure of animals in fenced areas or barns, presence of carcass dumps and livestock occurrence only in the surroundings of the study area (in the case of protected sites where animal husbandry is prohibited within the park). Type of grazing was divided into three levels according to the degree of vulnerability (1) animals roaming free and unattended all year around as the most vulnerable, (2)



(a)

(b)

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Fig. 2. Biomass (%) comparison of domestic and wild prey species present in grey wolf scats at (a) continental and (b) bioregional levels. Biomass consumption was estimated connecting prey's presence in scats with the species body weight.

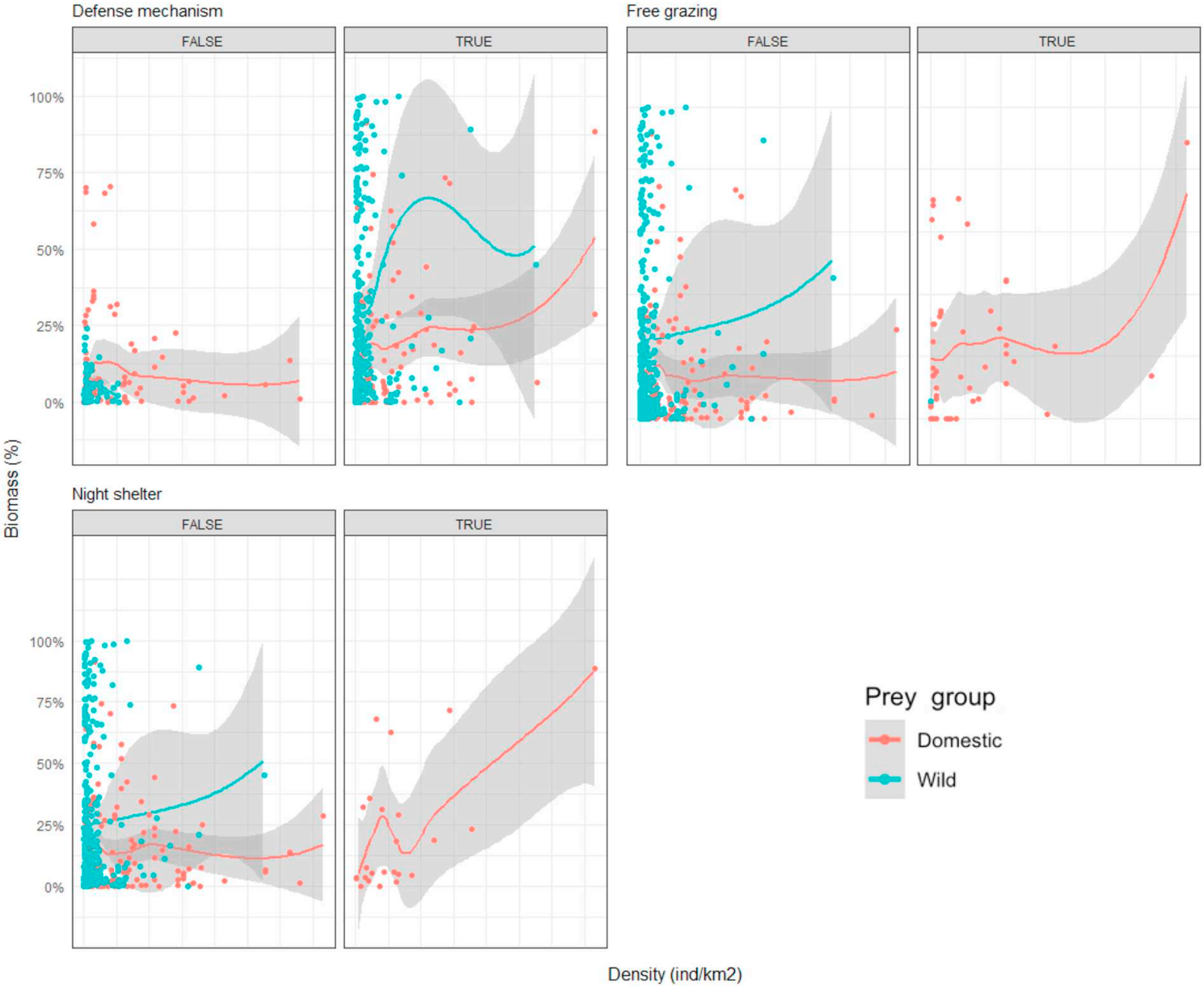


Fig. 3. Biomass (%) of prey present in wolf scats in relation to their density for significant ($P \le 0.003$) livestock management measurements +/− standard errors. The biomass percentage in relation with defence mechanisms (horns, antlers, spikes and fangs) is also presented for wild species.

grazing during certain seasons, and (3) livestock allowed to graze during day time, being kept in the barn at night. Carcass dumps were present in only nine of the studies, resulting in 16 data points where grey wolves could scavenge on dead animals at the farm's open-carcass dump (Chavez and Gese, 2005). These 16 data points were discarded from the analysis of domestic occurrence, since scavenging was not considered depredation. These events were confirmed to be scavenging, opposite to other instances, where it could not be confirmed if grey wolves did prey or scavenge carcasses. The exclusion of these studies did not significantly affect the selection of domestic species.

Mammals have evolved a wide variety of defence strategies to minimise risk of depredation (Caro, 2005), therefore presence/absence of anti-predator defence mechanisms (horns, antlers, spikes or fangs) were included for both wild and domestic groups. Rapid sprint speed and large size are both thought to decrease vulnerability to many predators (Sinclair et al., 2003; Walker et al., 2005), thus both variables were added as possible species traits driving grey wolves' preferences (Appendix E).

Scat content was expressed as percent biomass, as this technique is most the reliable to determine large carnivore diets (Davis et al., 2012; Klare et al., 2011). We calculated the mean biomass for yearly and seasonal studies. We used FO for all food categories included the “others” for the compositional analysis. We used percent biomass of all food categories for the models but excluded “others” because these groups did not form a consistent part of grey wolves' diet (FO < 13% in total) and there was very limited information about density data for these kinds of food items. Only 10 studies did not reach the minimum size of 59 scats necessary to identify principal prey remains occurring in >5% of scats (Trites and Joy, 2005), with 106 studies containing data from over 100 analysed scats. These were included in the analyses nonetheless.

2.2. Statistical procedures

Missing data, mainly prey species densities (19.9%), were imputed using the “mice” package (van Buuren, 2011) by drawing plausible values from a prediction distribution for each data point. We performed repeated multiple imputations ($m = 5$), until there were no significant differences between the distributions of original and imputed data (Appendix F). Multiple imputation is an advanced method in handling missing values. In contrast to single imputation, multiple imputation creates several datasets (m) by imputing missing values, based on the distribution of observed data, without the need to specify a joint distribution of predictor variables (White et al., 2011). These values take imputation uncertainty into consideration. Missing values are replaced by the average of the multiple imputed values (Hui et al., 2004). Single

Table 1

Prey group	Predictors	Estimate	Std error	t value	P
All	Intercept	−2.073	0.111	−18.626	2×10^{-16}
	Wild prey	0.499	0.144	3.472	0.001
	Density	0.199	0.060	3.302	0.001
	Body mass	0.415	0.096	4.341	1.7×10^{-5}
	Density:wild prey	0.408	0.105	3.886	1.1×10^{-4}
	Density:body mass	0.188	0.039	4.851	1.6×10^{-6}
	Wild prey:body mass	0.451	0.119	3.803	1.6×10^{-4}
	Body mass:speed	0.302	0.063	4.767	2.5×10^{-6}
Cox-Snell R^2	0591				
Domestic	Intercept	−2.565	0.360	−7.124	2×10^{-16}
	Defence mechanisms	4.733	0.951	4.980	1.9×10^{-6}
	Density	1.160	0.329	3.528	0.001
	Body mass	0.970	0.368	2.638	0.009
	Free grazing	0.776	0.159	4.879	2.9×10^{-6}
	Defence mechanisms:body mass	−3.853	0.908	−4.244	4.1×10^{-5}
	Body mass:Free grazing	−0.788	0.188	−4.200	4.8×10^{-5}
	Density:night shelter	1.132	0.218	5.191	7.5×10^{-7}
	Density:free grazing	−0.517	0.156	−3.308	0.001
Cox-Snell R^2	0.640				
Wild	Intercept	−2.525	0.295	−8.563	2×10^{-16}
	Defence mechanisms	1.107	0.302	3.669	0.003
	Density	0.481	0.162	2.968	0.003
	Density:body mass	0.501	0.067	7.476	6.8×10^{-13}
	Speed:body mass	0.970	0.376	2.582	0.010
Cox-Snell R^2	0.624				

imputation has been criticized for its bias (e.g., overestimation of precision) and ignorance of uncertainty about estimation of missing values, but if performed properly can give an accurate estimate of a real result. We performed repeated multiple imputations ($m = 5$), until there were no significant differences between the distributions of original and imputed data (Appendix F). Data were separated into two additional datasets, one for a total of 10 domestic prey species and another for 44 wild prey species, to compare grey wolf preferences among and within both groups.

Then, to identify the variables associated with grey wolf selection of domestic and wild prey, we ran Generalised Linear Models for Location, Scale and Shape (GAMLSS, Rigby and Stasinopoulos, 2007) using *R*. A complete list of all predictors used in our analysis is presented in Appendix E, with biomass percent as our dependent variable. The GAMLSS was fit to deal with some of the limitations associated with generalised additive models (GAM) and Generalised Linear Models (GLM). In GAMLSS, the exponential family distribution assumption for the response variable (Y) is relaxed and replaced by a general distribution family, including highly skewed and kurtotic distributions. Current updates of GAMLSS can handle up to 50 different types of distributions (Rigby and Stasinopoulos, 2007).

Our dataset had a higher number of zero responses than expected for a Poisson or negative binomial distribution. We registered 402 out of 729 events of 0% FO, even if the species was present in the study area. This means that a zero-inflated model that accounts for this excess of zeros was required. We therefore built our models separately for each dataset (wild and domestic prey species) using the zero/one- inflated beta regression (BEINF) type of distribution available in the 'gamlss' package in *R*. The beta-inflated distribution is used when the response variable takes values in a known bounded range. Appropriate standardisation can be applied to make the range of the response variable [0,1], i.e. from zero to one including the endpoints (Ospina, 2008). Spatial data (bioregion, biome and country) and prey species were coded as random effects since we expected similar effects of wolf diet preference across studies and prey groups. We ran the above-mentioned analysis to both the datasets with and without multiple imputation, corroborating that both results are qualitatively similar (Appendix F). Thus, we decided to use the multiple imputation dataset for our main analysis. We included interactions between explanatory variables and standardized the numeric predictors. We checked the residuals and worm plots (van Buuren and Fredriks, 2001) for each model afterwards (Appendix G).

3. Results

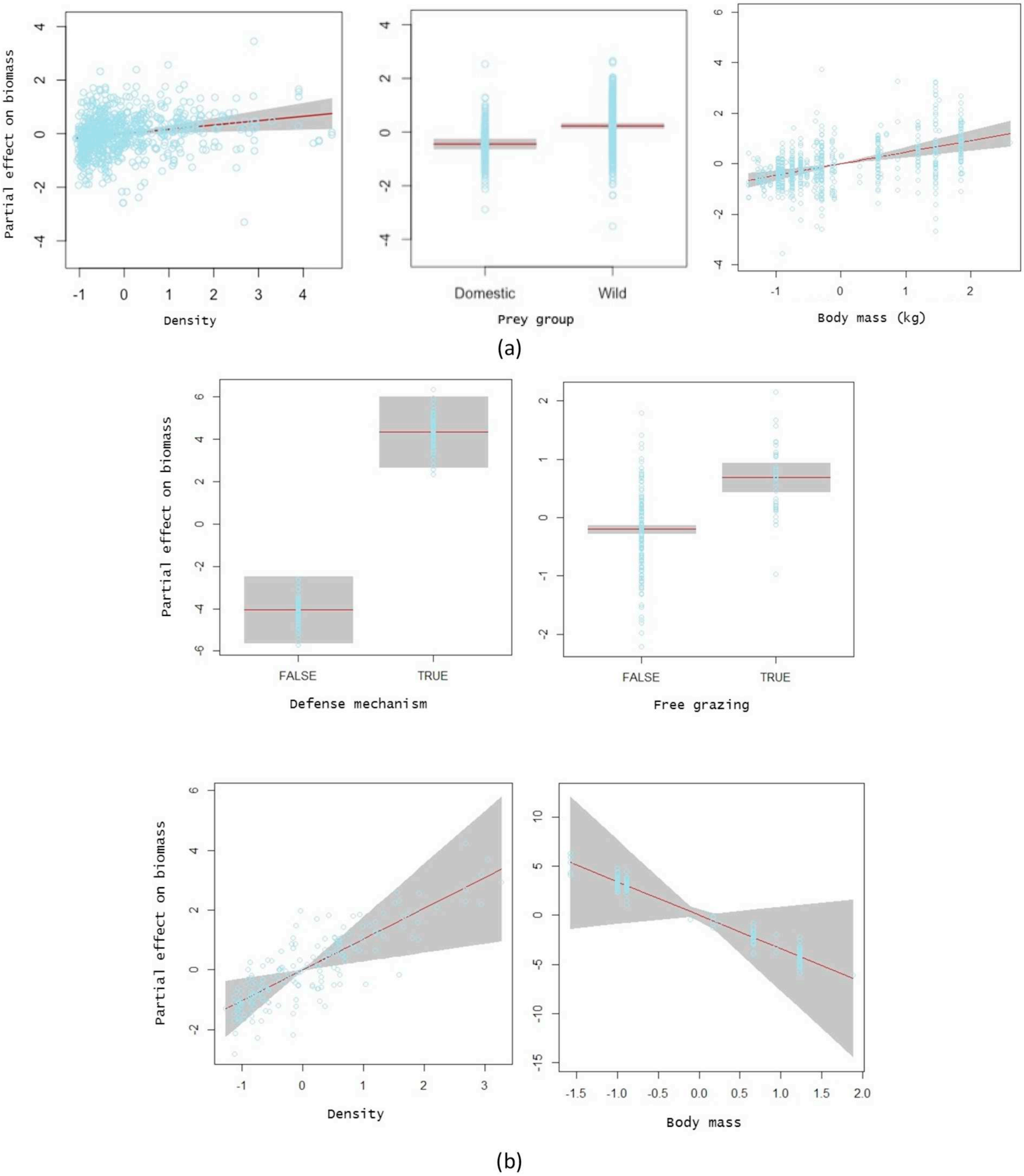
3.1. Literature review

We reviewed a total of 1877 literature sources, dating from 1944 to 2017. After meeting the selection criteria, we selected 119 studies, resulting in 729 data points. There was an increase in the number of studies published from 1945 to 1985 (peak = 85 studies), then a decline thereafter (Fig. 1a). Most of the studies were from Europe, particularly Italy, northern Spain and Central Europe with over 100 data points each (Fig. 1b).

About 65% of the domestic species present across studies were never found in grey wolf diets (FO = 0%) in comparison to only 47% of the wild ungulates never being consumed. It was common to have several domestic species not eaten by grey wolves in one study area even if they were present there.

Wild species were more prevalent in grey wolf diets (biomass percentage mean = 19 ± 27%) than domestic species (13 ± 19%) at the global level. Biomass percentage means of wild and domestic species were almost equal (wild biomass percentage mean = 14 ± 21%, domestic biomass percentage mean = 13 ± 19%) when taking into consideration only study sites where both prey types were present. We observed similar results when comparing grey wolf diets within continents, except for Asia, which had similar selection for both prey groups, with a mean FO of 12.5% for wild species and of 12.2% for domestic species (although the results in Asia were slightly different when using biomass consumption of domestic species with a mean biomass of 20% in comparison to a 13% of wild ungulates) (Fig. 2a). The wild-over-domestic selection pattern was evident consistently across bioregions, apart from the Asian bioregions of Mongolia (mean biomass of 11% for wild species versus 16% for domestic), Nepal (8% vs 10%), China (1% vs 49%), Pakistan (9% vs 21%), Iran (7% vs 42%) and South Russia (3% vs 23%) (Fig. 2b).

Percent of biomass of livestock in grey wolf diet was directly related to livestock management methods, particularly whether flocks could roam free and whether livestock were kept outside during the day. Livestock was preyed on much less when kept in a barn or farmyard and



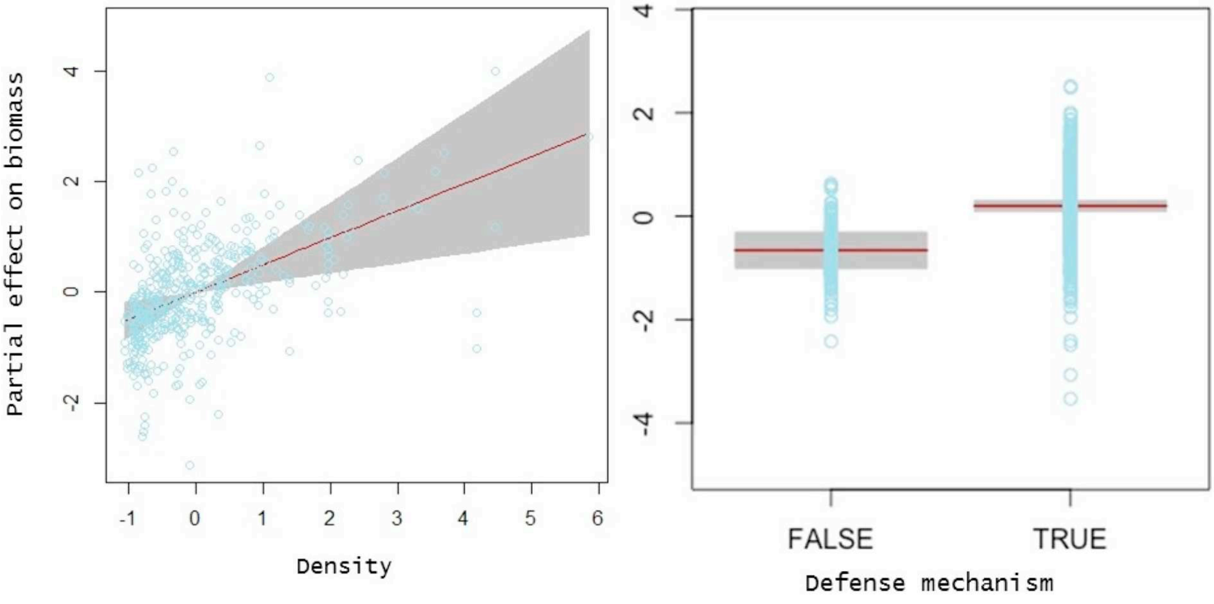
(a)

(b)

Fig. 4. Partial residual plots for the main models effects shown in Table 1 in (a) all species, (b) domestic species and (c) wild species datasets.This figure shows the data points after controlling for all other predictors in the model. , including the model residuals.

much more when left to graze without supervision (Fig. 3). However, there was an outlier to consider, for prey selection when animals were kept in barns during the night (Lagos, 2013, biomass over 86% for cattle). Anti-predator mechanisms were present in both wild and domestic species, i.e. horns in cattle (*Bos taurus*) and alpine ibex (*Capra ibex*). There was a much stronger selection of wild prey when comparing species with defensive traits from both groups. Selection of prey without any defensive mechanism was similar for domestic (i.e. domestic pigs) and wild groups (i.e. Przewalski's horses) (Fig. 3).

Grey wolf diets in Spain (8% mean wild biomass vs 18% mean domestic biomass) and Greece (13% vs 23%) differed from those in other bioregions by feeding mainly on livestock and other non-wild prey. Slightly lower percentages of domestic species differentiated the other southern European bioregions (domestic biomass of 11% for Italy and 8% for the Alps), while Scandinavian (0.1%) and central European (2%) grey wolves fed mainly on wild species. In contrast, North American study sites were consistently characterised by an almost exclusive selection of a few wild herbivore species (wild mean FO of 78%). In Asia, the results ranged from purely domestic selection in bioregions such as Mongolia (N = 29, domestic biomass of 16%), Pakistan (N = 13, 21%), Iran (N = 9, 21%), south Russia (N = 6, 23%) and China (N = 4, 49%), to high wild species selection in bioregions with more available data points such as India (N = 21, domestic biomass: 28%). Kyrgyzstan was the bioregion with the fewest data points



(c)

Fig. 4. (*continued*)

(N = 3) showing a dietary preference towards only wild species (Fig. 2b).

3.2. Drivers of biomass

Our GAMLSS model (Table 1) suggest that the type of prey (domestic or wild) does influence the percentage biomass consumed (Fig. 4a, $P = 0.001$), with wild prey being selected over domestic. We also found a significant effect over percent of biomass consumed in relation to prey abundance (Fig. 4a, $P = 0.001$) and body mass of prey (Fig. 4a, $P < 0.001$). We found a significant effect on prey selection on the interaction of body weight and maximal running speed. This indicates that grey wolves prefer faster species with high body mass. Although preference towards heavier prey was more associated wild species (Fig. 5a, $P < 0.001$). We found a similar effect on the interaction of body weight with animals' abundance, where grey wolves selected for heavy species with low densities, especially wild animals (Fig. 5a, $P < 0.001$).

For domestic species (Table 1), animals possessing defence mechanisms (Fig. 4b, $P < 0.001$) and left unattended and grazing freely for long periods of time were the most vulnerable to grey wolf attacks (Fig. 4b, $P < 0.001$), with biomass rates increasing up to 78%. We found a higher selection of more abundant animals (Fig. 4b, $P = 0.001$), but selection decreased for heavy prey (Fig. 4b, $P = 0.009$). The presence of small herds grazing freely and with high body weight were similarly important factors in determining prey selection (Fig. 5b). Animals enclosed at night were more vulnerable when present in bigger numbers (Fig. 5b, $P < 0.001$). We did not find a significant relationship of grey wolf selection for the other types of livestock husbandry.

For wild species (Table 1), the most significant effect on the biomass consumed was the presence of heavy prey in big numbers, followed by the presence of defence mechanisms (Fig. 4c, $P < 0.001$). We found a significant effect of prey abundance, with occurrence in scats increasing up to 48% for each extra individual per square kilometer (Fig. 4c, $P = 0.003$). There was a significant and positive effect of prey speed associated with animal weight, biomass rates increased significantly for faster animals with high weights (Fig. 5c, $P = 0.01$), and when present in smaller numbers (Fig. 5c, $P < 0.001$). All other variables, including their interactions, were not significant factors predicting overall wolf preferences towards wild species (Table 1).

4. Discussion

There is global interest in restoring large carnivores to their historic ranges, both for their own conservation and for the ecosystem services they provide (Ripple et al., 2014; Terborgh and Estes, 2010). Achieving this relies on the availability of suitable habitats and prey, as well as the ability to minimise human-carnivore conflicts. The grey wolf started to recolonise parts of its former range because of legal protections, natural recolonisation, reintroductions, and/or new habitat becoming available (Ansorge et al., 2006; Bangs et al., 1998; Bath and Buchanan, 1989). For grey wolves to successfully recolonise new areas requires an understanding of the factors that cause them to consume livestock. We addressed this issue at the global scale, and tested the broad hypothesis that depredation on livestock by grey wolves would be lower under circumstances where wild prey is abundant and where nonlethal livestock protection measures are in place. Our results suggest that grey wolves select wild prey when it is available, even when livestock is present at higher density, corroborating the first part of our hypothesis. This selection pattern is clearly seen in North America and Central Europe, where there is sparsely populated land and large populations of wild herbivores (Fuller, 1989; Mech, 1966; Müller, 2006; Novak et al., 2011; Thomson, 1952; Voigt et al., 1976).

In contrast, grey wolves mostly consumed livestock in Southern European countries and parts of Asia where large wild ungulates are largely extinct by humans. For example, grey wolves selected domestic ungulates in the Iberian Peninsula (Lagos, 2013; Torres et al., 2015; Vos, 2000), Italy (Ciucci and Boitani, 1998; Davis et al., 2012; Meriggi et al., 1991) and Greece (Migli et al., 2005), where wild ungulates are rare or even absent (Macdonald et al., 1980). In these areas, grey wolves have locally adapted to highly populated and intensively used areas by feeding mainly on other food resources and livestock. There were relatively few data available for Asia, with only 13% of the data points from this region. Nonetheless, data from Mongolia (Chen et al., 2011), China (Liu and Jiang, 2003), Southern Russia (Sidorovich et al., 2003), and Iran (Hosseini-Zavarei et al., 2013; Tourani et al., 2014) suggest intense selection of domestic ungulates by grey wolves. In India (Anwar et al., 2012; Habib, 2007; Jhala, 1993), Kyrgyzstan (Jumabay-Uulu et al., 2013) and Nepal (Chetri et al., 2017), grey wolves selected

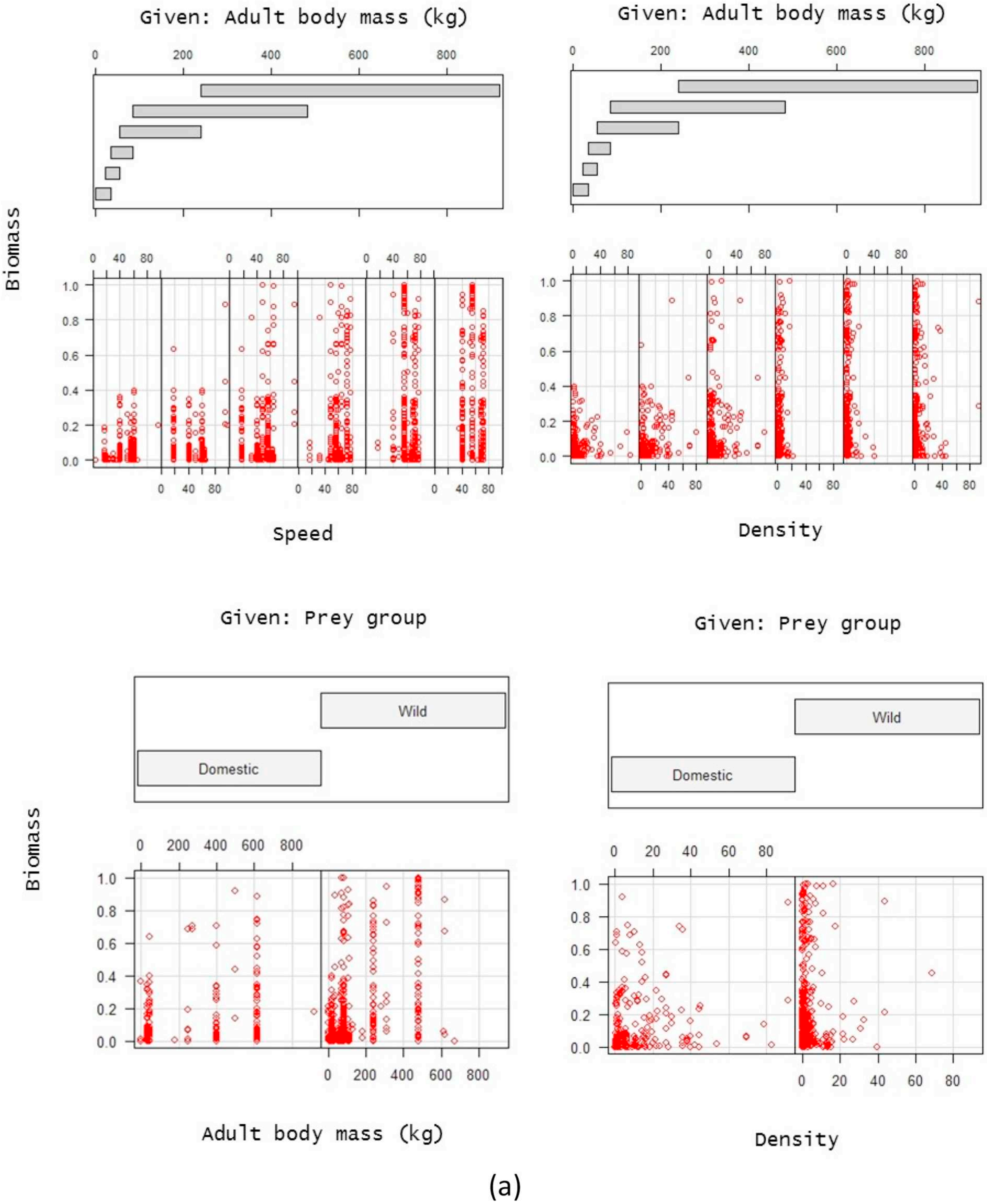


Fig. 5. Interaction plots representing visually the interaction between the main models effects shown in Table 1 in (a) all species, (b) domestic species and (c) wild species datasets. We define interaction when the effect of one independent variable differs based on the level or magnitude of another independent variable

wild ungulates over domestic species despite the high abundance of the latter. Pakistan showed an increase in livestock selection with its density. In terms of tackling the issue of livestock depredation by grey wolves, increasing wild prey populations may result in an increase of grey wolf density, potentially increasing the likelihood of conflict (Fuller et al., 2003; Mech and Barber-Meyer, 2015). However, several studies have suggested an increase of wild ungulate selection by grey wolves over livestock as wildlife abundances recover (Imbert et al., 2016; Meriggi et al., 2014). Our data mostly support this view, so the conservation of wild herbivores is important for successful wolf conservation.

Grey wolf preference towards unattended livestock was the most important driver of domestic species biomass consumption, corroborating the second part of our hypothesis. However, the presence of small flocks grazing freely, high densities of livestock being enclosed at night, and prey weight were important factors in determining prey selection (Table 1). Selection for livestock present in small numbers may be because these animals cannot aggregate in flocks as an antipredator

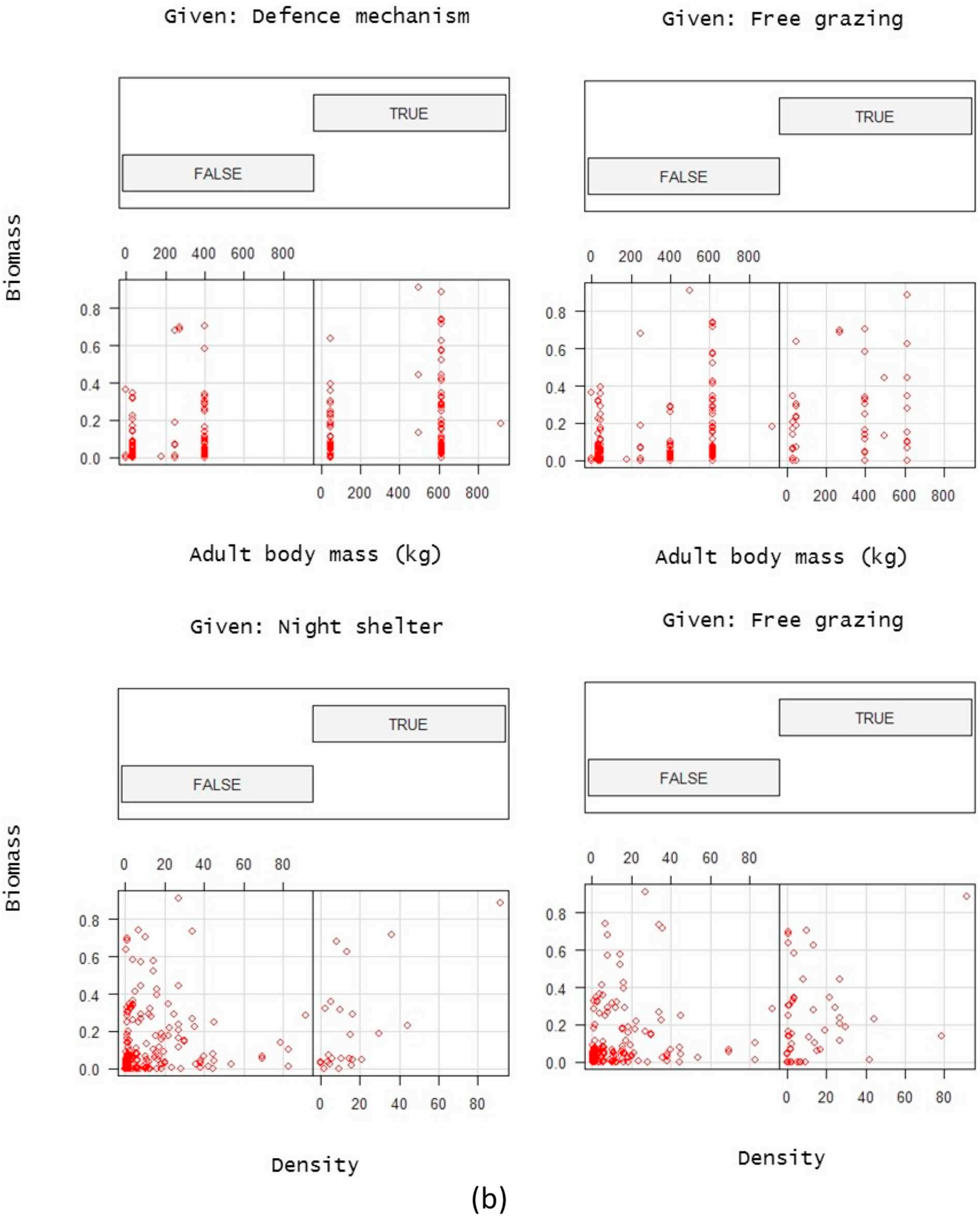


Fig. 5. (*continued*)

strategy leading to greater hunting success (Hamilton, 1971). Larger animals (>200 kg, i.e. cattle) were less likely to be preyed in comparison to smaller species such as sheep or goats that are more easily preyed (Fig. 5b), particularly when present in small groups. The increase of biomass consumed when animals were kept in shelters during the night was unexpected as this is seen as a measure of protection. However, this was likely due to an outlier (Lagos, 2013) with a biomass over 86% for cattle. Poor husbandry techniques are commonly used to explain high levels of depredation (Linnell et al., 1996; Meriggi and Lovari, 1996; Ciucci and Boitani, 1998). Our analyses found that the style of husbandry does affect livestock losses, with depredation increasing up to 78% in herds without any type of protection. In addition to conserving wild herbivores, it is therefore also important to implement appropriate livestock husbandry practices to minimise stock losses to grey wolves.

Grey wolf prey selection is determined by the risks that could arise during prey hunt, which is likely influenced by relative prey size, defence morphology (presence of horns, antlers, spikes or fangs) and

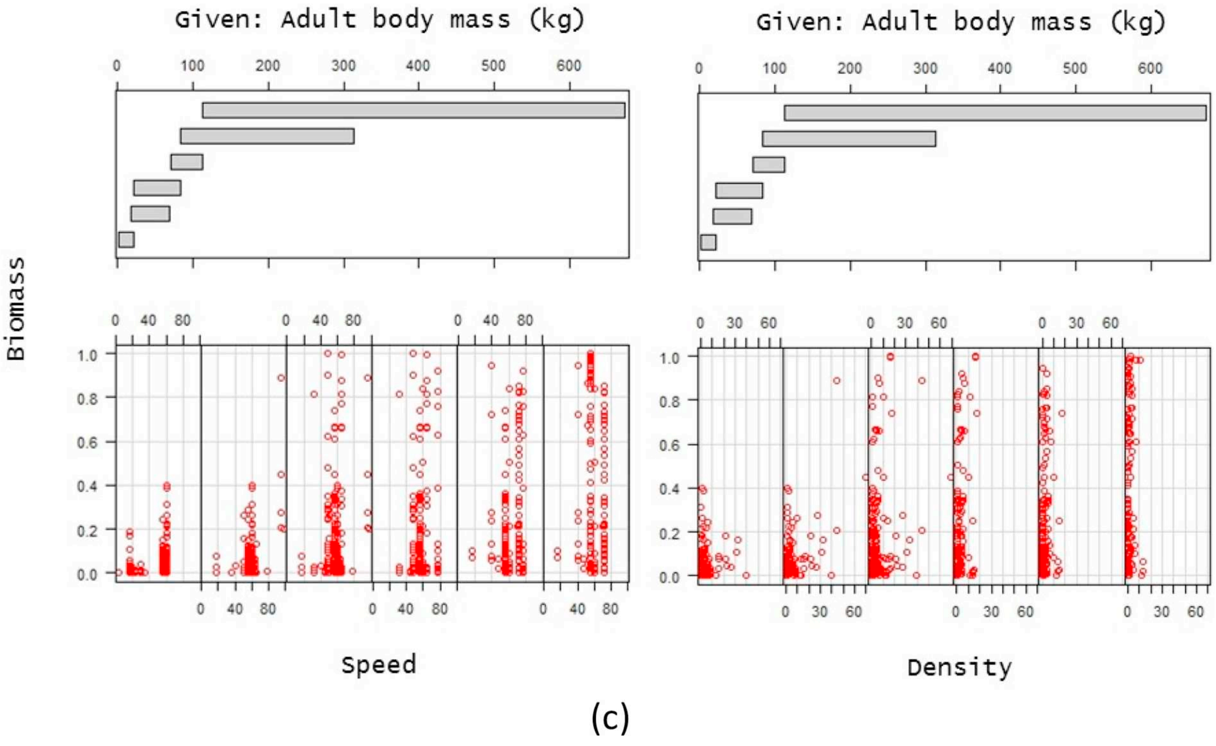


Fig. 5. (*continued*)

behavior (grouping) that may deter predators (Caro, 2005). Wildlife and domestic selection were highly influenced by the presence of defence mechanisms based on our results (Table 1). However, most of the species studied (67%) had a defensive trait, usually horns or antlers, and wolves are evolutionary predisposed to prey on ungulates that have defensive mechanisms (Mech and Peterson, 2003). The other factors we considered included animal abundance and weight. Animal abundance was the second most important driver of consumed biomass for wild ungulates. An increase of animal abundance (1 individual per square meter) could increase the consumed biomass up to 48%. There was a significant and positive effect of prey abundance associated to animal weight as well, with wolf preference towards heavier animals was detected when prey was present in smaller numbers, and conversely the selection of smaller species when these were more abundant (Table 1). Hunting success could be compromised when heavier, and therefore less vulnerable, species are present in aggregated herds. Bigger prey species are better able to defend themselves against predators being at the same time more exposed when present in small numbers (<10 individuals/km^2).

4.1. *Management implications*

Our main finding that grey wolves show a preference for wild prey and free-ranging livestock under different circumstances has important implications for facilitating coexistence between humans, livestock and grey wolves. Specifically, our results suggest that wild prey populations should be maintained and restored wherever possible to provide enough food for grey wolves and to minimise the likelihood that they will attack livestock. This is especially the case in highly human-populated areas where grey wolf and human habitats overlap and livestock are more vulnerable, such as the Iberian Peninsula, Italy and Greece, but also central Europe where there are increasing numbers of grey wolves (Ronnenberg et al., 2017). Second, livestock should be properly protected to minimise opportunities for wolf attacks. Unattended livestock can be subjected to repeated attacks in the same area since grey wolves can return to the kill site to keep on feeding, finding new vulnerable prey in the process (Karlsson and Johansson, 2010).

Many non-lethal methods have been tried to reduce livestock depredation (Breitenmoser et al., 2005). These include fencing (Musiani et al., 2003), confining livestock at night or during bad weather (Linnell et al., 1996; Schiess-Meier et al., 2007), repellents (Atkinson and Macdonald, 1994; Shivik et al., 2003; Smith et al., 2000a), livestock carcass disposal (Lagos and Bárcena, 2015), avoiding high risk areas or seasons, replacing vulnerable stock, adjusting calving seasons and location, guarding animals (Smith et al., 2000b), harassing, shooting non-lethal projectiles, relocating wolf populations (Bangs and Shivik, 2001; Bradley and Pletscher, 2005), fitting protective collars, or not removing horns from cattle. There is evidence that fencing and guardian animals can be effective in a range of scenarios (van Eeden et al., 2018b). Our results confirm that leaving animals unattended could significantly increase livestock depredation in any situation. When preventive measures fail, compensation programs have become common practice not only in Europe (Ciucci and Boitani, 1998; Echegaray and Vilà, 2010), where the disturbing lack of wild species make livestock management measures more difficult, but also in North America and Asia (Agarwala et al., 2010). However, many developing countries do not have the economic means to compensate livestock owners financially or to provide expensive proactive deterrents (Mishra, 1997), making livestock management measures the best solution to mitigate human-grey wolf conflicts.

Understanding the behavior and food preferences of wild species that conflict with humans is an essential first step for identifying mitigation strategies. Although we can only reveal broad patterns from our dataset, our results illustrate that identifying carnivore dietary preferences and patterns of livestock depredation associated with different management interventions can provide insight into improving coexistence between predators and livestock. In the future, our approach could be broadened to understanding the underlying behavioral mechanisms causing conflict between humans and other large carnivores or other species perceived to be pests.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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