

REVIEW

Food habits of the world's grey wolves

Thomas M. NEWSOME* *Desert Ecology Research Group, School of Biological Sciences, University of Sydney, New South Wales 2006, Australia; Global Trophic Cascades Program, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA and Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria 3125, Australia. Email: tnew5216@uni.sydney.edu.au*

Luigi BOITANI *Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Rome 00185, Italy. Email: luigi.boitani@uniroma1.it*

Guillaume CHAPRON *Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, SE - 73091 Riddarhyttan, Sweden Email: gchapron@carnivoreconservation.org*

Paolo CIUCCI *Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Rome 00185, Italy. Email: paolo.ciucci@uniroma1.it*

Christopher R. DICKMAN *Desert Ecology Research Group, School of Biological Sciences, University of Sydney, New South Wales 2006, Australia. Email: chris.dickman@sydney.edu.au*

Justin A. DELLINGER *School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA. Email: jad1nel2@gmail.com*

José V. LÓPEZ-BAO *Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, SE - 73091 Riddarhyttan / Research Unit of Biodiversity, Oviedo University, 33600 Mieres, Spain. Email: jv.lopezbao@gmail.com*

Rolf O. PETERSON *School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan 49931, USA. Email: ropeters@mtu.edu*

Carolyn R. SHORES *School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA. Email: shores.carolyn@gmail.com*

Aaron J. WIRSING *School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA. Email: wirsinga@uw.edu*

William J. RIPPLE *Global Trophic Cascades Program, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA. Email: bill.ripple@oregonstate.edu*

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*Correspondence author.

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ABSTRACT

1. Grey wolves *Canis lupus* have been studied extensively, but there has been no detailed review of the species' feeding ecology, despite growing debate about how to conserve wolf populations while limiting their impacts on wild or domestic ungulates. Here, we assess the extent to which the grey wolf diet varies among and within North America, Europe, and Asia.

2. We derived dietary data from searches of published literature. We grouped studies based on their bioregional location. We compared grey wolf diet among locations using non-metric multidimensional scaling and analysis of similarity. We assessed whether increased human impacts are associated with decreased grey wolf dietary diversity. Finally, using studies from southern Europe, we assessed whether the importance of wild ungulates in grey wolf diet has increased over time, coincident with a decline in domestic species in grey wolf diet over time.

3. We compiled dietary data from 177 studies incorporating 94607 scat and stomach samples. Grey wolf diet was dominated by large (240–650 kg) and medium-sized (23–130 kg) wild ungulates, but variation in the percentages of

wild ungulates consumed, along with variation in the percentages of domestic and smaller prey species consumed, contributed to the dietary differences found among and within continents.

4. We found no evidence that grey wolf dietary diversity varies globally, although the results from southern Europe suggest that grey wolves may switch their diets away from domestic species if more wild ungulates are available.

5. The diversity of prey consumed by grey wolves shows that the species is capable of surviving dramatic anthropogenic upheaval. However, there is an urgent need to increase our understanding of grey wolf foraging ecology in human-dominated landscapes, in order to determine whether restoration of depleted prey populations, coupled with effective damage-prevention measures, will reduce human-wolf conflicts.

INTRODUCTION

Before humans emigrated from Africa some 60000 years ago and populated the rest of the world, all continents were inhabited by a variety of megafauna (animals > 44 kg; Hofreiter 2007). These species included, for instance, the sabre-toothed cat *Smilodon populator*, marsupial lion *Thylacoleo carnifex*, woolly mammoth *Mammuthus primigenius*, and the short-faced bear *Arctodus simus*. However, during the Late Pleistocene and early Holocene (c. 24000 to 5000 before present), about two-thirds of the large mammal genera went extinct (Hofreiter 2007). Multiple explanatory hypotheses for this global extinction event have been proposed, but hunting and habitat changes caused by humans are likely to have been the primary drivers (Sandom et al. 2014). Human actions continue to cause extinctions of large-bodied species in most continents (Pimm et al. 2014), and those species that have survived are typically confined to reduced ranges (Laliberte & Ripple 2004, Ripple et al. 2014). In particular, large mammalian carnivores (≥ 15 kg) have experienced massive declines in their populations and geographic ranges around the world, and 77% of the 31 largest extant carnivores are still undergoing population declines (Ripple et al. 2014).

The grey wolf *Canis lupus* is a prime example of a large carnivore that has experienced recent population declines. Indeed, the species had one of the most extensive historical geographic distributions of any mammal, occurring throughout the northern hemisphere north of 15–20°N (Paquet & Carbyn 2003). However, during the 19th and 20th centuries (1800–2000), the grey wolf was eliminated by humans from much of its former range (Laliberte & Ripple 2004). As a consequence, in many places grey wolves became mainly restricted to remote and undeveloped areas with sparse human populations (Paquet & Carbyn 2003, but see Chapron et al. 2014, López-Bao et al. 2015b). In recent decades, grey wolf numbers have increased in some areas because of enhanced legal protections, natural recolonisation, and reintroductions (Chapron et al. 2014, Ripple

et al. 2014). Yet, there is still a deeply rooted hostility against the species because of its perceived impacts on human lives and livelihoods (Bruskotter & Wilson 2014, Dressel et al. 2015), various traditions and cultural practices, and political scapegoating (Chapron & López-Bao 2014, López-Bao et al. 2015a).

Throughout its range, the grey wolf's predatory habits and diet lie at the root of its conflict with humans (Naughton-Treves et al. 2003). Specifically, grey wolves, as predators, consume mostly meat, and are often accused of depleting populations of wild ungulates that serve as game for hunters, or of affecting the profitability of livestock farming (Bergstrom et al. 2009). Yet, there is growing interest in restoring grey wolf populations, both to conserve them and to harness their ecological services (Ripple et al. 2013, 2014). To facilitate informed discussion of grey wolf conservation and management, it is critical to develop a clear understanding of grey wolf dietary ecology in landscapes with varying levels of human influence. Grey wolves are now recolonising human-dominated regions in North America and Europe for the first time in many decades or even centuries, and insight from existing dietary studies will aid in predicting some of their ecological impacts (Mech 2012) and avoiding ecological surprises (Lindenmayer et al. 2010) that might undermine conservation and restoration goals. Indeed, a deep understanding of past ecological literature has been identified as an obvious and critically important part of formulating good hypotheses, framing alternative views of ecosystems and, in turn, developing ecological research (Lindenmayer et al. 2010).

In this paper we provide a comprehensive review of grey wolf diet at a global scale. To derive our results we reviewed field studies in which the diet of grey wolves was quantified from scats (faeces) and stomach contents. To evaluate large-scale spatial variation in grey wolf diet, we grouped studies into three continents that encompass the range of this carnivore: North America, Europe and Asia. We then grouped the studies according to their bioregional location within each continent. Our primary objective was to determine whether grey wolf diet varies among and within these

continents. Because grey wolves occur across a gradient of human landscape-transformation, from human-dominated regions to relatively undisturbed areas (Paquet & Carbyn 2003, Peterson & Ciucci 2003, Chapron et al. 2014), we expected that any dietary divergence would stem from differential use of anthropogenic foods and wild prey.

Our secondary objective was to test two specific predictions. Firstly, we explored whether increased human impacts on the landscape would result in a change in the diversity of prey consumed by grey wolves. We expected that dietary diversity would be lower in areas heavily modified by humans because human alteration of the globe has caused widespread environmental and ecological changes, including loss of biological diversity (Chapin et al. 2000). Secondly, as wild ungulate populations have been restored in southern Europe in recent decades, we tested specifically whether there is any evidence in the available literature on the diet of wolves in this region that the importance of wild ungulates in grey wolf diets has increased over time. We use the results to determine the extent to which grey wolves have modified their dietary preferences in human-altered ecosystems, and discuss the implications for conservation and management.

METHODS

Global review of grey wolf diet

We reviewed the literature on grey wolves and identified publications with a clear focus on diet. This literature was compiled through queries of Web of Science, JSTOR, Google Scholar and BIOSIS Previews for titles, abstracts and full texts with the search terms 'wolf' or '*Canis lupus*' and 'diet' with no restrictions on year or language applied (Appendix S1) and through the personal bibliography of one of the authors. Where large numbers of returns (>500) were obtained from the data base searches, we sorted the results by relevance, an automated feature of each search engine, to assist in determining which results were not relevant based on the search terms. We also cross-checked the reference lists of all papers found during the initial search. Any additional data found via the searches of reference lists, including books, conference presentations, and publically available theses and reports were included in our review.

We selected papers (Appendix S2) in which data were provided on the frequency of occurrence, relative occurrence, biomass or volume of prey species consumed by grey wolves from scat or stomach contents. We included dietary data from all subspecies of grey wolves, with the exception of domestic dogs *Canis lupus familiaris* and the New Guinea singing dog *Canis lupus hallstromi*. The African wolf *Canis lupus lupaster* was excluded because of

taxonomic ambiguity (Gaubert et al. 2012). The species name for the dingo (*Canis dingo*, previously *Canis lupus dingo*) has been revised and it is no longer considered a subspecies of extant grey wolves (Crowther et al. 2014); it was therefore excluded.

Summarising the data

We recorded the location (centroid), sampling length (start, middle and end), season (summer, autumn, winter, spring), source of dietary material (scat or stomach), analytical method (frequency, volume, or biomass calculation), and sample size (number of scats or stomachs) for each study, based on descriptions provided. Scat or stomach contents were recorded at the individual prey species level whenever possible, although some small prey items were grouped using categories commonly adopted in diet studies, such as fruit, birds, rodents, and rabbits/hares, for simplicity. To allow for a broad assessment of dietary preferences, we pooled the data from each study into 10 broad food categories based on adult body sizes (Appendix S3). The 10 food categories were: 1) domestic species; 2) large wild ungulates (240–650 kg); 3) medium-sized wild ungulates (23–130 kg); 4) medium-sized mammals (4–21 kg); 5) small mammals (0.1–2 kg); 6) rodents (~0.1 kg); 7) birds; 8) other (including large carnivores and fish); 9) garbage; 10) fruit. Where individual studies included dietary data from multiple locations in different habitats, we treated these as independent samples. For studies that reported dietary data for individual wolf packs, or on a yearly, seasonal or monthly basis, we calculated average values for each prey species or group. The occurrence of vegetation and invertebrates in grey wolf scats was infrequently reported so we excluded these categories in subsequent analyses.

To assess geographical variation in grey wolf diet we hierarchically grouped the studies at two different spatial scales. Firstly, we grouped the studies at the continent level (Fig. 1). Then, we grouped studies within each continent based on 14 biome boundaries determined by Olson et al. (2001; Fig. 1). Where studies occurred in the same biome but were geographically separated by over 100 km, we used finer scale ecoregion mapping (Olson et al. 2001) to assess whether the studies should be separated. This process resulted in nine bioregions in North America, eight in Europe and six in Asia (Fig. 1).

Reviewing the data set

Percentage frequency of occurrence per sample (%FO), expressed as the percentage of scats or stomachs containing a particular food taxon, is the most consistently used measure of the relative importance of prey taxa in carnivore diet (Klare et al. 2011). Wherever possible, we recorded

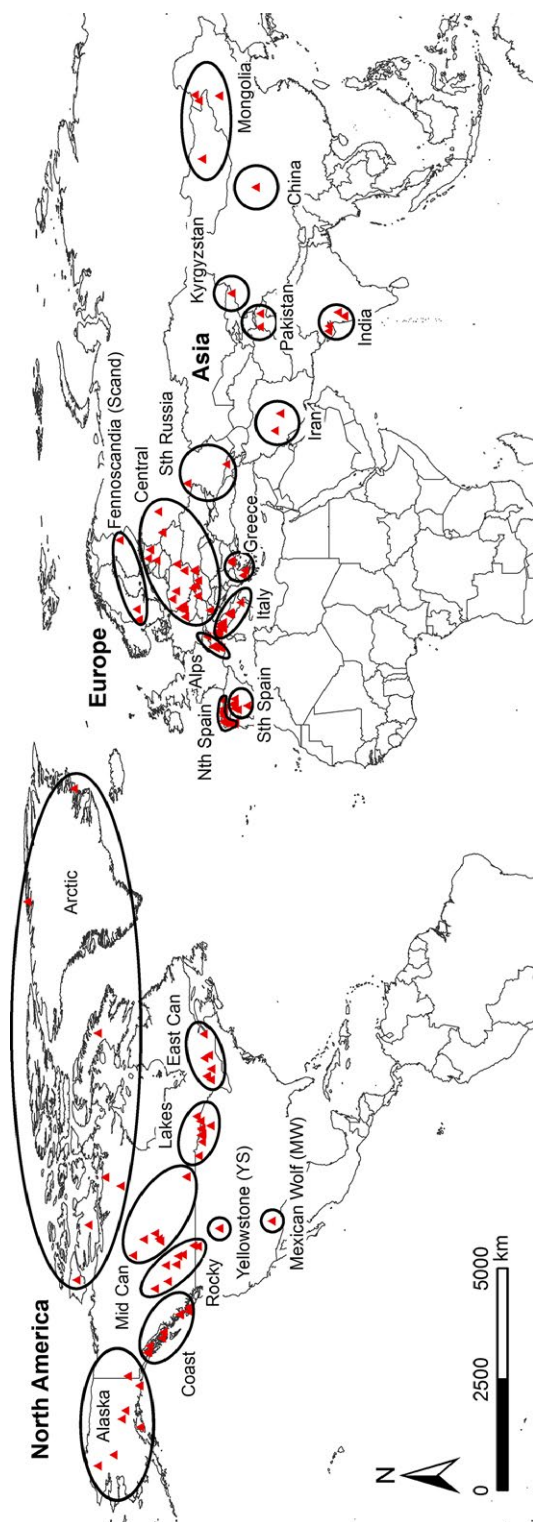


Fig. 1. Geographical distribution of the 177 grey wolf dietary studies (triangles) included in this review. Circles or ellipses enclose the bioregional groupings of studies within the continents: North America, Europe and Asia. Some study labels and bioregional boundaries have been moved slightly to accommodate the broad scale of mapping (1:125000000).

%FO to allow for comparisons among studies. However, %FO can yield different results to frequency of occurrence per food item, percentage volume of remains in each food category, or percentage biomass in scats (Klare et al. 2011). Thus, a common approach in dietary reviews is to exclude studies that do not use %FO (Doherty et al. 2015). Studies are also excluded on the basis of sample type (scat or stomach), sample sizes, and survey length (Doherty et al. 2015). However, under this approach, up to 40% of studies would have been removed from our review, greatly reducing our sample sizes and global coverage. Therefore, to assess whether we needed to exclude any studies we undertook two exploratory analyses.

Firstly, we calculated the average dietary content values for the 10 broad food categories in each bioregion in each continent. We repeated this step using a subset of the data with the following criteria for inclusion: 1) %FO was used; 2) dietary data came from scat contents; 3) >25 scats were sampled; 4) multiple seasons were sampled. After compiling the average values into separate tables, we converted them into a Euclidian distance matrix using the software package *ade4* (Dray et al. 2014) in *R* (Anonymous 2008). We then used a Mantel test (Mantel 1967) to evaluate the association between the full and subset distance matrices in each continent. As a second test, we ran a multivariate linear model using the *R* package *mvabund* (Wang et al. 2012). We tested for an effect of sampling length (in years), season (summer, autumn, winter, spring), source of dietary material (scat or stomach), analytical method (frequency, volume, or biomass calculation), and sample size (number of scats or stomachs) on the 10 broad food category values for each individual study in each continent. We used 1000 resampling iterations and analysis of variance to test for the overall effect of each variable on the 10 broad food category values. The results of these two tests confirmed that there were no statistical grounds to exclude studies from our review (Appendices S4 and S5). If the full and subset distance matrices had been different, we would have found non-significant *P* values for each continent comparison using the Mantel test. Moreover, we would have found significant *P* values if any of the different sampling variables influenced the dietary results within each continent. These scenarios did not occur, so all studies were included in subsequent analyses (Appendices S4 and S5). Since we included all studies, the importance of various prey taxa in the diet are expressed throughout the paper as averages of four measures: 1) percentage frequency of occurrence per scat or stomach (%FO); 2) percentage frequency of occurrence per food item; 3) percentage volume in scat or stomach samples; 4) percentage biomass in scat or stomach samples. In only the first of these measures, values may add up to >100%.

Assessing differences among and within continents

We assessed patterns of prey species composition in grey wolf diet among and within continents using non-metric multidimensional scaling and analysis of similarity (ANOSIM). We chose non-metric multidimensional scaling because it provides a graphical representation of the results, while ANOSIM provides a measure of dissimilarity (R) among and within selected groupings (Quinn & Keough 2002). We used the groupings of North America, Europe and Asia to assess differences in prey species composition among continents, and the bioregional groupings to assess differences in prey species composition among bioregions within each continent. For non-metric multidimensional scaling we used the Bray-Curtis coefficient to ordinate wolf dietary composition in each study in two dimensions using 100 random starts. The Bray-Curtis coefficient lessens the effects of the largest differences and is useful when comparing species' abundances or occurrences (Bray & Curtis 1957). We performed Monte Carlo randomisation to determine significance of the final stress values (a measure of goodness-of-fit), and used ANOSIM to test the hypothesis of no difference between two or more groups (Clarke 1993). ANOSIM uses the mean rank similarities of samples in different groups and of samples within the same groups to calculate a test statistic, R . We ran 999 random permutations to assess the statistical significance of the R statistic, and also conducted pair-wise ANOSIMs to determine which groups differed from each other.

Relationship between dietary diversity and human footprint index

We calculated the dietary diversity of grey wolves in each study by using Levins' measure of niche breadth (Levins 1968), standardised on a scale from 0 to 1 by using the following measure proposed by Hurlbert (1978):

$$B_A = \frac{B-1}{n-1}$$

where B_A = Levins' standardised niche breadth, n = the number of possible resource states (10 broad food categories), and B = Levins' measure of niche breadth expressed as:

$$\frac{Y^2}{\sum N_j^2}$$

where N_j = the number of individuals found in or using resource state j and $Y = \sum N_j$ (i.e. the total number of individuals sampled). Levins' B is highest when equal numbers of individuals occur in each resource state, indicating indiscriminate use among resource states, and lowest when all the individuals occur in only one resource state,

indicating maximum specialisation (Krebs 2014). We measured dietary diversity using the 10 broad food categories as the possible resource states, and then with domestic species and garbage excluded in case the presence of these human-derived foods influenced the results.

To derive a measure of human disturbance for each study area we used the global human influence index (human footprint index) calculated by Sanderson et al. (2002). The index has been calculated at a resolution of 1 km² and ranges from 0 to a maximum of 72: higher scores indicate greater human influence. This index was derived from four types of data as proxies for human influence including population density, land transformation, accessibility (roads, rivers, and coastlines), and power infrastructure, and it has been used as a broad measure of human disturbance in other ecological studies (e.g. Laliberte & Ripple 2004). To derive a single index number for each study we calculated the average values within a 50 km radius from the centroid of each study area by using the zonal statistics tool in the Spatial Analyst extension of Arc View v10.2 (Environmental Systems Research Institute Inc.: Redlands, CA, USA). The 50 km radius represents a total area of ~7500 km², thus allowing a value of human disturbance to be calculated over a broad study area that encompasses an area the size of multiple grey wolf home ranges (Boitani 1992, Paquet & Carbyn 2003). We then used a linear regression to model the relationship between dietary diversity and human footprint index using R (Anonymous 2008), to determine whether dietary diversity decreases with increasing human footprint index.

Case study in southern Europe

We used a linear regression to assess whether the occurrence of wild ungulates (large and medium-sized combined) and domestic species in grey wolf diet in southern Europe has changed over time and, in particular, whether it changed following wild ungulate restoration programs during recent decades (Boitani 1992) and following the conversion of agricultural land to forested areas in some places. To do this, we plotted the occurrence of wild ungulates and domestic species in grey wolf diet against the median date (year) in which each study was conducted. Data were selected from the following regions: Alps, Greece, North Spain, Italy, South Spain, and South Russia (see Fig. 1).

RESULTS

Review of grey wolf dietary studies

We inspected a total of 1903 returns during the literature search (Appendix S1). After examining the returns and cross-referencing, 146 individual references were considered

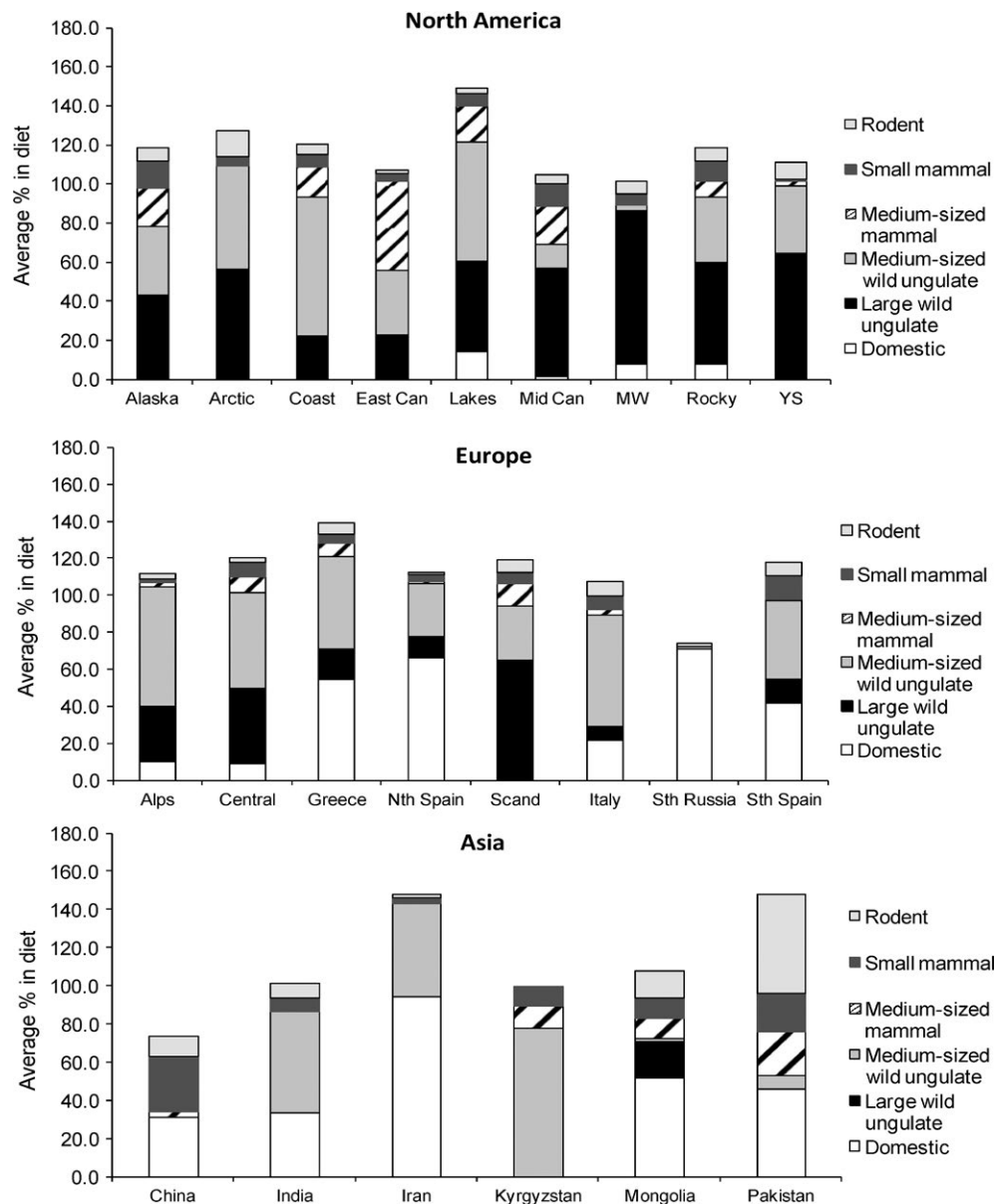


Fig. 2. The average percentage of six main food categories in the diet of grey wolves in different bioregions in each of the three continents (see Fig. 1 for locations and abbreviations). The most commonly used method to express the importance of each taxon in the diet was percentage frequency of occurrence per sample (%FO), but data from other methods are also included here. Since each scat or stomach may contain the remains of more than one prey taxon, the percentages as expressed by %FO may add up to >100%.

relevant. Seventeen of these references provided dietary data from multiple locations and, since we considered these to be independent, our final data set included 177 studies from North America ($n = 77$), Europe ($n = 85$) and Asia ($n = 15$; Fig. 1, Appendix S2). The data set included dietary contents from 94607 scat and stomach samples (average per study = 534). Ninety-one percent of dietary data were derived from contents in scats. Only 19 studies were conducted in single seasons. The average study length was 3.5 years, and in 69% of studies, enough detail was provided

in the results to calculate %FO. Studies spanned the time period from 1939 to 2014, but most studies (88%) were conducted after 1970.

Grey wolf diet was dominated by large and medium-sized wild ungulates in North America (Fig. 2), especially mule deer *Odocoileus hemionus* (average percentage in diet = 42%, $n = 13$ studies), elk *Cervus canadensis* (41%, $n = 20$), white-tailed deer *Odocoileus virginianus* (35%, $n = 28$), moose *Alces alces* (30%, $n = 54$), and caribou *Rangifer tarandus* (25%, $n = 19$). Black-tailed deer *Odocoileus*

hemionus columbianus had the highest average percentage in grey wolf diet at 74%, but this pattern was based on results from only two studies. Similarly, the average percentages of bison *Bison bison* (44%) and garbage (21%) were relatively high, but these were based on the results of four and three studies, respectively. Medium-sized mammals such as beavers *Castor canadensis* (21%) featured in a large number of studies ($n = 54$). In contrast, domestic species (including livestock) featured in only 10 studies in North America and comprised only 8% of grey wolf diet in those studies.

In Europe, grey wolf diet was dominated by medium-sized wild ungulates, especially wild boar *Sus scrofa* (24%, $n = 76$), roe deer *Capreolus capreolus* (24%, $n = 66$), and chamois *Rupicapra rupicapra* (21%, $n = 9$). The percentage of the diet consisting of large wild ungulates was also high, especially moose (31%, $n = 12$) and red deer *Cervus elaphus* (20%, $n = 38$). However, large wild ungulates featured in fewer studies ($n = 52$) than medium-sized wild ungulates ($n = 81$). Overall, domestic species formed a much higher percentage of grey wolf diet in Europe (33%, $n = 73$) than in North America (Fig. 2). Domestic pigs *Sus scrofa domestica* (16%, $n = 19$), goats *Capra aegagrus hircus* (17%, $n = 36$), and horses *Equus caballus* (16%, $n = 28$) comprised a higher overall percentage of grey wolf diet than sheep *Ovis aries* (9%, $n = 45$), and cattle *Bos* spp. (9%, $n = 40$), although there was high variation in the occurrence of domestic species among studies. In comparison to North America, grey wolves in Europe consumed fewer medium-sized mammals (7%, $n = 28$), but garbage and fruit featured in three times as many studies ($n = 39$).

Grey wolf diet in Asia was dominated by domestic species (50%, $n = 14$) and medium-sized wild ungulates (36%, $n = 10$; Fig. 2). Of the domestic species, the highest percentage was made up of poultry (38%, $n = 2$), followed by goats (21%, $n = 10$), yak *Bos grunniens* (21%, $n = 2$), horses (17%, $n = 4$), sheep (15%, $n = 13$), and then cattle

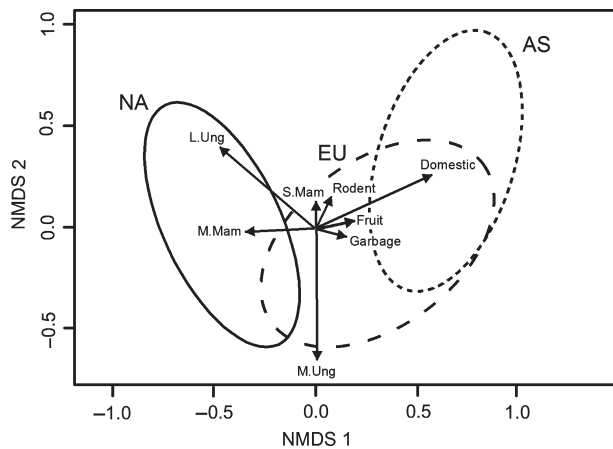


Fig. 3. Non-metric multidimensional scaling ordination of grey wolf diet by continents. Vectors displayed are significant at $P < 0.07$. The 95% confidence interval ellipses are displayed for North America (NA), Europe (EU) and Asia (AS). M.Mam = medium-sized mammal, S.Mam = small mammal, L.Ung = large wild ungulate, M.Ung = medium-sized wild ungulate.

(12%, $n = 9$). Blackbuck *Antelope cervicapra* (53%, $n = 4$), wild sheep (44%, $n = 2$) and gazelles *Gazella subgutturosa* (31%, $n = 1$) were the most dominant medium-sized wild ungulates. In some instances, rodents and medium-sized mammals were consumed in relatively high percentages (Fig. 2), especially civets *Paguma alarvata* (20%, $n = 1$) and marmots *Marmota* spp. (12%, $n = 5$). Similarly, the percentage of fruit in grey wolf diet in Asia (10%, $n = 2$) was relatively high compared to that in North America (5%, $n = 7$).

Differences among continents

There were significant differences in grey wolf dietary composition among continents (Table 1). The variable-loading results showed that eight of the ten broad food categories contributed significantly ($P < 0.05$) to the ordination axis (Appendix S6). In particular, differences in the importance of large wild ungulates and medium-sized mammals were the primary features of dietary differences between North America and the other two continents (Fig. 3). The high percentage of domestic species in Asia was the primary feature of dietary differences between Asia and the other two continents, whereas medium-sized wild ungulates were most important in the diets of wolves in Europe (Fig. 3). Pairwise ANOSIMs supported the group positions determined by the ordination. For example, there was more overlap in the diet of grey wolves in North America and Europe ($R = 0.23$; $P = 0.001$) than between the diet of grey wolves in North America and Asia ($R = 0.56$; $P = 0.001$; Table 1).

Table 1. Non-metric multidimensional scaling and analysis of similarity (ANOSIM) results comparing grey wolf diet among continents and among bioregions within continents (see Fig. 1 for locations).

Trials	Stress (P)*	Non-metric r^2	ANOSIM R (P)
Continents, Overall	14.8% (0.059)	0.98	0.26 (0.001)
Continents			
Asia vs. Europe			0.16 (0.006)
Asia vs. N. America			0.56 (0.001)
Europe vs. N. America			0.23 (0.001)
Bioregions			
N. America	12.0% (0.03)	0.99	0.27 (0.001)
Europe	10.8% (<0.01)	0.99	0.39 (0.001)
Asia	9.5% (0.08)	0.99	0.34 (0.03)

*The P -value for stress is based on Monte Carlo randomisation.

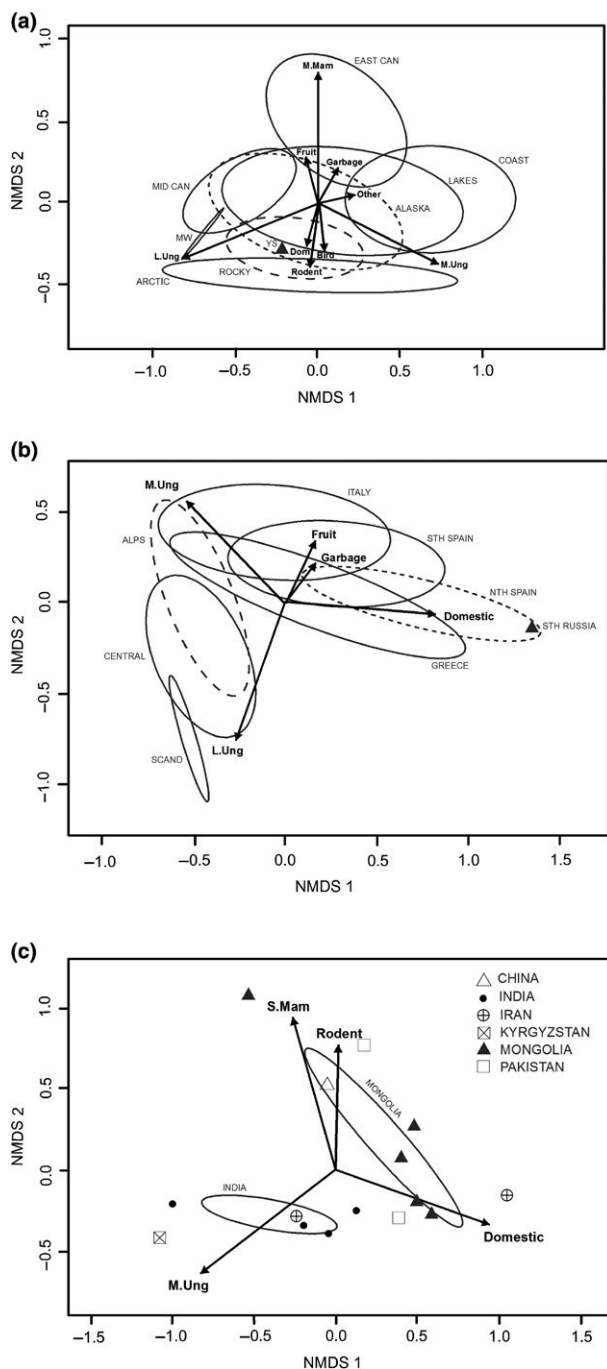


Fig. 4. Non-metric multidimensional scaling ordination of grey wolf diet in (a) North America, (b) Europe, and (c) Asia (see Fig. 1 for locations and abbreviations). Vectors displayed are significant at $P < 0.07$. The 95% confidence interval ellipses are displayed. Bioregions with a sample size of one (YS, Kyrgyzstan and China), or two (Sth Russia) were excluded from the analyses, but their positions on the ordination axis are shown. Positions for all Asian studies are shown in addition to 95% bioregional confidence ellipses, since $n \leq 5$ for all bioregions. M.Mam = medium-sized mammal, S.Mam = small mammal, L.Ung = large wild ungulate, M.Ung = medium-sized wild ungulate, Dom = domestic.

Differences among bioregions within continents

We detected significant differences in grey wolf dietary composition among bioregions within continents (Table 1). In North America, variable-loading results for the ordination showed that eight of the ten broad food categories contributed significantly ($P < 0.05$) to the ordination axis (Fig. 4a, Appendix S7). The importance of medium-sized mammals, especially beavers, in East Canada (43%, $n = 12$), was the primary feature of dietary differences between East Canada and the other North American bioregions (Fig. 4a). In contrast, the relatively high percentage of medium-sized wild ungulates (53%, $n = 5$, mainly caribou), large wild ungulates (57%, $n = 6$, mainly muskoxen), and rodents (13%, $n = 7$) in the Arctic was a key feature of dietary differences between the Arctic and the other North American bioregions (Fig. 4a). The Coastal bioregion was also separated on the ordination axis, and this separation was mainly characterised by a high percentage of medium-sized wild ungulates (71%, $n = 9$, primarily mule deer, black-tailed deer and mountain goats *Oreamnos americanus*) and to a lesser extent by species in the 'Other' food category (primarily fish and other marine species; Appendix S7).

In Europe, variable-loading results for the ordination showed that five of the ten broad food categories contributed significantly ($P < 0.05$) to the ordination axis (Table 1, Fig. 4b, Appendix S8). In particular, the high percentage of large wild ungulates in Scandinavia (65%, $n = 3$, mainly moose) was a key feature of dietary differences between Scandinavia and the other bioregions (Fig. 4b). In contrast, the high percentage of medium-sized wild ungulates contributed to the separation of the Alps (64%, $n = 6$, mainly chamois) and Italy (60%, $n = 19$, mainly wild boar and roe deer) on the ordination plot from the other bioregions (Fig. 4b). High percentages of both medium-sized wild ungulates (52%, $n = 26$, mainly roe deer and wild boar) and large wild ungulates (41%, $n = 26$, mainly red deer and moose) contributed to the separation of the Central Europe bioregion from the others (Fig. 4b). In contrast, high percentages of domestic species contributed to the separation of North Spain (66%, $n = 17$, mainly cattle, horse and goat) and South Russia (71%, $n = 2$, mainly pigs and cattle) from the other bioregions on the ordination plot (Fig. 4b).

In Asia, there were significant differences in grey wolf dietary composition among bioregions (Table 1), although few studies were included in the analysis ($n = 15$). Only four of the ten broad food categories contributed significantly ($P < 0.05$) to the ordination axis (Fig. 4c, Appendix S9). India was separated on the ordination because relatively high numbers of medium-sized wild

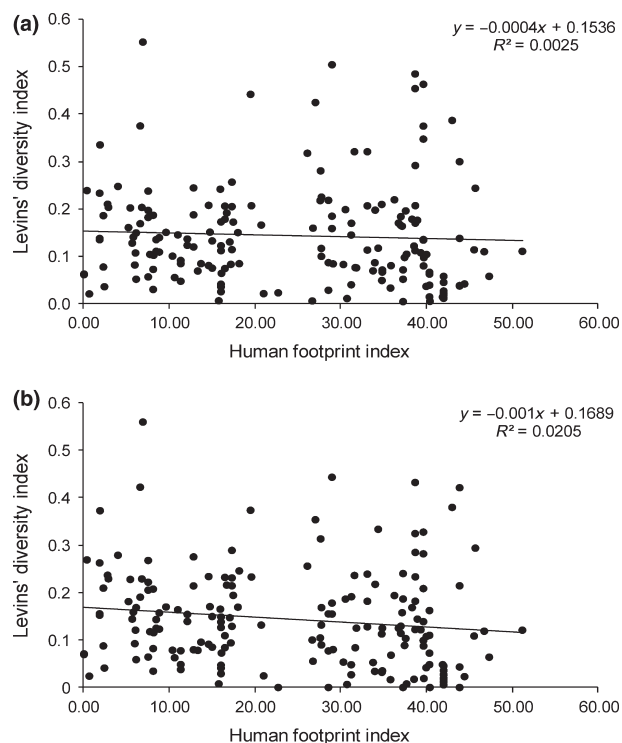


Fig. 5. Grey wolf dietary diversity plotted against an index of human influence (human footprint index). In (a), dietary diversity is based on the percentages of all prey noted in wolf dietary studies incorporated in this review. In (b), dietary diversity is based on wild prey only, i.e. excluding domestic species and garbage. Human footprint index is based on Sanderson et al. (2002) and is calculated as the average value within a 50 km radius of each study.

ungulates were eaten (53% of the diet, $n = 4$, mainly blackbuck). In the other bioregions, the diet of grey wolves was dominated by small mammals, rodents or domestic species (Fig. 4c).

Dietary diversity and human footprint index

There was no evidence that grey wolf dietary diversity increased or decreased with human footprint index, based on a linear regression model ($r^2 = 0.002$, $F_{1,175} = 0.47$, $P = 0.49$; Fig. 5a). This result occurred irrespective of whether or not domestic species and garbage were excluded from the dietary diversity calculations ($r^2 = 0.02$, $F_{1,175} = 3.65$, $P = 0.06$; Fig. 5b).

Case study in southern Europe

When grey wolf diet was assessed throughout southern Europe, there was evidence that the importance of wild ungulates in grey wolf diet has increased over time ($r^2 = 0.08$, $F_{1,50} = 4.82$, $P = 0.03$; Fig. 6a). This trend

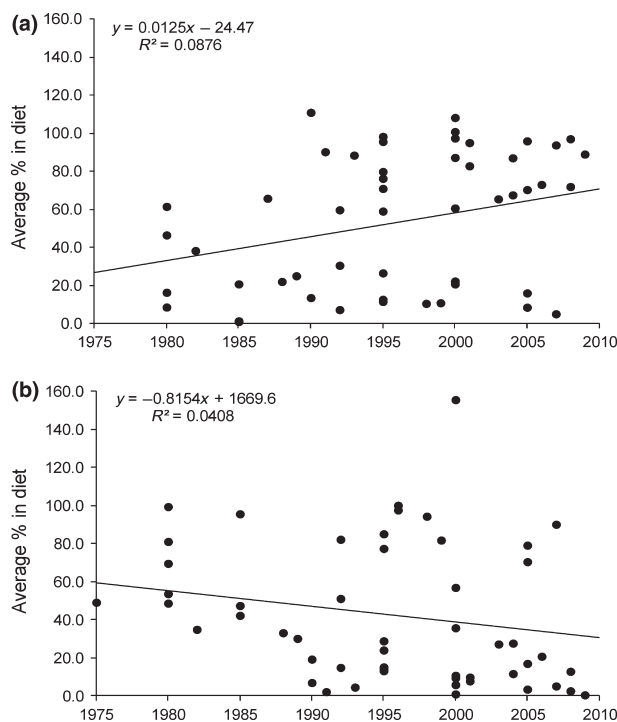


Fig. 6. Average percentages of (a) large and medium-sized wild ungulates and (b) domestic species in grey wolf diet, plotted against the median date (year) in which the studies were conducted. Data were taken from studies conducted in the southern European regions: Alps, Greece, North Spain, Italy, South Spain, and South Russia (see Fig. 1 for locations). The most commonly used method to express the importance of each taxon in the diet was percentage frequency of occurrence per sample (%FO), but data from other methods are also included here. Since each scat or stomach may contain the remains of more than one prey taxon, the percentages as expressed by %FO may add up to >100%.

corresponded to a decline in domestic species in the diet over time, although the linear regression was not significant ($r^2 = 0.04$, $F_{1,51} = 2.16$, $P = 0.14$; Fig. 6b).

DISCUSSION

Humans have triggered waves of animal extinctions and driven biodiversity loss and declines that are comparable to previous mass extinction events during Earth's history (Barnosky et al. 2011, Dirzo et al. 2014, Ceballos et al. 2015). However, species' vulnerability to extinction are highly variable (Isaac & Cowlishaw 2004), and different biological traits, such as ecological flexibility and resilience, may provide a degree of protection from external threats and thus allow populations to recover rapidly from depletion (Cardillo et al. 2004). Grey wolf populations are recovering in parts of North America and Europe (Chapron et al. 2014, Ripple et al. 2014), and the species has managed to persist in human-dominated landscapes

(Chapron et al. 2014). Accordingly, it is perhaps unsurprising that our review of 177 studies from North America, Europe and Asia demonstrates that grey wolves can survive on a wide array of foodstuffs, or that we found clear dietary differences among and within continents (Figs 3 and 4). Moreover, the unexpected finding that grey wolf dietary diversity, both with and without considering domestic species and garbage, is not lower in areas heavily modified by humans supports the idea that grey wolves have flexible foraging strategies and can live in a range of ecological conditions, including areas with high densities of humans (Fig. 5; e.g. >150 inhabitants per km²; Chapron et al. 2014). Nevertheless, our analysis identifies several knowledge gaps and there are many challenges to developing a sustainable conservation model for grey wolves throughout the globe, particularly in human-dominated landscapes. Below, we highlight several novel insights about the implications of global information on the feeding ecology of grey wolves for conservation and management.

In North America, large wild ungulates and medium-sized mammals dominated grey wolf diet, whereas in Europe and Asia, the diet was dominated by medium-sized wild ungulates and domestic species, respectively (Fig. 3). The results from North America and Europe support the assumption that grey wolves are obligate carnivores whose use of prey generally depends on the availability of wild ungulates (Paquet & Carbyn 2003). In Asia, the abundance of wild ungulates is generally lower than in North America and Europe (Ripple et al. 2015) so the grey wolves' reliance on domestic species was expected. Maintaining and restoring wild ungulate populations should thus remain a priority for grey wolf conservation (Ripple et al. 2014). The key threats to wild ungulates include un-sustainable hunting for meat by humans, competition with livestock, and habitat loss (Ripple et al. 2015). Therefore, a suite of initiatives is required to conserve wild ungulates adequately, including changes to hunting harvests (Jonzén et al. 2013), broader protection of favourable habitats to reduce the amount of land converted to agriculture (Ripple et al. 2015), and where necessary, reintroductions of locally extinct wild ungulate species (Boitani 1992).

A possible consequence of wild ungulate population depletion is that grey wolves will consume more human-provided foods, including garbage if it is accessible, and domestic species if they are vulnerable to predation. This putative relationship is supported by the large amount of garbage and domestic animal species in grey wolf diet in Asia and some parts of Europe (Fig. 2). For instance, in the Yazd province in central Iran, where there is a moderately low abundance of wild prey, grey wolves fed almost exclusively on farmed chicken, domestic goats and garbage (Tourani et al. 2014). In central Greece, where roe deer

are very rare, domestic pigs, goats, and sheep dominated grey wolf diet (Migli et al. 2005). Similarly, free-ranging mountain ponies are the main prey of wolves in Western Galicia (Spain), where wild ungulates (roe deer and wild boar) are absent or their density is quite low (López-Bao et al. 2013). Prey switching to domestic species by grey wolves has also been demonstrated in Belarus, where a sixfold increase in livestock consumption was recorded when wild ungulate densities were at a low level (Sidorovich et al. 2003). These studies, among others, highlight that domestic prey consumption might be related to the density and diversity of wild ungulates, including both common and threatened species. Indeed, our case study in southern Europe suggests that consumption of livestock by grey wolves has decreased over time, coincident with an increase in their consumption of large and medium-sized wild ungulates (Fig. 6).

Although correlative, similar results to ours from southern Europe have been used to support the idea that grey wolves prefer wild prey over domestic species; see Meriggi and Lovari (1996). However, some caution is required when interpreting the result of our analysis and that of Meriggi and Lovari (1996). Firstly, the low *r*-squared values in our analysis indicate a relatively weak relationship between the percentage of wild ungulates/domestic species in grey wolf diet and the median date (year) in which the studies were conducted (Fig. 6). Such variability could reflect differences in local conditions between studies. Secondly, neither our analysis nor that of Meriggi and Lovari (1996) involved measuring grey wolf depredation on livestock over the period of interest. This is important to note, because domestic prey consumption as revealed by dietary studies does not necessarily reflect the level of conflict, i.e. the true or perceived economic loss. Thirdly, neither analysis controlled for the accessibility of wild versus domestic prey, both of which are influenced by independent factors. Indeed, patterns of livestock depredation cannot be described only in terms of ecological predator-prey dynamics but must be analysed in relation to local husbandry techniques. In the absence of data on these aspects and an adequate sampling scheme to test the hypotheses, it is not legitimate to draw firm conclusions on the relationship between wild and domestic prey frequency in grey wolf diet. Therefore, future research needs to be focussed on whether restoring wild ungulates will reduce human-wolf conflicts, to avoid a scenario where increases in wild ungulate availability result in grey wolf population growth or increased presence of wolves attracted by potential prey (Treves et al. 2004, Bradley & Pletscher 2005), and then in turn, increased depredation on livestock.

Clearly, a key factor that influences livestock depredation by grey wolves is the availability and vulnerability of the livestock themselves, which is strongly influenced by

livestock type (cattle, sheep, goat) and husbandry techniques. By implication, livestock producers could promote healthy wild ungulate populations, in at least some cases, by implementing husbandry techniques that reduce the availability and vulnerability of cattle and other livestock to grey wolves and other predators. Non-lethal methods such as the use of fladry, guardian animals and electric, audio or visual deterrents have, for example, been shown to deter grey wolves from livestock or other food sources (Musiani et al. 2003, Shivik et al. 2003). Approaches that maintain or enhance range conditions, such as livestock rotation, could also indirectly benefit wild ungulates by increasing forage quality. These practices come at a cost to the livestock producer, so they often require financial incentives and investment in public outreach to create sociopolitical support (Chapron et al. 2014). For example, in 1996 the Swedish government implemented a performance-payment strategy based on the number of carnivore reproductions and/or the regular and occasional occurrence of large carnivores (Zabel & Holm-Müller 2008). Such pre-emptive payments need to be high enough to ensure full compensation for stock losses, and the potential for abuse of the system means that monitoring is required, but this initiative could be a viable solution for wolf-livestock conflicts in other parts of the world.

If grey wolf predation on livestock does change in relation to the availability of wild ungulates, it may be necessary to consider whether there is adequate supplementary prey available. Supplementary prey can be defined as prey species that comprise major elements of the diet at times, but contribute minimally at others and are generally ancillary to staple prey (Newsome et al. 1983). Prey that supplement grey wolf diet during wild ungulate shortages (or while grey wolves are denning and using rendezvous sites) include beavers, lagomorphs, microtine rodents, birds, fish and, on occasion, other carnivores (Paquet & Carbyn 2003). The importance of supplementary prey to grey wolves has been acknowledged in previous dietary reviews (e.g. Okarma 1995, Paquet & Carbyn 2003, Peterson & Ciucci 2003, Zlatanova 2014). Our analysis offers several insights into the importance of supplementary prey in the diet of grey wolves across the globe. For example, in East Canada, medium-sized mammals (mainly beavers) comprised 43% of grey wolf diet on average, and variation in the relative importance of this prey group was the primary feature of dietary differences among bioregions within North America (Fig. 4a). Similarly, the occurrence of species in the 'Other' food category (notably fish and other marine species) was close ($P = 0.07$) to being a significant contributor to the differences in grey wolf diet among bioregions in North America; grey wolves consumed fish and/or seals *Phoca* spp. in most studies ($n = 8$) we included from the Coastal bioregion. Indeed, when salmon *Oncorhynchus* spp. become

available, they may occur in up to 70% of grey wolf scats, making them important supplementary prey, or even staple prey depending on definitions (Darimont et al. 2008). In Europe, smaller prey (including medium-sized mammals, small mammals, rodents and birds) did not contribute significantly to variation on the ordination axis (Fig. 4b, Appendix S8); a result that stems from the relatively small amount of supplementary prey consumed by grey wolves throughout Europe (Fig. 2). In contrast, grey wolves consumed relatively large amounts of rodents in Asia (Figs 2 and 4c), but this pattern was accompanied by high percentages of domestic species consumed in five out of the six bioregions assessed (Fig. 2).

The lack of supplementary prey in some regions raises several concerns for grey wolf conservation. For example, the dietary results from the Mexican Wolf bioregion in North America, and to a lesser extent from Yellowstone National Park, indicate that grey wolves in these areas rarely consume small prey species (Fig. 2). A possible explanation is that these wolves selected for larger prey over all other available species. However, an alternative explanation is that the abundance of small supplementary prey is low in these study systems. In support of the latter explanation, Brown (2002) indicated that even rabbits and hares are in short supply, leaving only cattle and elk as potential prey for Mexican wolves *Canis lupus baileyi*. Rabbit harvests in Arizona and Colorado have fallen precipitously in recent decades (Ripple et al. 2013), and extremely low rabbit densities were found recently in an Arizona survey (Frery & Ingraldi 2011). The lack of small and medium-sized mammals in some western states (USA) may be due at least in part to coyotes *Canis latrans* preying on these animals, especially where coyote abundance is likely to have increased after grey wolf extirpation in the early 20th century (by the 1930s; Ripple et al. 2013). With respect to fish as supplementary prey, there have been widespread declines in native salmon stocks over the last century in California, Oregon, Idaho, and Washington due to habitat loss, inadequate passage and flows caused by hydropower, agriculture, logging and other developments (Nehlsen et al. 1991). Conversion of agricultural land for livestock grazing has also severely affected plant and animal communities; studies indicate that these domestic species have had numerous and widespread negative effects on western USA ecosystems (Beschta et al. 2013). Restoring supplementary prey species should thus be a management priority in those areas where wolves prey on a very narrow spectrum of large wild ungulate species in order to buffer against potential variation in main prey abundance (Fig. 2). However, it may also be necessary to consider other factors, including changes in environmental and agricultural policies, grey wolf pack sizes, social dynamics and even the prey preferences of different individual grey wolves. Such factors could influence whether

grey wolves select supplementary prey, even during periods of wild ungulate declines.

Although it is not possible from our analyses to assess fully and precisely why grey wolf diet varies among and within continents, our results can be interpreted with confidence for several reasons. First, our sample size was large ($n = 177$ studies) in comparison to that of similar dietary reviews (e.g. Bojarska & Selva 2012). Second, the studies we reviewed were conducted under many different ecological conditions (Figs 1 and 5). Finally, our analytical approach ensured that our results were not biased by sampling length, season of study, source of dietary material, analytical method, or sample size (Appendices S4 and S5). However, we acknowledge that rigorous attempts to determine wolf preference for any kind of prey can be fraught with methodological problems (Peterson & Ciucci 2003), especially because scat and stomach contents do not necessarily reflect predation; indeed, scat and stomach contents may also reflect scavenging of wild and especially domestic prey carcasses (Cuesta et al. 1991, Ciucci et al. 1996). As such, if predation is assessed solely through food habits it could misrepresent actual predation rates (Wilson & Wolkovich 2011). In addition, in most studies we reviewed (69%), %FO was used, a measure that has some disadvantages over alternative analytical techniques (Klare et al. 2011). For example, %FO can over-represent small prey items, whereas volume and biomass calculations can be influenced by varying scat sizes (Klare et al. 2011). Differential digestion of body parts may also introduce error in the estimation of prey consumed, although %FO is useful for documenting rare prey items (Klare et al. 2011). Finally, it was impossible for us to select study site locations randomly within each continent, further adding to the level of bias.

Despite those potential shortfalls, it is abundantly clear from our results that grey wolves have extremely flexible foraging capabilities, and that they eat a wide range of prey whether or not humans are around. This potentially gives grey wolves a survival advantage under global change (Clavel et al. 2011). However, our findings have broader implications when considering the ecological relationships between wolves and their environment. Recent studies, for example, suggest that grey wolves can exert strong top-down effects on ecosystems by suppressing their main prey and lower order competitors (Ripple et al. 2014). There is growing concern, however, that humans are modifying the ecological role of predators, especially where humans provide supplementary foods including garbage, livestock, carcasses, and crops (Newsome et al. 2015). Most studies assessing the ecological role of grey wolves have been conducted in National Parks or wilderness areas, where grey wolves feed primarily on large wild ungulates. Much less is known about the ecological role of grey wolves when they feed on other kinds of foods.

It is possible that the availability of human-provided foods could subtly alter the ecological relationships of grey wolves, both intra-specifically (e.g. pack size, dispersal, density) and inter-specifically (e.g. wild-prey relationships, hunting behaviour, trophic interactions, and bottom-up and top-down patterns), relative to those in comparatively closed systems with low or no human interference. For example, the provision of human-provided foods influences the movements, activity, dietary preferences, group sizes, and population dynamics of dingo populations in Australia (Newsome et al. 2013a, b, c, 2014). Grey wolves also appear commonly to take advantage of human-provided foods; livestock and/or garbage is present in the diet of grey wolves in 66% of studies in this review. Therefore, conservation of grey wolves in places where anthropogenic subsidies are used heavily (e.g. parts of Europe and Asia) may not necessarily result in the expected ecological services that grey wolves can provide. While this does require further investigation (Wilson & Wolkovich 2011, López-Bao et al. 2015b, Newsome & Ripple 2015), minimising human-driven prey accessibility should be incorporated into management strategies that aim to avoid conflicts and to prevent alteration of ecological and evolutionary processes (see also Wilmers et al. 2003).

CONCLUSION

One of the biggest obstacles to grey wolf recovery is the concern about wolf impacts on livestock and subsequent persecution. Our results show that future research needs to be focussed on ascertaining whether maintaining healthy populations of wild prey, both small and large, could assist in conserving grey wolf populations, while also reducing their impacts on livestock. However, the ability of grey wolves to survive on diets consisting of rodents, birds, small mammals and garbage does suggest that another obstacle to their recovery may not be lack of habitat or prey, but societal acceptance (Dressel et al. 2015). Therefore, it is critical that we increase our understanding of grey wolf foraging ecology in a broader range of habitats, so that human attitudes and management decisions can be based on scientific knowledge. Without such knowledge, management strategies for grey wolves may continue to be focussed on lowering perceived risks to humans and their activities, rather than also incorporating the benefits of grey wolves to human society and the environment (*sensu* Bruskotter & Wilson 2014).

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REFERENCES

- Anonymous (2008) *R: A Language and Environment for Statistical Computing*. Version 2.92. R Foundation for Statistical Computing, Vienna, Austria.
- Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Bergstrom BJ, Vignieri S, Sheffield SR, Sechrest W, Carlson AA (2009) The Northern Rocky Mountain gray wolf is not yet recovered. *BioScience* 59: 991–999.
- Beschta RL, Donahue DL, DellaSala DA, Rhodes JJ, Karr JR, O'Brien MH, Fleischner TL, Deacon Williams C (2013) Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management* 51: 474–491.
- Boitani L (1992) Wolf research and conservation in Italy. *Biological Conservation* 61: 125–132.
- Bojarska K, Selva N (2012) Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Review* 42: 120–143.
- Bradley EH, Pletscher DH (2005) Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. *Wildlife Society Bulletin* 33: 1256–1265.
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Brown DE (2002) *The Wolf in the Southwest: the Making of an Endangered Species*. High-Lonesome Books, Silver City, New Mexico, USA.
- Bruskotter JT, Wilson RS (2014) Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conservation Letters* 7: 158–165.
- Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biology* 2: e197.
- Ceballos G, Ehrlich PR, Barnosky AD, Garcia A, Pringle RM, Palmer TM (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* 1: e1400253.
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL et al. (2000) Consequences of changing biodiversity. *Nature* 405: 234–242.
- Chapron G, López-Bao JV (2014) Conserving carnivores: politics at play. *Science* 343: 1199–1200.
- Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H et al. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1518–1519.
- Ciucci P, Boitani L, Pelliccioni ER, Rocco M, Guy H (1996) A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biology* 2: 37–48.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9: 222–228.
- Crowther MS, Fillios M, Colman N, Letnic M (2014) An updated description of the Australian dingo (*Canis dingo* Meyer, 1793). *Journal of Zoology* 293: 192–203.
- Cuesta L, Barcena F, Palacios F, Reig S (1991) The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia* 55: 239–254.
- Darimont CT, Paquet PC, Reimchen TE (2008) Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecology* 8: 14.
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the anthropocene. *Science* 345: 401–406.
- Doherty TS, Davis RA, van Etten EJB, Algar D, Collier N, Dickman CR, et al. (2015) A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography* 42: 964–975.
- Dray S, Du-four A-B, Thioulouse J (2014) Package "ade4" v1.6-2. <https://cran.r-project.org/web/packages/ade4/index.html>.
- Dressel S, Sandström C, Ericsson G (2015) A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology* 29: 565–574.
- Frary VF, Ingraldi M (2011) *Response of Northern Goshawk (Accipiter gentilis) Prey within the Eagar South Wildland Urban Interface Forest Treatment*. Research Branch, Arizona Game and Fish Department, Flagstaff, Arizona, USA.
- Gaubert P, Bloch C, Benyacoub S, Abdelhamid A, Pagani P, Djagoun CAMS, Couloux A, Dufour S (2012) Reviving the African wolf *Canis lupus lupaster* in North and West Africa: a Mitochondrial lineage ranging more than 6000 km wide. *PLoS ONE* 7: e42740.
- Hofreiter M (2007) Pleistocene extinctions: haunting the survivors. *Current Biology* 17: R609–R611.
- Hurlbert SH (1978) The measurement of niche overlap and some relatives. *Ecology* 59: 67–77.
- Isaac NJ, Cowlshaw G (2004) How species respond to multiple extinction threats. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271: 1135–1141.
- Jonzén N, Sand H, Wabakken P, Swenson JE, Kindberg J, Liberg O, Chapron G (2013) Sharing the

- bounty—adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. *Ecological Modelling* 265: 140–148.
- Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41: 294–312.
- Krebs CJ (2014) *Ecological Methodology*, 3rd ed. (in prep). Addison-Wesley Educational Publishers, Inc. <http://www.zoology.ubc.ca/~krebs/books.html>.
- Laliberte AS, Ripple WJ (2004) Range contractions of North American carnivores and ungulates. *BioScience* 54: 123–138.
- Levins R (1968) *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, New Jersey, USA.
- Lindenmayer DB, Likens GE, Krebs CJ, Hobbs RJ (2010) Improved probability of detection of ecological “surprises”. *Proceedings of the National Academy of Sciences* 107: 21957–21962.
- López-Bao JV, Sazatornil V, Llaneza L, Rodríguez A (2013) Indirect effects of heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters* 6: 448–455.
- López-Bao JV, Blanco JC, Rodríguez A, Godinho R, Sazatornil V, Alvares F et al. (2015a) Toothless wildlife protection laws. *Biodiversity and Conservation* 24: 2105–2108.
- López-Bao JV, Kaczensky P, Linnell JDC, Boitani L, Chapron G (2015b) Carnivore coexistence: wilderness not required. *Science* 348: 871–872.
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209–220.
- Mech LD (2012) Is science in danger of sanctifying the wolf? *Biological Conservation* 150: 143–149.
- Meriggi A, Lovari S (1996) A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33: 1561–1571.
- Migli D, Youlatos D, Iliopoulos Y (2005) Winter food habits of wolves in central Greece. *Journal of Biological Research* 4: 217–220.
- Musiani M, Mamo C, Boitani L, Callaghan C, Gates CC, Mattei L, Visalberghi E, Breck S, Volpi G (2003) Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. *Conservation Biology* 17: 1538–1547.
- Naughton-Treves L, Grossberg R, Treves A (2003) Paying for tolerance: rural citizens’ attitudes toward wolf depredation and compensation. *Conservation Biology* 17: 1500–1511.
- Nehlsen W, Williams JE, Lichatowich JA (1991) Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16: 4–21.
- Newsome TM, Ripple WJ (2015) Carnivore coexistence: trophic cascades. *Science* 347: 383.
- Newsome AE, Catling PC, Corbett LK (1983) The feeding ecology of the dingo II. Dietary and numerical relationships with fluctuating prey populations in south-eastern Australia. *Australian Journal of Ecology* 8: 345–366.
- Newsome TM, Ballard G-A, Dickman CR, Fleming PJS, Howden C (2013a) Anthropogenic resource subsidies determine space use by Australian arid zone dingoes: an improved resource selection modelling approach. *PLoS ONE* 8: e63931.
- Newsome TM, Ballard G-A, Dickman CR, Fleming PJS, van de Ven R (2013b) Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography* 36: 914–925.
- Newsome TM, Stephens D, Ballard G-A, Dickman CR, Fleming PJS (2013c) Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming domestic dogs (*C. l. familiaris*) in the Tanami Desert, Australia. *Wildlife Research* 40: 196–206.
- Newsome TM, Ballard G-A, Fleming PJS, Ven R, Story GL, Dickman CR (2014) Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* 175: 139–150.
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR (2015) The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography* 24: 1–11.
- Okarma H (1995) The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica* 40: 335–386.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC et al. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51: 933–938.
- Paquet PC, Carbyn LN (2003) Gray wolf *Canis lupus* and allies. In: Feldhamer GA, Thompson BC, Champan JA (eds) *Wild Mammals of North America: Biology, Management, and Conservation*, 483–510. JHU Press, Baltimore, Maryland, USA.
- Peterson RO, Ciucci P (2003) The wolf as a carnivore. In: Mech D, Boitani L (eds) *Wolves: Behavior, Ecology and Conservation*, 103–130. University of Chicago Press, Chicago, Illinois USA and London, UK.
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344: 1246752.
- Quinn GP, Keough MJ (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Ripple WJ, Wirsing AJ, Wilmsers CC, Letnic M (2013) Widespread mesopredator effects after wolf extirpation. *Biological Conservation* 160: 70–79.

- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.
- Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M et al. (2015) Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience* 52: 891–904.
- Sandom C, Faurby S, Sandel B, Svenning J-C (2014) Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133254.
- Shivik JA, Treves A, Callaghan P (2003) Nonlethal techniques for managing predation: primary and secondary repellents. *Conservation Biology* 17: 1531–1537.
- Sidorovich VE, Tikhomirova LL, Jedrzejska B (2003) Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. *Wildlife Biology* 9: 103–111.
- Tourani M, Moqanaki EM, Boitani L, Ciucci P (2014) Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78: 117–121.
- Treves A, Naughton-Treves L, Harper EK, Mladenoff DJ, Rose RA, Sickley TA, Wydeven AP (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* 18: 114–125.
- Wang Y, Naumann U, Wright ST, Warton DI (2012) mvabund - an R package for model-based analysis of multivariate abundance data: the mvabund R package. *Methods in Ecology and Evolution* 3: 471–474.
- Wilmers CC, Stahler DR, Crabtree RL, Smith DW, Getz WM (2003) Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters* 6: 996–1003.
- Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution* 26: 129–135.
- Zabel A, Holm-Müller K (2008) Conservation performance payments for carnivore conservation in Sweden. *Conservation Biology* 22: 247–251.
- Zlatanov D (2014) Adaptive diet strategy of the wolf (*Canis lupus* L.) in Europe: a review. *Acta Zoologica Bulgarica* 66: 439–452.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Search terms used to identify grey wolf dietary studies. Country name refers to the 69 countries within grey wolf range according to spatial data from the 2009 IUCN Red List of Threatened Species.

Appendix S2. Full list of studies included in this review.

Appendix S3. Broad food categories used to summarise the diet of grey wolves. Average adult body sizes were obtained from the PanTHERIA data base (<http://esapubs.org/archive/ecol/E090/184/#data>).

Appendix S4. Mantel test results comparing a full data set to a subset of data. The full data set incorporated the average dietary contents values for all studies in each bioregional grouping in each continent. The subset of data only included studies in which %FO was used, dietary material was derived from scat contents, >25 scats were sampled, and scats were sampled in multiple seasons and years. Dietary contents values were based on 10 broad food categories (see Appendix S3).

Appendix S5. Results of the multivariate linear models testing for an effect of different sampling variables on the diet of grey wolves at the individual study site level in each continent. Dietary contents values were based on 10 broad food categories (see Appendix S3). Numbers reported refer to the overall test statistics (analysis of variance with 1000 re-sampling iterations). Response variables included sampling length (in years), season (summer, autumn, winter, spring), source of dietary material (scat or stomach), analytical method (frequency, volume, or biomass calculation), and sample size (number of scats or stomachs). Note that all papers from Asia had the same source of dietary material (scats) so the test is not applicable (n/a) to this variable.

Appendix S6. Dissimilarity boxplots and variable loading results for grey wolf broad food categories at the continental level.

Appendix S7. Dissimilarity boxplots and variable-loading results for grey wolf broad food categories in North America.

Appendix S8. Dissimilarity boxplots and variable-loading results for grey wolf broad food categories in Europe.

Appendix S9. Dissimilarity boxplots and variable-loading results for grey wolf broad food categories in Asia.