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Original investigation

Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*)Sophie Ståhlberg^{*,1}, Elena Bassi, Viviana Viviani, Marco Apollonio

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ABSTRACT

Wolf (*Canis lupus*) diet is determined by several ecological factors which can differ with latitude and human impact on the environment. Here we aim to compare Northern and Southern Europe with respect to wolf feeding habits. Scats were collected and analysed for nine years in South-central Scandinavia and four years in Tuscany, Italy, where prey density, predator-prey size relation and habitat heterogeneity, were compared in different ecological perspectives. Consumption followed prey density in Scandinavia but not in Tuscany and the main prey species, moose and wild boar respectively, were more seasonally age diversified in Scandinavia than in Tuscany. Most likely, the risk of injury was an important factor in prey age selection, especially in Tuscany. Diet composition in Scandinavia showed a negligible variance while in Tuscany, temporal and spatial variation were clearly recognised. The underlying mechanism is most likely related to the limited ecological diversity of landscape in Scandinavia contrasted with the higher variability of South European landscapes resulting in higher variation in prey abundance and consequently prey choice.

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Introduction

An animal exhibits a preference for a particular type of food when the proportion of that type in the animal's diet is higher than its proportion in the environment (MacArthur and Pianka, 1966). Amongst carnivores, ranked preferences are seen most clearly when actively selecting prey items that are the most profitable in terms of energy intake per unit time spent handling prey, i.e. the "functional response", classified by Holling (1959a,b). Wolves (*Canis lupus*) are highly adaptive and behaviourally flexible carnivores that have evolved to hunt prey widely ranging in size, although they are most commonly categorised as cursorily hunters of large ungulates (Peterson and Ciucci, 2003). Wolves are opportunistic and when wild prey species are absent or scarce, they utilise other food sources such as domestic animals, garbage, carcasses, marine species and vegetation (Salvador and Abad, 1987; Darimont et al., 2003; Gazzola et al., 2005, 2007; Stahler et al., 2006; Watts et al., 2010). Moreover, wolves can both scavenge and

predate, and they switch between the two strategies depending on what is most profitable (Stephens and Krebs, 1986). Wolves in Europe are most often territorial and hunt within their home range where the prey species are determined by the habitat resources and threats. Home range and territory size increase with latitude and Jędrzejewski et al. (2007) predicted that they range, on average, between 140 km² at 40°N in southern Europe, and 950 km² at 60°N in northern Europe. In North America, Fuller et al. (2003) found a positive correlation between wolf density and abundance of ungulates on a latitudinal scale, whereas Cubaynes et al. (2014) suggests that space rather than prey abundance is the limiting resource due to the intrinsic density-dependent mechanism, i.e. intraspecific aggression. Other factors affecting wolf diet in addition to prey species ecology and latitudinal differences in habitat attributes include human predation (Sidorovich et al., 2003), agricultural policies (Llaneza and López-Bao, 2015), climate changes (Wilmers et al., 2007; Mech and Fieberg 2014) and the genetic structure of populations (Jędrzejewski et al., 2012). During the past decades, many studies have been carried out to define wolf food habits in different areas, and one common result is that ungulates are the primary preys across the wolf distribution range in Scandinavia and Italy (Sand et al., 2005; Mattioli et al., 2011). Nearly all ungulate species are used by wolves within their range, and it seems that in each local area, wolf become very skilled on hunting a particular species

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(Sand et al., 2012). No previous studies have investigated the latitudinal variation in wolf diet with associated cause-specific factors between Scandinavia and Italy, which may well be interesting for future recovery and re-establishment of the wolf population in Europe. Contrary to radio/GPS tracking, scat analysis represents a cheap and non-invasive way to assess wolf diet (Reynolds and Aebischer, 1991; Teerkin, 1991). Scat analysis allows for both qualitative and quantitative assessment of the diet (Ballard et al., 1987; Gade-Jorgensen and Stagegaard, 2000) and makes collection of large samples feasible. While scat analysis has been used extensively in Italy regarding the feeding ecology of wolves (Mattioli et al., 1995, 2011; Capitani et al., 2004; Gazzola et al., 2007; Milanesi et al., 2012), this technique has been less widely adopted in Scandinavia (Scandinavian Wolf Research Project: <http://skandulv.nina.no>; Olsson et al., 1997). In this study, we used scat analysis for determining prey selection in two different European areas: one in Scandinavia, mainly South-central Sweden where the majority number of wolves inhabit, and the other in North-central Italy, Tuscany region. The objective of this study was to compare the wolf diet in these two areas, which show clear differences in terms of higher prey density and availability (Melis et al., 2009) and habitat heterogeneity (Storöen et al., 2015) in Italy compared to Scandinavia, as well as climate (Geffen et al., 2004; Melis et al., 2009) which can be valuable when analysing the ongoing wolf recolonization of the Alps and other parts of Western Europe. We tested the hypothesis that habitat features determine the outcome of the wolf diet, as these regulate prey distribution and abundance (Jędrzejewski et al., 2004; Houle et al., 2010; Milanesi et al., 2012; Mattisson et al., 2013) in the different areas. We predicted that (1) the prey species with the highest density is selected by wolves, (2) predator-prey size relationship has higher effect on wolf predation in Scandinavia as the main prey species is larger than in Tuscany, and (3) habitat heterogeneity will affect the wolf diet variance.

Material and methods

Study areas

Fig. 1.

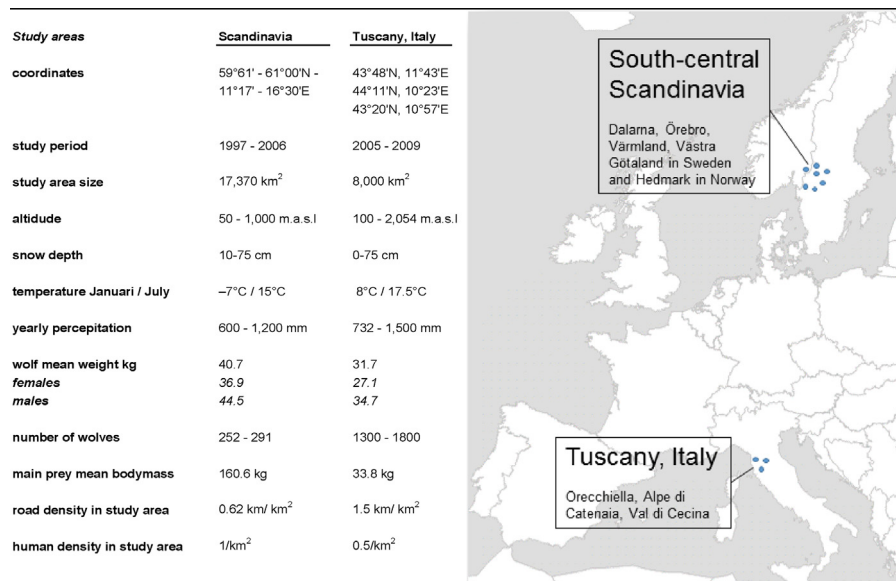


Fig. 1. Wolf territories in Northern and Southern Europe with associated data values (see Wabakken et al., 2010; Swedish Meteorological and Hydrological Institute; National Veterinary Institute; Swedish National Atlas, 1991; Galaverni et al., 2015; Arezzo Provincial Veterinary Department).

South-central Scandinavia

Data were collected in south-central Scandinavia, hereafter abbreviated SCA, in 18 wolf territories located in the counties Värmland, Dalarna, Örebro, Västra Götaland and two in Norway, Våler and Rømskog; (1) Leksand, (2) Hasselfors, (3) Grangårde, (4) Nyskoga, (5) Hagfors, (6) Tyngsjö, (7) Tisjön, (8) Furudal, (9) Dals-Ed, (10) Koppang, (11) Filipstad, (12) Årjäng, (13) Bogrängen, (14) Glaskogen, (15) Uttersberg, (16) Malung, (17) Atndalen, (18) Gravendal, (19) Rømskog N, (20) Våler N. Boreal temperate forest in the cold temperate climate zone with snow cover 3–6 months/year. Coniferous forest (taiga) is the dominant vegetation type and locally in the mountains, tundra is present. SCA's boreal forests (300,000 km² in Norway and Sweden) are among the most intensively exploited forests in the world, with less than 5% virgin forest left standing. The vegetation is dominated by coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Common deciduous species included birch (*Betula pubescens*), willow (*Salix* spp), aspen (*Populus tremula*), and alder (*Alnus incana*, *A. glutinosa*). Moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are the wolves main prey species (Sand et al., 2005, 2008) and other prey species available are beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), and black grouse (*Tetrao tetrix*). Other large or medium-sized mammalian predators present in wolf territories are brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*) and, in a few, wolverine (*Gulo gulo*). Due to extensive logging, the study areas are easily accessible to humans by a network of gravel forest roads (Eriksen et al., 2009).

Tuscany, Italy

Tuscany, hereafter abbreviated TUS, is located in North-central Italy and is a probable source of dispersing wolves to the Alps (Scandura et al., 2001; Fabbri et al., 2007). Wolf habitat differs geographically and three areas with wolf territories were examined in TUS. Previous studies have been carried out in the Tuscan provinces which we are taking into consideration (Mattioli et al., 1995, 2004, 2011; Ciucci et al., 1996; Apollonio et al., 2004). The three study areas in TUS are Alpe di Catenia in Arezzo Province, Orecchiella in Lucca Province and Berignone in Pisa Province. We estimated

one or two packs in each area. Wolf main ungulate prey species in the Northern Apennines, wild boar and roe deer, has increased significantly between 1977 and 2004 (Meriggi et al., 2011). The only other mammalian predator in TUS predating on ungulates is the red fox. The Tuscan study areas were quite different, thereof the descriptions are provided separately:

Alpe di Catenaia (43°48'N, 11°43'E). The study area is 120 km² and includes a small protected area of 27 km² in the centre. There is more than 80% forest cover with coppice, high trunk forests of Turkey oak (*Quercus cerris*) and chestnut (*Casanea sativa*) at lower elevation, and of beech (*Fagus sylvatica*) at upper ranges. Moreover, conifers such as pine and black pine (*Pinus nigra*), white spruce (*Abies alba*), Douglas fir (*Pseudotsuga* spp) are interspersed into deciduous woods. Prey species are wild boar (*Sus scrofa*) and roe deer. Sheep (*Ovis aries*) and goats (*Capra hircus* spp.) are present in open areas throughout the year.

Orecchiella (44–11°N, 10–23°E). It is included in a temperate cold climate zone, characterised by high rainfall mainly concentrated in autumn and spring. Summer rains are extensive, although irregular by the influence of the Mediterranean climate. Conifers and beech dominates the high forest landscape and at lower altitudes, it is possible to find Turkey oak and chestnut. Other species of trees and shrubs are: ash (*Fraxinus excelsior*), laburnum (*Laburnum anagyroides*), blackthorn (*Prunus spinosa*), the mountain ash (*Sorbus aria*) and the rowan tree (*Sorbus aucuparia*). Prey species are mouflon (*Ovis orientalis musimon*), red deer (*Cervus elaphus*), roe deer, and wild boar.

Val di Cecina – Berignone (43–20°N, 10–57°E). The Val di Cecina can be considered a transition zone between the two major Italian climatic regions: the Mediterranean with summer drought and the Central European, with no dry period summer time. Wooded hills composed of deciduous and evergreen oak forests of downy oak *Quercus pubescence*, French oak *Q. robur* and holm oak *Q. ilex*. Prey species are wild boar, fallow deer (*Dama dama*), roe deer, mouflon and small mammals. Sheep and goats are present in open areas throughout the year.

Sampling design for scat collection

Scats were collected along systematic transects of 1–2 km 1–2 times per month in each territory, in re-sealable plastic bags and frozen until laboratory analysis. They were identified in the field as most likely corresponding to wolves based on size (diameter > 2.5 cm), shape and the presence of mammal prey remains such as hair, bones, claws and hooves or feathers.

Laboratory analysis

In SCA, the scats were frozen and prior to the analyses, dried for 48 h at 90 °C (±5 °C). After the drying process, dry weight of the scats were taken (0.01 g precision). The procedure to analyse the scat contents followed Spaulding et al. (1997). Each scat was broken apart by hand and the single prey items were sorted. If there was more than one prey item found in the scat, we assumed that the macro and micro components originated from the found items in the same proportion (Ciucci et al., 1996). We identified the macro components in the scats (e.g. hairs, hooves, teeth, bone fragments) with the help of reference manuals (Moore et al., 1974; Debrot et al., 1982; Teerink, 1991) and a reference collection developed at the Grimsö Research Station. The hairs were first examined visually concerning colour pattern, length, thickness, and thereafter identified microscopically by medullary pattern and cuticular scale (Teerink, 1991). With the help of a reference grid we visually estimated the relative volumetric proportion for each prey item identified in a scat (Reynolds and Aebischer, 1991). The distinction into juvenile and adult cervid was carried out mainly

due to the characteristic hair pattern of young animals. We were able to distinguish between juvenile and adult from birth to the first autumn moult in August/September. It is very difficult to distinguish between juveniles and adults during the winter season by looking only at the hairs (Peterson et al., 1984; Ciucci et al., 1996), why we applied the age class distribution for consumed cervids described by Pedersen et al. (2005) according to: moose (adult:yearling:calf) 80:10:10 and roe deer (adults:fawns) 50:50, to make a reasonable differentiation into juveniles and adults.

In Italy, the scats were kept dry and frozen at –30 °C, scat were washed in a sieve of 0.5 mm and the prey remains (hair and bones), fruit and grasses found in every scat were dried at 68 °C for 24 h. Prey remains were identified through comparison to a reference collection of mammal hair, bones, and teeth. This identification was based mainly on the macroscopic characteristics of hairs and bones following Mattioli et al. (2004, 2011); nevertheless, if necessary, identification through microscopical analysis were performed too, with the support of references glasses and guide. Wild boar remains were divided into three weight classes: new-born piglet (<10 kg), piglet (10–35 kg), and adult (>35 kg). Concerning the summer season, cervid remains were classified into two classes according to the first moult (September–October): fawn (<5 months) and adult (≥5 months). Of the scats containing cervids in TUS, 37% were collected in summer and could be considered for evaluation of the seasonal prey age results. We excluded cervids in order to avoid bias from the seasonal prey age class analysis of winter as, when bones were absent in the scats, fawns could not be identified during their first winter by hair only.

In order to estimate the contribution of each species in the diet, in terms of volume, we categorised each food item in a scat by 5% steps (i.e. <5%; 6–10%; 11–15%) as described by Russell and Storch (2004). We calculated the average volume (AV%) for each food item. The AV% was defined as $V_i/N \times 100$ where V_i is the total volume of a given food item i , and N is the total number of scats.

Prior to the analyses the observers were trained in identifying scat contents by practicing with reference material and scats. As recommended by Ciucci et al. (1996), a blind test was performed with 50 scat samples to assess the accuracy of identification by the laboratory personal in both SCA and TUS. The errors were below the threshold of 5% (Mattioli et al., 2004). For the analysis, the year was divided in two seasons, according to the wolf biology: summer, and winter. As SCA has earlier winter and later summer periods than TUS, summer is considered as one month shorter in SCA. Thus, summer is between the 1st of May and the 30th of September in SCA, and from the 1st of May to the 31st of October in TUS; while winter is between the 1st of October and the 30th of April in SCA, and from the 1st of November to the 30th of April in TUS.

Estimated biomass in scats

To estimate the biomass intake, we used the Whole Scat Equivalents (WSE), which summarises the relative dry volume for a given food item within the scat sample (Angerbjörn et al., 1999), for the SCA data and the AV% for the Italian data as these methods used differed locally. Yearly biomass ingested from the food items were estimated on the basis of the known relationship between prey biomass consumed per collectable scat produced, using three calculations; Floyd et al., 1978; Weaver, 1993 and Ruhe et al., 2003 (Table 2). Calculations are presented with the Floyd equation: $y = 0.383 + 0.02x$, Weaver equation: $y = 0.439 + 0.008x$ and Ruehe equation $y = 0.731 + 0.00406x$, where the x = assumed live weight of prey species and y = estimated biomass consumed per scat. For seasonal biomass calculation, we used the Weaver equation since neither Floyd nor Ruehe have been based on large ungulates such as moose (Table 4). Assumed live weights of prey species were gath-

ered from previous studies and adjusted according to prey type consumption, i.e. juvenile:adult relation.

Prey preference

Manly's preference index, α_i is a useful measure for quantifying predator preference in selective predation as it includes a random number of prey types of both constant and changing prey densities. To investigate prey preference, Manly's Alpha preference index, also known as Chesson's index (Chesson, 1978) was used: $\alpha_i = (r_i/n_i) * [1/\sum(r_j/n_j)]$ where prey type r_i or r_j is the proportion in the diet and n_i or n_j the proportion in the environment. Manly's alpha ranges from 0 to 1; r_i and r_j are the proportions (biomass) of prey type i or j in the wolf diet, n_i and n_j are the proportions (biomass) of prey type i or j in the environment. Unselective predation occurs if $\alpha_i = 1/m$ (m = total number of prey types). Prey species i is preferred if α_i is greater than $1/m$, whereas negative selection is found if α_i is less than $1/m$. Conversely, if $\alpha_i = 1/m$, less of prey type i occurs than expected by random feeding, i.e. prey type i is avoided by the predator.

Niche width

The calculations of niche width were based on seven prey groups in SCA and eight in Italy.

Levin's Food Niche Breadth (FNB) index (Levins, 1968) was used to measure specialisation quantitatively for the wolf diet composition within SCA and TUS. Levin's index is defined as $B = 1/\sum p_j^2$ where p_j = proportion of fractions of items in the diet that are of food category j . Levin's Food Niche Breadth can be standardised and expressed in a scale from 0 to 1 with the help of an equation, $BA = (B-1)/(n-1)$ where BA = Levin's standardised FNB, n = number of possible resource states.

Niche overlap

The calculations of niche overlap between wolf territories were based on the same prey groups as used in niche width. To calculate niche overlap, Pianka's index (Pianka, 1973) was used: $O_{jk} = \sum (p_{ij} * p_{ik}) / [\sum p_{ij}^2 * \sum p_{ik}^2]$ where O_{jk} is Pianka's measure for niche overlap between predator j and predator k , p_{ij} is the proportion of prey type i in relation to the total amount of prey ingested by predator j , p_{ik} is the proportion of prey type i in relation to the total amount of prey consumed by predator k , and m is the total number of prey types. The calculations were based on the relative biomass of the prey types. The index ranges from 0, i.e. no overlap, to 1, i.e. complete overlap.

Dataset accuracy

The use of re-sampling techniques (e.g. bootstrapping) to produce confidence intervals around estimates of dietary composition (Reynolds and Aebischer, 1991) are used to avoid misleading conclusions about elusive, difficult to observe and occurring in low population densities predator feeding habits (Davis et al., 2012). For evaluating the accuracy in our conclusions, we generated the confidence intervals of each year as well as seasons by bootstrapping. We used a parametric bootstrap approach to calculate variances for the diet of each year, calculated 10,000 bootstrap estimates to obtain the standard error for the estimated diet components and examined the mean of the bootstrap distribution to assess bias in the estimates (Efron and Tibshirani, 1993). Bootstrapping is a technique that has previously been useful in the analysis of predator diets (e.g. Karanth and Sunquist, 1995; Davis et al., 2012).

Prey abundance

In SCA, moose density was on average 126/100 km² and roe deer density on average 57/100 km² from pellet counts in seven of the territories (Eriksen et al., 2009; Sand et al., 2012; Gervasi et al., 2012).

In TUS, due to the habitat and species heterogeneity between the three study areas, to estimate ungulate density we combined data obtained using different methods; drive census, as described in Davis et al. (2012), especially for roe deer and wild boar, observations from vantage point for cervids and mouflon, and red deer were also censused by counting roaring males during the rut season, as described in Mattioli et al. (2004). The average prey densities in the three Tuscan areas showed that roe deer had the highest density of 2510 individuals/100 km², wild boar 691/100 km², fallow deer 286/100 km², red deer 191/100 km², and mouflon 325/100 km². Roe deer and wild boar were present in all study areas. Human hunting of wild ungulates is a very widespread activity, both in SCA (Cederlund and Bergström, 1996) and in TUS. Roe deer in SCA, and wild boar in TUS are harvested by humans in relation to their densities. Furthermore, there is a somewhat lower proportion of human harvest of moose in SCA and roe deer in TUS in relation to their densities.

Statistical analysis

When results were normally distributed, statistical significance was tested with independent samples *t* test, ANOVA and post-hoc Tukey HSD test. When data was not normally distributed, Mann Whitney and Kruskal Wallis tests were used and a single-factor ANOVA applied to the data raked across all samples when different sample sizes. Data was analysed using IBM SPSS Statistics 21 and StatSoft Statistica 10, R for bootstrapping.

Results

In SCA, a total of 2159 scats (803 in summer and 1334 in winter) were collected and analysed from 20 wolf territories (two in Norway), between 1997 and 2006. Of these, 90.5% contained wild ungulates, 5.7% small mammals, 0.7% birds, 0.5% domestic animals, 0.6% other prey and 2.5% vegetarian (berries and grass). In TUS between 2005 and 2009, a total of 542 scats were collected and analysed (Alpe di Catenai, $n = 266$; Val di Cecina (Berignone), $n = 156$; Orecchiella, $n = 120$). Of these, 268 were collected during summer and 274 during winter. Scat content contained 89.8% wild ungulates, 1.4% small mammals, 3.2% domestic animals, 1% other preys and 5.5% fruit, berries and grass (Table 1).

From the bootstrapping resample, it is possible to notice that the Swedish dataset showed a continuous and stable image from 1997 to 2006 with negligible temporal, prey species-specific or food item variance. On the contrary, the Tuscan dataset 2005–2009 (excluding 2007) showed a greater variance than the SCA one (Table 2). In SCA, the highest biomass intake concerned wild ungulates (89.1%), whereas those of small mammals and domestic animals were comparatively lower (10.4% and 0.6%, respectively). TUS showed an even highest level of biomass intake concerning wild ungulates (95.1%), whereas domestic animals and small mammals were comparatively lower (3.4% and 1.5%, respectively).

Niche width and overlap

Levin's Food Niche Breadth was broader in TUS ($B = 4.0$) than in SCA ($B = 2.5$) and consequently the standardised niche breadth was higher in TUS ($BA = 0.23$) than in SCA ($BA = 0.12$). This results in

Table 1

Wolf feeding habits in Sweden and Italy. Diet composition is expressed as frequency of occurrence of item (FO/I), indicating total *n* of scats and %. Average assumed prey weight is reported for all age classes. Prey density expressed in individuals/km². Hunting harvest expressed in individuals/km², reported by the Swedish Hunters Association for Hunting and Wildlife Management 2005–2009 in all countries, and local hunting teams in Alpe di Catenai (no hunting reports available from Orecchiella or Berignone). Availability is defined as prey density (individuals/km²) available for wolves after human predation. Selection indicates prey Manley's preference index α , and for sample accuracy, 95% confidence intervals (CI) were calculated using bootstrap.

food item	FO/I						weight			density	human hunt	availability	selection	bootstrap 95% CI	
	summer n	summer%	winter n	winter%	total n	all seasons%	summer	winter	all seasons	ind/km2	ind/km2	ind/km2	Manly's	lower	upper
SWEDEN															
moose <i>Alces alces</i>	499.6	65.1	968.2	78.8	1468	73.5	116.7	192	160.6	1.26	0.36	0.9	0.79 [*]	73.48	73.52
undetermined cervid <i>Cervidae</i>	91	11.9	126.8	10.3	218	10.9								10.89	10.91
roe deer <i>Capreolus capreolus</i>	54.5	7.1	119.2	9.7	174	8.7	17.1	20	18.8	0.57	0.47	0.1	0.21 ^{**}	8.69	8.71
beaver <i>Castor fiber</i>	31.1	4.05	0.2	0.02	31	1.6	18	18	18					1.59	1.61
hare <i>Lepus europaeus</i>	10.5	1.37	0.1	0.01	11	0.5	3.5	3.5	3.5					0.44	0.56
badger <i>Meles meles</i>	16.9	2.2	3.3	0.27	20	1	10.5	10.5	10.5					0.99	1.01
small mammals <i>Rodentia</i> , Insectivora	13	1.69	0.1	0.01	13	0.7	0.025	0.025	0.025					0.69	0.71
birds <i>Aves</i>	6.3	0.82	9.3	0.75	16	0.8								0.77	0.83
insects		0	0.1	0	0	0									
undetermined carnivore <i>Carnivora</i>	4.9	0.64	0	0	5	0.2									
undetermined mammal <i>Mammalia</i>	0.5	0.07	0	0	1	0									
domestic animals	9.7	1.26	1	0.08	11	0.5	25	25	25					0.49	0.51
fruit/berries	4.4	0.57	0	0	4	0.2									
plant material	22.9	2.98	0.2	0.02	23	1.2									
wolf (grooming)	2.2	0.29	0.2	0.01	2	0.1									
TOTAL	767.5		1228.7		1996										
ITALY															
wild boar <i>Sus scrofa</i>	87.5	32.5	123.3	48.2	210.75	40.1	33.2	34.5	33.8	6.91	5.89	1.02	0.36 [*]	40.05	40.15
roe deer <i>Capreolus capreolus</i>	59.75	22.2	70.8	27.7	130.5	24.9	20.7	24	22.4	25.1	3.64	21.46	0.063 ^{**}	24.86	24.94
red deer <i>Cervus elaphus</i>	18.5	6.9	7	2.7	25.5	4.9	39.1	102.5	70.8	1.91	***		0.169 ^{**}	4.88	4.92
fallow deer <i>Dama dama</i>	37.75	14	14.8	5.8	52.5	10	23.9	55.4	39.7	2.86	***		0.074 ^{**}	9.98	10.02
mouflon <i>Ovis orientalis</i>	24.5	9.1	14.3	5.6	38.75	7.4	22.9	23.8	23.4	4.88	***		0.33 [*]	7.37	7.43
hare <i>Lepus europaeus</i>	4	1.48	1.5	0.59	5.5	1	3	3	3					0.99	1.01
small mammals <i>Rodentia</i> , Insectivora	6.5	2.41	0.3	0.1	6.75	1.3	0.03	0.03	0.03					1.29	1.31
domestic animal	9	3.34	7.5	2.94	16.5	3.1	55.8	55.8	55.8					3.09	3.11
fruit/berries	9	3.34	2.5	0.98	11.5	2.2								2.18	2.22
plant material	9	3.34	7.8	3.03	16.75	3.2								3.19	3.21
fox <i>Vulpes vulpes</i>	2	0.74	1	0.39	3	0.6									
mustelid <i>Mustelidae</i>	0	0	2	0.78	2	0.4									
non identified	2	0.74	1	0.39	3	0.6								0.59	0.61
other	0	0	2	0.78	2	0.4								0.39	0.41
TOTAL	269.5		255.5		525										

* Selective.

** Negative selection.

*** Inadequate number of records reported.

Table 2

Yearly biomass consumed expressed in kg and%. Calculations are presented with the Floyd equation (1978): $y = 0.383 + 0.02x$, Weaver equation (1993): $y = 0.439 + 0.008x$ and Rühle equation (2003): $y = 0.731 + 0.00406x$ when x is the assumed average weight of prey.

SWEDEN	%WSE	Floyd			Weaver			Rühle		
		kg/scat	kg	%	kg/scat	kg	%	kg/scat	kg	%
moose	79.6	3.60	6117.6	95.6	1.72	2933.3	92.5	1.38	2353.3	87.3
roe deer	9.4	0.76	153.2	2.4	0.59	118.9	3.8	0.81	162.9	6.0
small mammals	1.3	0.38	10.4	0.2	0.44	11.9	0.4	0.73	19.8	0.7
beaver	2.9	0.74	45.3	0.7	0.58	35.5	1.1	0.80	49.0	1.8
hare	5.2	0.45	49.9	0.8	0.47	51.5	1.6	0.75	82.2	3.0
badger	1.1	0.59	13.8	0.2	0.52	12.1	0.4	0.77	18.0	0.7
domestic animals	0.6	0.88	10.8	0.2	0.64	7.8	0.2	0.83	10.2	0.4
			6400.9			3171.1			2695.4	
ITALY	%AV									
wild boar	43.8	1.08	237.1	43.2	0.74	162.6	41.9	0.86	203.1	43.6
roe deer	27.1	0.91	121.9	22.2	0.59	90.8	23.4	0.82	120.7	25.9
red deer	5.3	1.80	51.6	9.4	1.05	28.9	7.4	1.02	29.2	6.3
fallow deer	10.9	0.88	69.5	12.7	0.76	44.7	11.5	0.89	52.7	11.3
mouflon	8.0	0.85	37.1	6.8	0.74	27.3	7.0	0.83	36.0	7.7
hare	0.7	0.44	1.7	0.3	0.46	1.8	0.5	0.74	2.9	0.6
small mammals	0.7	0.38	1.5	0.3	0.44	1.7	0.4	0.73	2.9	0.6
domestic animal	3.4	1.50	27.8	5.1	0.88	16.4	4.2	0.96	17.8	3.8
			548.3			374.2			465.4	

a higher inter-areas niche overlap in SCA ($O_{jk} = 0.85$) than in Italy ($O_{jk} = 0.63$) using Pianka's index.

Seasonal prey age class variation

In SCA the main source of biomass consumed was by one third from moose during summer, and nearly exclusively during winter. The selection of moose calves increased significantly in summer in respect to winter ($U = 1,443.5$, $n = 216$, 18 , $P = 0.05$). However, when comparing summer and winter seasons (Table 3), the second prey choice, roe deer, in summer is more variable, explicitly in SCA. Other prey species were fairly evenly distributed during summer, however, nearly absent during winter.

In TUS wild boar was the most selected all year around. Young weighing 10–35 kg were most selected in winter, while no significant difference in use of age classes was found in summer. Roe deer was the secondly used prey species. The use of fallow deer, mouflon and red deer increased during summer, in relation to fawning season. Highest source of biomass in TUS came primarily from wild boar and secondly from roe deer all seasons, closely followed by fallow deer during the summer season. All other ungulate species as well as domestic species, had a fairly evenly distribution as biomass source during the winter season.

Territorial variances

Calculating the diet at the scale of territory separately, Table 4 shows the variance within SCA and TUS. Using Manly's alpha preference index, wolves in SCA clearly showed positive preference for moose (and consequently, the negative preference for roe deer). The highest prey species preference was seen in moose all seasons except for one territory where roe deer was the most preferred all seasons and another territory where it was selected in winter and not in summer. TUS showed highest preference of wild boar, mouflon and fallow deer (and consequently negative preference of roe deer all seasons), with a substantial seasonal variation (Table 4).

Discussion

Density and age class dependent prey selection

The results in this study confirmed that the major component of wolf diet comes from wild ungulates followed by a minor part of

small mammals and domestic animals. As we expected, moose was the main prey in Scandinavian wolf diet, having the highest density values. The intensive forest management may have resulted in an increased production of moose forage (Edenius et al., 2002), along with intensive and selective human harvest of moose in SCA contributing to high rates of reproduction via structuring the population towards a high proportion of productive females (Nilsen and Solberg, 2006). In this study, where moose was the main prey in SCA and wild boar in TUS, it was appropriate to compare the three equations, Floyd, Weaver and Rühle, for a comprehensive view as prey size differed in the two study areas and the equations have different original prey species anchorage. According to the three different equations (Table 2), the level of biomass differed among areas most strongly with Floyd's equation, which showed a higher intake per scat. In Italy, wild boar was the main prey species, yet less numerous than the second selected prey species, roe deer. However, wild boar was the most selected prey species in Alpe di Catenaiia but not in the two other Tuscan areas as shown with Manly's Alpha preference index (Table 4). This was likely related to the strongly different ungulate communities of the three areas taken into account, generating changes in prey composition and density of the sample through years. Thus, for the Tuscan areas, our first prediction was not supported by the data analysis as roe deer had the highest density of all prey species, yet wild boar, mouflon and fallow deer were the most selected. In spite of negative preference using Manly's Alpha preference index, roe deer was the second prey choice as well as the second largest source of biomass in both SCA and TUS with the exception of summer in SCA. It has been shown that wolf hunting success is lower due to longer chase distance, fewer encounters and less predator-naïve behaviour in roe deer than in moose in SCA (Wikenros et al., 2009), but no similar studies have been published from Italy. When present at high density, roe deer can be a profitable prey for wolves because of the high encounter rate and low handling time (Huggard 1993a; Mattioli et al., 2004; Sand et al., 2005), nevertheless, roe deer selection was low in TUS in relation to their density (Ciucci et al., 1996; Capitani et al., 2004; Mattioli et al., 2011; Davis et al., 2012). Remarkable was the high number of available roe deer in Alpe di Catenaiia after human predation, with a relatively small use by the wolf when compared to wild boar. Besides predation risk from wolf, brown bear and red fox, vigilance may be higher in Swedish roe deer as another predator, Eurasian lynx, is a stalking predator forcing higher anti-predator behaviour investment (Wikenros et al., 2015), even if this

Table 3
Biomass consumed expressed in kg and per cent in summer and winter using three equations by Floyd et al., 1978; Weaver, 1993 and Rütche et al., 2003.

	Summer					Winter				
	assumed weight (kg)	WSE/AV%	biomass consumed/scat (kg)	biomass consumed (%)	biomass consumed/scat (kg)	assumed weight (kg)	WSE/AV%	biomass consumed/scat (kg)	biomass consumed (%)	biomass consumed/scat (kg)
SWEDEN										
moose	116.7	62.3	137	29.8	1102.2	192	73.3	1.98	95.8	1931.2
roe deer	17.1	8.9	0.58	12.5	462.4	20	7.5	0.60	3.0	59.9
beaver	18	1.6	0.44	9.5	352.7	18	0.8	0.44	0.2	4.7
hare	3.5	3.8	0.58	12.7	468.1	3.5	1.6	0.58	0.6	12.4
badger	10.5	1.3	0.47	10.2	375.0	10.5	0.9	0.47	0.3	5.6
domestic*	25	2.1	0.52	11.4	420.0	25	0.3	0.52	0.1	2.1
small mammals	0.025	1.2	0.64	13.9	513.1	0.025	0.1	0.64	0.0	0.9
					3693.5					2016.8
TUSCANY										
wild boar	33.2	37.1	0.70	39.1	69.9	34.5	52.0	0.67	49.3	95.0
roe deer	20.7	19.2	0.60	17.4	31.1	24	25.9	0.63	23.2	44.8
red deer	39.1	8.7	0.75	9.8	17.5	102.5	5.0	1.26	9.0	17.3
fallow deer	23.9	17.1	0.63	16.2	28.9	55.4	6.4	0.88	8.0	15.4
mouflon	22.9	10.1	0.62	9.4	16.8	23.8	5.8	0.63	5.2	10.0
hare	3.0	0.59	0.46	0.4	0.7	3	0.39	0.46	0.3	0.5
small mammals	0.03	0.63	0.44	0.4	0.7	0.03	0.12	0.44	0.1	0.2
domestic*	55.8	5.5	0.89	7.3	13.1	55.8	3.9	0.89	5.0	9.6
					178.8					192.7

has had a limited effect on habitat selection by roe deer after lynx expansion in SCA (Samelius et al., 2013). In TUS however, roe deer has only two predators, wolf and red fox (Bassi et al., 2012), the latter predating solely on fawns during the first post-birth weeks (Jarnemo and Liberg, 2005). Our data clearly showed wide variations in seasonal prey age class variation, e.g. in TUS, different age classes showed that young wild boar were clearly selected during winter. During summer, there was a more varied distribution of prey selection, covering several species with a higher proportion of cervids, especially red deer, fallow deer and mouflon, due to the availability of fawns (Table 1).

Influence of prey size on selection

The body size difference in Scandinavian and Italian wolves was not the only reason for Italian wolves predating on smaller ungulate species. No larger ungulates than red deer are present in TUS and choosing young wild boar during winter may suggest that they were not only preferred due to lack of experience and developed anti-predator behaviour. Optimal foraging strategy (Stephen and Krebs, 1986), highlights the importance of predators' selection of the most profitable prey, profitability being the ratio between energy gain and handling time. Depending on the prey species density, encounters may occur frequently or rarely and the time and risk when killing varies with prey size and behaviour. Moreover, within a prey species, there are differences in sex-, age- and size groups which affects kill rate and risk of injury. The proportion of moose calf increased from 2% during winter to 25% during summer in SCA, even though the largest part of the scat content consisted of adult moose. Calves offer a relatively small amount of biomass per kill, which results in a higher kill rate per time unit during the vegetative growth period (Sand et al., 2008). However, body size increases rapidly resulting in higher biomass intake per kill for predators. There was no significant seasonal difference in adult wild boar predation and Tuscan wolves switched seasonally to mainly other ungulates than wild boar during the summer season. Adult wild boar can cause serious injury or death to predators, and albeit the Apennine wild boar is somewhat smaller than in other parts of Europe, it can be energy beneficial targeting younger individuals. Moose can also cause injury or death to predators but as the Scandinavian moose may be naïve due to a long period of wolf absence, their anti-predator behaviour has not yet had enough time to adjust to the re-colonising wolves (Sand et al., 2006). Moose in North America may rapidly have adjusted their anti-predator behaviour after only one generation in re-colonising predator areas (Berger et al., 2001), however, the delayed behavioural response covering several generations as in Scandinavia, is a general finding in large-bodied ungulates when exposed to cursorial predators (Thacker et al., 2011). Moose is nearly four times larger than the SCA wolves, compared to wild boar in relation to the Italian wolves that are virtually equal in weight, calculated all seasons. In SCA, selection of adult moose and roe deer was greater than on juveniles all seasons, while in TUS, wild boar juveniles were more selected than adults all seasons and juvenile red deer more selected than adults during summer, suggesting a stronger avoidance of injury by Tuscan wolves. However, we argue that the more than tenfold increase of moose calf in wolf diet in SCA during summer, and the more than doubled increase of young wild boar in TUS during winter, associates with the size difference relation between predator and prey, and consequently the investment in avoidance of injury.

The effect of habitat and prey species composition heterogeneity

The composition of wolf diet changes according to the temporal and spatial availability of prey species in its territory (Jędrzejewski et al., 2002; Kauffman et al., 2007; Mattisson et al. 2013) and these

Table 4

Manly's α selectivity index and Levins index reported for each territory in SCA and TUS. N represents the number of scats used for the calculation. Manly's index is calculated for both season and for the entire year, while Levins index is only for the two season; this latter index is expressed in a scale from 0 – 1, 0 being none to 1 being complete.

			Manly's α	Levins FNB
SCANDINAVIA		n	preference	niche width
Bogragen	summer	36	moose 0.87	0.2448
	winter	24	no roe deer	0.4347
	all seasons		moose 0.91	
Dals-Ed	summer	73	moose 0.68	0.325
	winter	34	roe deer 0.72	0.381
	all seasons		roe deer 0.51	
Filipstad	summer	21	moose 0.78	0.3197
	winter	50	moose 0.8	0.171
	all seasons		moose 0.8	
Grangärde/Gravendal Glaskogen	summer	76	moose 0.74	0.214
	winter	217	moose 0.81	0.182
	all seasons		moose 0.79	
Hagfors	summer	100	moose 0.8	0.2604
	winter	81	moose 0.82	0.154
	all seasons		moose 0.81	
Hasselfors	summer	72	moose 0.69	0.2347
	winter	205	moose 0.65	0.256
	all seasons		moose 0.66	
Leksand	summer	111	moose 0.87	0.1617
	winter	280	moose 0.89	0.0987
	all seasons		moose 0.89	
Nyskoga	summer	93	moose 0.94	0.102
	winter	123	moose 0.96	0.0835
	all seasons		moose 0.95	
Tisjön	summer	84	moose 0.96	0.2208
	winter	48	moose 0.75	0.3957
	all seasons		moose 0.87	
Tyngsjö	summer	15	no roe deer	0.257
	winter	110	moose 0.92	0.1601
	all seasons		moose 0.93	
Årjäng	summer	48	moose 0.77	0.2789
	winter	6	no roe deer	0.8
	all seasons		moose 0.79	
Våler, Norway	summer	73	moose 0.65	0.3228
	winter	9	roe deer 0.77	0.8406
	all seasons		moose 0.6	
TUSCANY				
Alpe di Catenai	summer	129	wild boar 0.69, red deer 0.38	0.3602
	winter	152	wild boar 0.75	0.1703
	all seasons		wild boar 0.69	
Orecchiella	summer	55	red deer 0.46, mouflon 0.8	0.5543
	winter	66	mouflon 0.41	0.5613
	all seasons		mouflon 0.57	
Val di Cecina (Berignone)	summer	98	fallow deer 0.47, mouflon 0.44	0.379
	winter	47	fallow deer 0.3, mouflon 0.28	0.6419
	all seasons		fallow deer 0.41, mouflon 0.39	

tendencies are confirmed also by our results. Even if SCA territories were larger than TUS ones, TUS presented a higher heterogeneity in terms of number of prey species; the prey community was composed by only two prey species in SCA and by a total of five species in TUS. Different latitudes may reflect on abiotic and biotic habitat heterogeneity, however, the level of human utilisation of the landscape too determines wolf diet diversification. The intensively exploited forest industry in SCA prevents rich species diversity opposing to the abandoned former agricultural areas in the Apennines, allowing re-forestation and species diversification. Earlier studies have shown that small-bodied ungulates are limited by snow depth, vegetation productivity and forest cover (Huggard, 1993b; Okarma et al., 1995; Jędrzejewski et al., 2002; Ratikainen

et al., 2007; Melis et al., 2009), all attributes of which TUS has superior conditions for successful roe deer, fallow deer and red deer reproduction and diversification. Forestry practice can be developed without huge economical losses for the forest industry, yet benefitting biodiversity including ungulates (Beguín et al., 2015) and consequently large carnivores. Finally, the more varied landscape of TUS, with elevations ranging from 100 to 2,500 m.a.s.l and vegetation moving from Mediterranean scrubs to high mountains pastures is a further reason promoting its higher variability within region variability. According to our third hypothesis, we expected that the Tuscan diet resulted to be more heterogeneous than the Scandinavian: Levin's and Pianka's index values seem to confirm our third hypothesis.

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