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SHORT COMMUNICATION

What does the wild boar mean to the wolf?

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Abstract Generalist predators are expected to shape their diets according to the local availability of prey species. In turn, the extent of consumption of a prey would be influenced by the number of alternative prey species. We have tested this prediction by considering the wild boar and the grey wolf: two widespread species whose distribution ranges overlap largely in Southern Europe, e.g. in Italy. We have reviewed 16 studies from a total of 21 study areas, to assess whether the absolute frequency of occurrence of wild boar in the wolf diet was influenced by (*i*) occurrence of the other ungulate species in diet and (*ii*) the number of available ungulate species. Wild boar turned out to be the main prey of the wolf (49% occurrence, on average), followed by roe deer (24%) and livestock (18%). Occurrence of wild boar in the wolf diet decreased with increasing usage of roe deer, livestock, and to a lower extent, chamois and red deer. The number of prey species did not influence the occurrence of wild boar in the wolf diet. The wild boar is a gregarious, noisy and often locally abundant ungulate, thus easily detectable, to a predator. In turn, the extent of predation on this ungulate may not be influenced so much by the availability of other potential prey. Heavy artificial reductions of wild boar numbers, e.g. through numerical control, may concentrate predation by wolves on alternative prey (e.g. roe deer) and/or livestock, thus increasing conflicts with human activities.

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Introduction

The composition of prey communities is expected to influence the diet of predators (e.g. Sinclair et al. 2003; Garrott et al. 2007; Baudrot et al. 2016). In turn, large carnivores play a pivotal role in ecosystems, as their action may generate cascading effects on lower trophic groups (e.g. Fortin et al. 2005; Beschta and Ripple 2009; Suraci et al. 2016). Feeding habits have evolved to maximise fitness and subject to constraints imposed by availability of food resources (MacArthur and Pianka 1966). Generalist predators are expected to shape their diet according to the local availability of prey species (Terraube et al. 2014; Baudrot et al. 2016).

The wild boar *Sus scrofa* is the most widespread ungulate in the world, favoured by its ecological plasticity, popularity as a game species and particularly high reproductive rate (Barrios-Garcia and Ballari 2012; Massei et al. 2014). In Europe, its main predator is the grey wolf *Canis lupus* (Newsome et al. 2016), a generalist carnivore (e.g., Mech 1970; Okarma 1997; Davis et al. 2012) which feeds mainly on meso-large mammals, especially ungulates (Meriggi and Lovari 1996; Meriggi et al. 2011; Newsome et al. 2016). In the last few decades, because of reintroductions and improved management (Apollonio et al. 2010), numbers of wild ungulates have increased all over Europe and have been the main determinants of range expansion and population growth of the wolf (Okarma 1997; Chapron et al. 2014; Galaverni et al. 2015). When wild prey is available, the wolf tends to prefer it to livestock (Meriggi and Lovari 1996). In particular, the wild boar is an important prey in Mediterranean countries, with variable frequencies of occurrence across areas (e.g. Meriggi et al. 1996; Barja 2009; Bassi

et al. 2012). Abundance of wild boar in the diet of wolves should lead to a decreased predation on livestock (Meriggi et al. 2011). However, Meriggi and Lovari (1996) reported that the presence of several wild ungulate species is necessary to reduce predation pressure on livestock. Thus, it is unclear whether the use of wild boar could be influenced by the richness of the prey community, as well as by livestock availability.

In our review, we have assessed the importance of wild boar for the wolf diet in Italy. In particular, we have evaluated whether the occurrence of wild boar in the diet of the wolf could depend on number of potential prey species, i.e. large ungulates. We predicted that the importance of wild boar in the wolf diet would decrease when the spectrum of potential prey species increases.

Materials and methods

We have reviewed information from eight published papers and eight grey' sources (e.g. dissertations and technical reports) on food habits of wolves in Italy, estimated through scat analyses (Fig. 1). There are indications that shifts in diet of large predators are not season dependent (e.g. wolf: Patalano and Lovari 1993; Iberian lynx: Ferreras et al. 2010; common

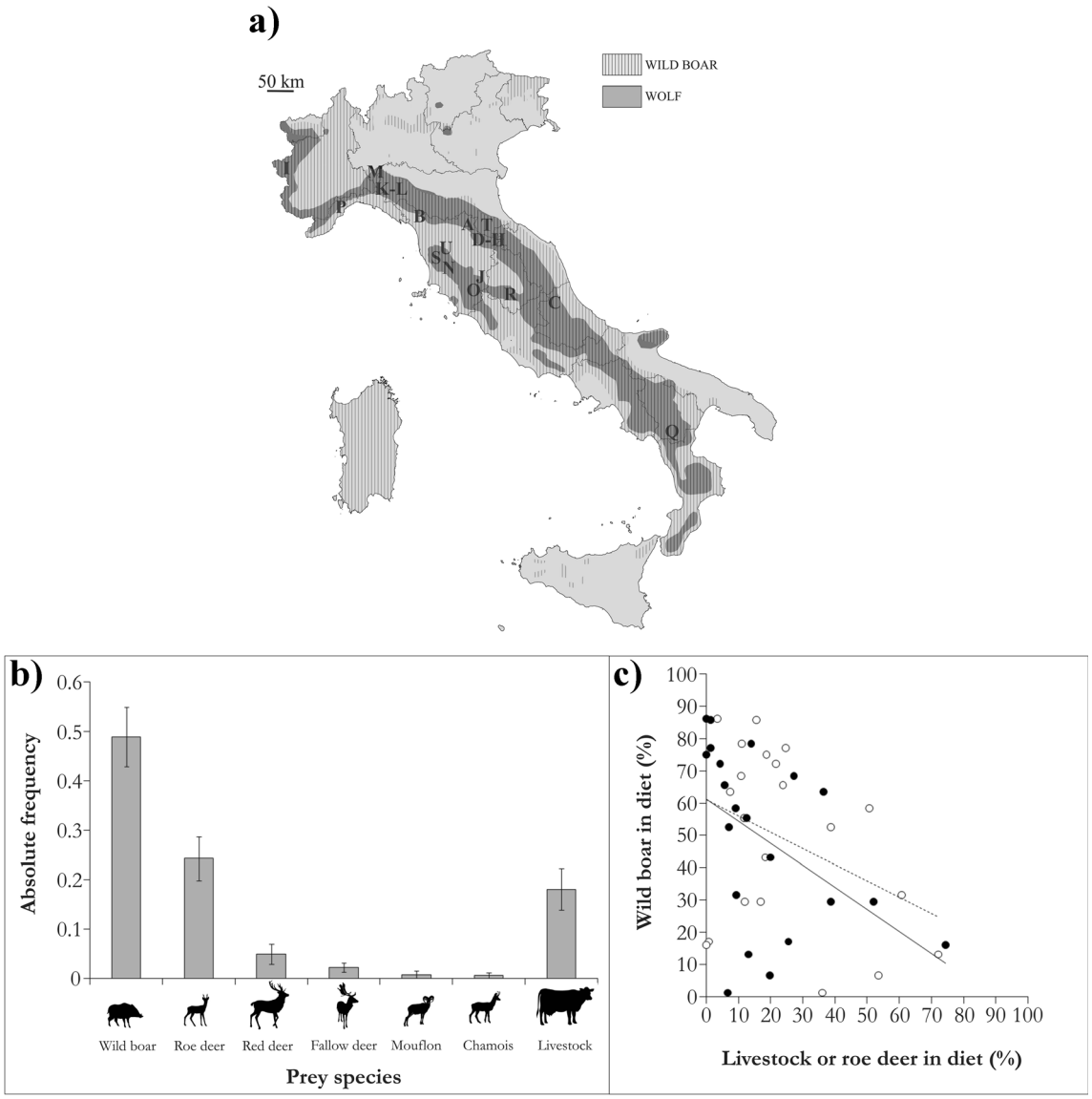

Fig. 1 **a** Distribution of study areas: *A* Mattioli et al. 1995; *B* Ciucci et al. 1996; *C* Patalano 2003; *D–H* Mattioli et al. 2004; *I* Gazzola et al. 2005; *J* Bargagli 2006; *K–L* Milanesi et al. 2012; *M* Meriggi et al. 2015; *N* Mori unpublished 2010–2015; *O* Mori unpublished 2013; *P* Brielli 2011; *Q* Borrelli 2010; *R* Vercillo and Ragni 2012; *S* Benatti 2015; *T* Lovari et al. 1995; *U* Boitani and Ciucci 1996. Distribution map of wolf and wild boar are taken from Lovari and Riga (2016) **b** absolute frequency of ungulate prey in the diet of the wolf and **c** absolute frequency of occurrence of wild boar in the diet of the wolf in relation to abs. frequency of occurrence of livestock (*empty circles*, *dotted line*) and roe deer (*black circles*, *solid line*)

and snow leopards: Lovari et al. 2013). For the wolf, Newsome et al. (2016, Appendix S5) concluded that the season is not a significant source of bias in assessment of diet.

We collated data on (*i*) absolute frequency of wild boar in the diet of wolves (i.e. number of scats with occurrence of wild boar/number of analysed scats, to avoid the interdependence bias of relative frequencies, see also Meriggi and Lovari 1996) and (*ii*) number of potential meso-large prey (i.e. ungulates: wild boar, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, fallow deer *Dama dama*, both species of chamois *Rupicapra rupicapra* and *Rupicapra pyrenaica*, mouflon *Ovis aries*, small livestock: sheep/goat, large livestock: cattle/equid). Mean absolute frequencies of each ungulate species were calculated across study areas (n = 21, from 16 sources). In 10 out of 21 study areas, the general category livestock' has been used. In turn, we calculated the absolute frequency of livestock, pooling together data relevant to single species, when available.

We used general linear models to assess relationships between the absolute frequency of wild boar in the diet of wolves (response variable) and the composition of the assembly of potential prey (i.e. the number of species), as well as the frequency of occurrence of other prey in diet (predictor variables). We detected collinearity between frequencies of occurrence of red deer and chamois in the wolf diet (correlation coefficient: r = 0.78); in turn, we considered the frequency of red deer only, because this prey species was comparatively more important for the wolf (see Fig. 1). Model selection was conducted through the 'MuMIn' package (Bartòn 2012) of the R software, fitting all possible models (n = 26). We used the Akaike's Information Criterion corrected for small sample sizes (AIC_c). Models were selected for inference if they had $\Delta AIC_c \leq 2$ units (Burnham and Anderson 1998) and if their AIC_c was lower than that of any simpler, nested alternative.

Results and discussion

The wild boar was the staple of the wolf diet (abs. frequency, mean ± standard error: 0.49 ± 0.06, occurring in all the studies), followed by roe deer (0.24 ± 0.04, found in 95.2% studies) and livestock (0.18 ± 0.04, found in 90.6% studies) (Fig. 1). Other ungulates were never the main prey of the wolf, but for the red deer in the upper Susa Valley (Gazzola et al. 2005), where wild boar presence was negligible (Gazzola et al. 2007). Fallow deer was reported as a prey in 42.9% studies, red deer in 33.3%, whereas both mouflon and chamois occurred in 9.5% studies each. Only the best model was retained for inference, including the effects of frequencies of roe deer, livestock and red deer (K = 5, log-likelihood = −87.500, AICc = 189.0, ΔAICc = 0.000, weight = 1.000). Thus, in contrast to our prediction, models did not support any effect of the number of potential ungulate prey species on the absolute frequency of wild boar in the wolf diet, but occurrence of livestock, roe deer and, to a lesser extent, that of red deer decreased with increasing absolute frequency of wild boar in diet (Fig. 1; Table 1).

Since the 1970s, land use changes (e.g. urbanisation and countryside abandonment by humans), the establishment of new protected areas, the implementation of national and international laws regulating hunting, as well as translocations of wildlife, have enhanced the numerical increase and range expansion of herbivore species in most of Europe (Acevedo and Cassinello 2009; Carnevali et al. 2009). Differently from roe deer, the wild boar is gregarious and noisy while moving, making itself easily detectable because of grunts, pungent smell and squeals (Cahill et al. 2003; Massei et al. 2014). In Europe, in the last few decades, the wild boar has been facing a sharp increase in numbers and distribution range (Massei et al. 2014), raising management concerns (Barrios-Garcia and Ballari 2012). Intensive hunting pressure is known to alter the spatial behaviour and social grouping of this ungulate (Maillard and Fournier 1995; Keuling et al. 2008), increasing its clumped distribution within wooded and protected areas (Tolon et al. 2009; Scillitani et al. 2010). Furthermore, postnatal body growth occurs more slowly in wild boar (Gaillard et al. 1992; Ježek et al. 2011) with respect to roe deer (Portier et al. 2000), the second most popular prey species for the wolf in the study areas covered by our review (Fig. 1). Most wild boar groups include a high number of juveniles, i.e. subadult individuals and piglets (e.g. Dardaillon 1988; Fernàndez-Llario et al. 1996), which fall well within the optimal prey size for the wolf (Gazzola et al. 2005).

Fallow deer (Gilbert 1968) and mouflons (Bon et al. 1990; Le Pendu et al. 1995) also live in medium-large sized groups, even where hunting pressure occurs (Svensson 2012), but these species, allochthonous in Europe, were much less common than wild boar in the areas of our review (i.e. always <5% in absolute presence for mouflon, up to 6% for fallow deer Carnevali et al. 2009; Benatti 2015). Several methodological flaws are inherent to most food habit studies, e.g. relating scat content to consumed prey and prey availability (Putman 1984), in turn even more so to reviews which have to rely on results obtained by other researchers. The wild boar is a prey twice as abundant as the roe deer (the second prey) in the

Table 1 Variables influencing the absolute frequency of occurrence of wild boar in the diet of the wolf in Italy estimated through general linear models; summary of the selected model (Multiple r^2 = 0.663; Adjusted r^2 = 0.604)

Predictor	*B*	s.e.	*p*
Intercept	94.522	8.835	<0.001
Livestock	−1.087	0.221	<0.001
Roe deer	−0.873	0.205	<0.001

wolf diet (Fig. 1). Therefore, even allowing for some approximation, we suggest that the wild boar makes an ideal prey species for the wolf.

Wild boar are often subjected to control operations to reduce strongly their density (e.g. Barrios-Garcia and Ballari 2012; Massei et al. 2014). One may speculate that a heavy artificial reduction of their local numbers, i.e. more than 50–70% over large areas (as several regional authorities have advocated recently through the media, in Italy), would deprive the wolf of its main prey species, thus intensifying predation on roe deer, a valued game animal, and livestock, in turn exacerbating the human-wolf conflict. Preventive actions to limit damage to agriculture and to livestock (e.g. appropriate fences, trained shepherd dogs, pragmatic legislation on wolf management), as well as different intensities of control of wild boar numbers in relation to ecological/agricultural vocation of areas, may be alternative/complementary measures to reduce human-wildlife conflicts.

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