Original Research Article

# Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes

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## A R T I C L E   I N F O

## A B S T R A C T

In ecologically pristine ecosystems, top-down effects of apex predators play a fundamental role in shaping trophic cascades and structuring ecosystems, but in human-modified landscapes anthropogenic effects may markedly alter the ecological role of predators. In particular, human-provisioned food subsidies represent a serious concern for the conservation of apex predators, even though little empirical attention has been given to this aspect in assessing conservation outcomes. To assess the extent to which anthropogenic food subsidies affected feeding ecology of a protected wolf (*Canis lupus*) population in a human-modified landscape, we integrated scat-analysis (n = 1141 from 4 packs; Jan 2005–Mar 2009) and winter field inspections of Global Positioning System telemetry re-locations (n = 595 clusters and 96 single locations from 5 wolves in 5 packs and 3 floaters; 2008–2011) of wolves living in a historical national park of central Italy hosting both wild prey and livestock at high densities. We revealed that livestock dominated the wolf diet (mean biomass = 63.3 ± 14.2% SD), secondarily supplemented by wild prey (36.7 ± 5.3%, mostly wild boar [*Sus scrofa*], roe deer [*Capreolus capreolus*], and red deer [*Cervus elaphus*]). During winter, we revealed a higher propensity of wolves to scavenge (72.5%; n = 91 feeding events) rather than killing prey, and feeding behavior was affected by prey type (i.e., domestic vs wild ungulates) as the large majority of scavenged carrions (75.8%) were livestock carcasses abandoned on the ground that died for causes different from predation. Feeding behavior of wolves was not affected by social affiliation (i.e., pack members vs solitary wolves), indicating that pack members, even if aided by cooperative hunting, were equally likely than solitary wolves to scavenge rather than killing prey; yet, 27.5% of winter feeding events involved predation, exclusively targeted to wild prey. Our findings indicate that large livestock carrion subsidies may strongly depress predatory behavior in wolves, despite the occurrence of an abundant wild prey community, and have relevant ecological, evolutionary and management implications. Reliance on human-provided livestock carrion subsidies likely alters the ecological role of wolves by reducing their top-down cascading effects on the ecosystem, and this has relevant implications for the conservation of wolves and other apex predators in national parks. Accordingly, we call for more strict regulations to govern livestock management and practices and argue that, at least in national parks, conservation goals of apex predators need to explicitly consider their ecological role.

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## 1. Introduction

Top-down effects of apex predators through trophic cascades are increasingly recognized as having a major role in regulating ecosystem structure and functioning through direct (density-mediated) and indirect (behaviourally-mediated) impacts on both herbivores and mesopredators (Estes et al., 2011; Ripple et al., 2014; Newsome and Ripple, 2015a). Concurrently, bottom-up factors such as habitat characteristics and food availability can also affect trophic dynamics, by acting in synergy with apex predators and mesopredators relationships (Ritchie and Johnson, 2009). Humans can alter the potential for trophic cascades by directly or indirectly impacting apex predators, mesopredators and their prey due to a wide range of anthropogenic factors in human-modified landscapes (Dorresteijn et al., 2015; Newsome and Ripple, 2015a). Humans can interfere with top-down effects of apex predators in prey populations by harvesting (Barnosky et al., 2004), by altering the perception of predation risk in anthropogenic landscapes by both predators and prey (Ordiz et al., 2013; Lodberg-Holm et al., 2019), or by affecting food resources for prey, mesopredators and apex predators (i.e., anthropogenic bottom-up effects; Kuijper et al., 2016). In particular, human-provided food subsidies to apex predators, including easily accessible livestock, may result in behavioral and population-level effects that can potentially affect trophic cascades and impair ecosystem functioning (Kuijper et al., 2016).

Most apex predators are also facultative scavengers, promptly consuming carrions when available (DeVault et al., 2003; Selva et al., 2005; Wilson and Wolkovich, 2011). Scavenging plays a significant role in structuring food webs, as it represents an energy transfer among trophic levels with no changes on the demography of the consumed species or energy expenditure by the predator to chase and kill its prey (Wilson and Wolkovich, 2011). Availability of carrion basically depends on the cause and location of animal mortality, and facultative scavengers often rely on deaths due to disease, malnutrition, and accidents as well as animals killed by other predators (DeVault et al., 2003). In human-modified landscapes, activities such as intensive farming (Ripple et al., 2013) or game hunting (Wilmers et al., 2003) can expectedly increase carrion supply for facultative scavengers, thereby reinforcing other forms of food subsidies to apex predators.

Among apex predators, wolves (*Canis lupus*) are well known to be opportunistic carnivores and facultative scavengers (Mech and Boitani, 2003), whose feeding ecology has been extensively investigated throughout its range (Peterson and Ciucci, 2003; Newsome et al., 2016). Several studies highlighted the plasticity of wolves in using anthropogenic food sources such as garbage and livestock in human-modified landscapes, especially when the latter is not properly defended (Salvador and Abad, 1987; Meriggi et al., 1991; Vos, 2000; Hosseini-Zavarei et al., 2013). Indeed, human-provided food subsidies may even represent the main food source for wolves living in areas with low availability of wild prey (e.g., Boitani, 1982; Ciucci et al., 1997; Hovens and Tungalaktuja, 2005; Tourani et al., 2014). Reviews at the continental and global scales, however, show that wolves tend to prefer wild over domestic ungulates where both are available (Zlatanova et al., 2014; Newsome et al., 2016). Accordingly, the restoration of wild ungulate communities, and the protection of livestock, have been viewed as an effective strategy to support wolf recovery and conservation in many European countries, also aimed at reducing wolf-human conflicts (Imbert et al., 2016). Nevertheless, wolves and other apex predators may be attracted by livestock and other anthropogenic food subsidies not only where wild prey are scarce but also due to their greater energetic profitability compared to wild ungulates (Newsome et al., 2015). As a consequence, wolf depredation levels may reflect not only the scarcity of wild prey populations but also the accessibility to livestock, determined by prevailing husbandry and surveillance practices (Newsome et al., 2016). In addition, wealthy and high-density wild prey communities will tend to support higher wolf density and productivity (Baker et al., 2008), therefore facilitating increased depredation levels if livestock is not properly attended (Treves et al., 2004). Accordingly, conservation efforts aimed at reducing wolf depredations, and more in general at enhancing the ecological role of wolves, should focus not only on re-establishing wild prey communities but also on reducing access to anthropogenic food subsidies, including livestock (Newsome et al., 2017). In this context, it is important to recognize that especially large livestock (i.e., cattle, horses) carrion, if not promptly removed from the open, may provide large amounts of high-quality and profitable food to wolves, often quite predictable in space and time where livestock farming is regularly conducted (Ciucci et al., 2018). Not only consumption of livestock carrions by wolves can increase depredations levels but, similarly to other human-provided food subsidies, it may also markedly alter individual and population aspects of wolf behavior and ecology, hampering their potential to shape cascading effects through the ecosystem (Kuijper et al., 2016; Newsome et al., 2017). Enhancing our knowledge on the use of anthropogenic food subsidies by wolves is therefore critical to better understand the effects of food subsidies on predators, their communities and ecosystems (Oro et al., 2013; Newsome et al., 2015; Kuijper et al., 2016). Additionally, this could be beneficial to inform conflict management, as well as and the current discussion on conservation strategies of apex predators at the global scale (Chapron et al., 2014; Gilroy et al., 2015; Gompper et al., 2015; Lòpez-Bao et al., 2015; Newsome and Ripple, 2015b).

To investigate the dependency by wolves on anthropogenic food subsidies in a human-modified landscape, we studied wolf feeding ecology in the Abruzzo, Lazio and Molise National Park (PNALM), a protected area in central Italy historically repatriated with a rich and diversified community of wild ungulates to reinforce wolf conservation. Among the few critical strongholds of Italian wolves when they were on the brink of extinction in the early 70s (Zimen and Boitani, 1975), the PNALM pioneered wolf conservation through conflict mitigation measures, closure of garbage dumps, and the reintroduction of roe (*Careplus capreolus*) and red (*Cervus elaphus*) deer (Tassi, 1976; Boscagli, 1985). Currently, wolves occur at high densities (i.e., 5 wolves/100 km$^2$) in the park and adopt habitat-mediated spatio-temporal patterns complementary to human activity to enhance their survival and fitness (Mancinelli et al., 2018, 2019). Livestock grazing is allowed in the PNALM, as provisioned by the Italian National Law on protected areas (LN 394/91; http://www.parks.it/federparchi/leggi/394.html), and this dual

mandate (i.e., wolf conservation and livestock grazing) makes the PNALM emblematic of potentially conflicting management goals in protected areas in human-modified landscapes.

Despite the relevant ecological and social changes that have occurred in the PNALM since historical conservation efforts to recover wolves and their wild prey populations, surprisingly only one study has been conducted on the feeding ecology of wolves about 10 years after the first roe and red deer reintroduction efforts (Patalano and Lovari, 1993). In those conditions, when wild ungulate populations were still relatively small and patchily distributed, almost equal amounts of domestic and wild ungulates constituted the bulk of the wolf diet (Patalano and Lovari, 1993). In our study, we combined scat-analysis and winter field inspections of Global Positioning System (GPS) locations from collared wolves to investigate wolf feeding ecology and behaviour in the PNALM. In particular, our aims were 1) to assess the extent to which wolf feeding ecology was affected by anthropogenic food subsidies, accounting for inter-pack and seasonal variation, in an area where wild ungulates had been historically repopulated, and 2) to determine the relative importance of predation vs scavenging by wolves, accounting for both prey type (i.e., wild vs domestic ungulates) and social affiliation, contrasting pack members with floaters (i.e., nomadic solitary individuals); specifically, due to cooperative hunting in wolf packs as a factor facilitating predation (Mech and Peterson, 2003), we predicted that scavenging would be more frequent in floaters compared to pack members (2.a), and that pack members, relative to floaters, would more frequently kill wild compared to domestic prey (2.b). Beyond documenting the feeding ecology of a protected wolf population, our findings have relevant implications for the role that national parks have for the conservation of apex predators in human-modified landscapes.

## 2. Materials and methods

### 2.1. Study area

Our study area was centered in the PNALM, including the park and its external buffer zone (1294 km$^2$), located in the central Apennines (Italy; Fig. 1). The area is typically mountainous, with elevations ranging from 400 to 2285 m.

Vegetation types are dominated at higher altitudes by pure stands of beech (*Fagus sylvatica*) forests and, at lower altitudes, by mixed forests where other species (*Quercus* spp., *Acer* spp.) predominate. Above 1800 m, the beech forests give way to alpine grasslands, whereas valley bottoms are mostly covered by abandoned and seasonally cultivated fields near human settlements. Mean monthly temperatures range from 2 °C in January to 20 °C in July, with rainfall most frequent in spring and fall and snow cover generally extending from mid-December to March (Piovesan et al., 2003). Average human density is 14.6 inhabitants/km$^2$, though most of the population is clustered in few, small villages (Ciucci et al., 2015). The park, established in 1923, is the oldest national park in Italy and represented one of the few strongholds where wolf survived during their historical minimum in Italy (Zimen and Boitani, 1975). During our study, at least 8 wolf packs overlapped portions of our study area, each comprising 2−9 wolves ($\bar{x} \pm SD = 5.3 \pm 2.8$ wolves/pack), with a relatively high density (>5 wolves/100 km$^2$) and a tight territorial mosaic, likely consistent with saturation levels (Mancinelli et al., 2018). Apennine brown bears (*Ursus arctos marsicanus*) are also present in the area at a density of about 40 bears/1000 km$^2$ (Ciucci et al., 2015). Free-ranging dogs may be occasionally present especially around villages, either in the form of working dogs or owned free-ranging dogs. The PNALM features a rich and diversified community of wild ungulates, comprising wild boar (*Sus scrofa*), red deer, Apennine chamois
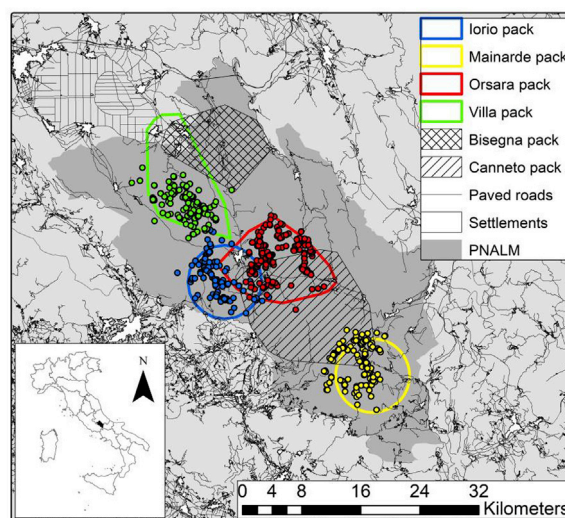


**Fig. 1.** Location of the Abruzzo Lazio and Molise National Park in Italy (inlet) and distribution of the 1141 wolf scats (dots) analyzed to quantify diet composition in 4 wolf packs (colored in the figure), whose territories are depicted using the 100% minimum convex polygon based on GPS telemetry, or approximated by 5 km-buffers centered at home sites and comprising most of snow-tracking trajectories (Iorio and Mainarde packs).

(*Rupicapra pyrenaica ornata*) and roe deer. Red deer have been reintroduced during 1972–1987, and since then they have been steadily increasing in numbers and range, locally reaching densities up to >14/km$^2$ in 2010 (Lovari et al., 2014). However, red deer densities are heterogeneously distributed across the PNALM, as shown by spring estimates based on pellet count within the territories of the four wolf packs we studied (see below), ranging from 0.6 to 4.2 red deer/km$^2$ in the Iorio and Orsara packs, respectively (Grottoli and Ciucci, 2008). Wild boar also occurred at a relatively high density, though unknown, and were widely distributed across the study area, while roe deer were less abundant and distributed at lower altitudes (R. Latini, pers. comm.). Apennine chamois had a clustered distribution at higher elevations, with a minimum of 500 counted in 2009 (http://www.camoscioappenninico.it), but showing negative trends possibly due to competition with the increasing red deer population (Lovari et al., 2014; Ferretti et al., 2015).

Multiple uses are predominant in the park, and livestock husbandry, forestry, and tourism are important economic activities (Ciucci et al., 2014). In 2009, an average of 67 livestock farms/100 km$^2$ in the study area raised about 28,664 livestock heads, with highest densities of sheep (*Ovis aries*; 1359 sheep/100 km$^2$), followed by goats (*Capra hircus*; 351 goats/100 km$^2$), cattle (*Bos taurus*; 344 cattle/100 km$^2$), and horses (*Equus caballus*; 161 horses/100 km$^2$) (Galluzzi, 2014). Although it is broadly intended that livestock grazing within national parks should be compatible with the protection of landscapes and ecosystems, neither the National Law on protected areas (LN 394/91) nor the PNALM management plan make explicit reference to how livestock grazing should be managed. Whereas sheep and goats are grazed according to traditional husbandry methods (i.e., active surveillance by shepherd and livestock guardian dogs, and night-enclosure in predator-proof shelters and corrals), cattle and horses are generally left free-ranging, mostly during the summer but locally also during the winter. Births of horses and cattle are unattended by farmers and peak in April–May and May–June, respectively. Livestock carcasses, including animals dead for causes different from predation are often abandoned on the ground as the local health authority exempts farmers from their removal due to the remoteness of the sites and inaccessibility of mountainous terrain (Ciucci et al., 2014).

### 2.2. Field methods

#### 2.2.1. Scat collection

From January 2005 to March 2009 we systematically collected non-weathered and collectable wolf scats year-round in four of the eight packs, sampled within the study area to be representative of different ecological and anthropogenic conditions (Iorio, Mainarde, Orsara and Villa packs; Fig. 1). Complementary to systematically searching wolf scats along trails and routes used by wolves across each pack territory, we also collected scats along snow-trajectories or at locations of GPS-collared wolves to enhance sampling efficiency (Ciucci et al., 2018). For the scope of the analysis, we reduced autocorrelation among collected scats using a 2-week time interval between successive collections, thereby decreasing the chance of sampling scats produced by the same feeding event; we also averaged scats of the same age and content if collected at the same site (i.e., along the same snow-trajectory, the same kill/scavenging site or scent-post; Ciucci et al., 2018).

Wolf pack territories were delineated by means of GPS-telemetry (Mancinelli et al., 2018), snow-tracking, wolf-howling, and non-invasive genetic sampling (Boggiano et al., 2013). We estimated the time since deposition of collected scats based on the last sampling effort, the scat's appearance, exposure of the collection site and weather conditions (Ciucci et al., 1996) or, for GPS-collared wolves and snow-tracking sessions, according to the date the wolves frequented the site. Scats collected along systematic routes were discriminated from those of dogs based on a conservative, multi-criteria approach (i.e., size and content of scats, their location, previous knowledge of scent-marking sites, presence of other signs and the seasonal occurrence of dogs in the area; Ciucci et al., 1996). As presence of free-ranging dogs increased during summer, we conservatively discarded many scats including a number of probable wolf scats. This approach drastically decreased the chances of including dog scats in the sample, as supported by a random subsample of 90 scats collected using these criteria, all subsequently assigned to wolves based on molecular data (Boggiano et al., 2013).

#### 2.2.2. GPS cluster checks

From December through March, from 2008–2009 to 2010–2011, we searched for evidence of winter feeding activity by field surveying GPS locations of adult wolves, previously fitted with GPS collars within a broader ecological study (Mancinelli et al., 2018, 2019), including 5 pack members belonging to 5 different packs and 3 floaters (i.e., solitary and nomadic individuals; Fuller et al., 2003) (Supplementary Material Table S1). To identify wolf feeding sites we programmed GPS collars to obtain one location every 0.5–1 h; to extend expected battery life, we limited this acquisition rate to one 10-day period at the beginning of each month during winter, alternating it to a reduced 6 fix/day acquisition rate during the rest of the month and the year (Mancinelli et al., 2018). In the period of high acquisition rate, aided by the presence of the snow, we attempted to explore all clusters of wolf locations compatible with feeding events. To this aim, we plotted (ArcGIS, version 10.2.2), on a daily basis, all locations acquired during the previous 24 h and, based on the assumption that wolves spend at least 30 min on medium-large prey, we defined a cluster as two or more successive locations with a maximum distance between them ≤ 200 m (Sand et al., 2005). To confirm social affiliation of collared wolves and to search for additional indication of feeding activity, in addition to GPS clusters and aided by snow cover we also occasionally visited single GPS locations acquired during the previous 24-hr period (Sand et al., 2005). To minimize disturbance, we did not visit feeding clusters until at least 2

days after the last GPS location on the site and we avoided surveying clusters previously identified as resting or refuges sites. Upon field surveys, we intensively searched for prey remains or foraging indications within a 50-m radius around all clustered or single locations. If prey remains were found, we then classified the site as a kill-site, if evidence of predation was available (e.g., chase in the snow, trampled or broken vegetation, arteriosus blood on rocks and stumps, injuries on prey carcasses corresponding to subcutaneous hematoma; Demma et al., 2007, Sand et al., 2005, 2008); otherwise, if none of the above evidence was detected and the age of the carcass was estimated to be older than the date the wolves visited the site, we classified the site as a scavenging site. In all cases, we identified the prey or carrion species and, based on bone remains, estimated two broad age classes (i.e., juveniles, <8−10 months, and adults, >18 months). To avoid misclassifying older kills revisited by wolves as scavenging sites, we did not consider heavily consumed and disarticulated carcasses estimated to be older than about one week. In addition, we did not return to already surveyed feeding sites if wolves re-visited them, assuming successive visits represented repeated use of the same carcass (Webb et al., 2008).

## 2.3. Analyses

### 2.3.1. Diet quantification

We used traditional lab procedures (Ciucci et al., 1996) to process scats, and the point-frame method (Ciucci et al., 2004) to identify undigested prey remains and quantify their occurrence. Mammal hairs in each scat were recognized by microscopic examination of the cuticular pattern and the medulla using a reference manual (Teerink, 1991) and through comparison to hairs from mammals collected in the study area. Wild and domestic ungulate species were further classified as juveniles (≤4−5 months) and adults (>4−5 months) on the basis of microscopic hair features detectable from birth to the first autumn molt (Ciucci et al., 1996). Accuracy of observers (n = 3) in identifying mammal hairs was preliminarily evaluated through a blind test on a sample of 120 hairs of mammal species collected from local populations. Observers were evaluated both at the species and age levels, with an average reported accuracy of 99.1% (±0.9) and 98.5% (±0.4) for species and age class identification, respectively.

To quantify the scat content we used the percentage of occurrence based on the number of equivalents (i.e., the relative volumetric proportions of a prey species in a scat summed across all scats containing that species; Floyd et al., 1978). Equivalents thus return the number of scats expected if each was composed solely by that particular prey species. For the aim of the analysis, using the number of equivalents, instead of single occurrences, further reduces autocorrelation among collected scats. To correct frequency data into ingested biomass (i.e., accounting for the bias due to variation in prey size; Floyd et al., 1978), we used Weaver's (1993) regression model by using weights of prey species from the literature and accounting for differences among sexes (limited to adults) and age classes (Supplementary TextS1). Non-food items (i.e., plant material, soil and rocks), as well as food-items with a seasonal occurrence per pack < 3% were excluded from further analyses (Ciucci et al., 1996).

### 2.3.2. Statistical modelling

We used log-linear models to assess spatial (wolf pack) and temporal (season) effects on diet composition based on scat data (Ciucci et al., 2018). Log-linear models are one of the specialized cases of Generalized Linear Models (GLMs) for Poisson-distributed data and represent a valuable tool to analyze multi-way contingency tables (Agresti, 1990). We limited log-linear modelling to scats collected from October 2006 to September 2008 due to an insufficient sample size obtained in other seasons and years (Table S2). Because we could not account for an annual effect due to a limited sample size, we pooled data across years and, similarly, we aggregated livestock species in two broad categories, large livestock (cattle and horses) and sheep/goats. For the scope of modelling, we distinguished two seasons, summer (Apr−Sep) and winter (Oct−Mar), to account for differences in the annual life cycle of wolves and their wild prey, and an increased livestock availability during summer. Using the *stats* R package (R Core Team, 2019) with a log-link function, we applied log-linear modelling based on a 3-dimensional table (i.e., pack, season, and prey category), with the number of equivalents for each prey category as the response variable (Ciucci et al., 2018). To find the most parsimonious model based on the Akaike Information Criterion (AIC; Anderson and Burnham, 2002) we used the *AICcmodavg* R package (Mazerolle, 2019) following a stepwise procedure from the saturated to the main-effect model. Finally, we used the pseudo-$R^2$ estimate (Nagelkerke, 1991) to provide a measure of the goodness-of-fit of the best supported model. Based on GPS-cluster checking data, and using the same R packages above, we also applied GLMs using a logit-link and wolf ID as a random factor to assess if the likelihood of scavenging (0) vs predation (1) was affected by prey type (domestic vs wild), social affiliation (loner vs pack member), or both.

## 3. Results

### 3.1. Wolf diet based on scat analysis

We collected a total of 1232 wolf scats, of which 146 were averaged as considered non-independent contributing 55 scats to the final dataset, for a final sample size of 1141 scats for the analysis. Average annual sample size per pack was 73 ± 52 SD scats, and seasonal sample size averaged 43 ± 29 SD and 40 ± 26 SD scats per pack during summer and winter, respectively

(Table S2). Overall, we identified a total of 19 food categories in the whole scat sample, comprising 10 species of wild and 6 of domestic mammals, plus traces of birds, fruits, insects, plant material and garbage (Supplementary material; Table S3). Limited to food items, and based on the number of equivalents, ungulates were the most frequently consumed prey ($99 \pm 2\%$), comprising wild ($52 \pm 16\%$) and domestic ($48 \pm 12\%$) species. Although wild and domestic ungulates were consumed in similar proportions, the latter predominated in terms of biomass (Table 1).

Specifically, cattle and horses predominated the overall diet, followed by wild boar, roe deer and red deer in similar proportions (Table 1). Sheep and goats, even though frequently consumed, cumulatively contributed <10% of the biomass ingested, and Apennine chamois were only marginally consumed (Table 1). The global model was the most supported (Pseudo-$R^2 = 0.73$; see Table S4 for model selection) and, accounting for differences in sample size, it revealed that both wild ungulates and sheep/goats were less frequently consumed by wolves than cattle and horses (Table 2).

Diet composition varied markedly across packs (Fig. 2, Table S5) and, to a lesser extent, by seasons in some of the packs we studied (Table S6).

Compared to wolves of the Iorio pack, wolves of the Orsara and Villa packs were more likely to consume roe deer, red deer and wild boar rather than large livestock (Fig. 3, Table 2), the same being true for the Mainarde pack but limited to wild boar. In particular, compared to the Iorio pack, the odds of consuming red deer rather than large livestock were highest in the Orsara and the Villa packs (Table 2), where it contributed 26% and 6% of the biomass ingested, respectively (Fig. 2, Table S5). The odds of consuming wild boar were highest in the Mainarde and Villa packs (Table 2), where it contributed 21% and 17% of the biomass ingested, respectively (Fig. 2, Table S5), and, similarly, the odds of consuming roe deer were highest in the Villa and Orsara packs (Table 2), where it contributed 19% and 17%, respectively, of the biomass ingested. Compared to the Iorio pack, wolves in the Mainarde, Orsara and Villa packs also showed higher odds of consuming sheep/goats rather than large livestock (Table 2). In all these packs, however, cattle and horses still predominated (Mainarde and Villa packs) or contributed similarly to wild ungulates (Orsara pack) in terms of biomass (Fig. 2). Two- and three-way dietary interactions revealed no appreciable seasonal differences in diet composition (Table 2), with the sole exception of a greater summer consumption of roe deer in the Villa pack, where it represented the main wild ungulate prey, and of sheep/goats in the Orsara pack (Table S6).

Juveniles of both wild and domestic ungulates represented an important portion of the wolf diet during summer (Table S6), with piglets represented 58% of wild boar remains, fawns 43% of roe deer remains, and calves 52% of red deer remains (Supplementary material, Fig. S1).

### 3.2. GPS cluster checks

We identified 702 clusters out of 8314 GPS locations (1454 hourly locations and 6860 half-hourly locations) collected during the 10-day winter periods (Table S1). We inspected in the field a total of 595 (84.8%) clusters, that were constituted by a mean of 9.8 ($\pm$13.1 SD) GPS locations (range: 2−137). During the same period, we also field inspected 74 (5.6%) single GPS locations. In total, we found 95 feeding sites (87 within clusters and 8 at single locations), including 25 kill-sites, 66 scavenging sites, and 4 sites were wolves fed at illegal butchery discards (Fig. 3 and Supplementary material, Table S1).

Overall, we found 12 species of wild and domestic mammals being consumed by wolves (Table S7); except the hedgehog (*Erinaceous europaeus*), all were already identified in the scat remains. Excluding feeding at butchery discards, most feeding behavior by wolves (n = 91 feeding events) involved scavenging (72.5%), the large majority of which involving livestock carcasses (75.8%; mostly sheep and horses, followed by cattle and goats; Fig. 4).

As indicated by the best selected model, winter feeding behavior was essentially determined by prey type (Table 8), as wild ungulates, relative to domestic ones, had much higher chances of being predated rather than scavenged ($\beta = 4.27 \pm 1.01$SE, p < 0.001) by wolves. Accordingly, all winter kills (n = 25) involved wild prey, mostly red deer, followed by

**Table 1**
Consumption (%) of wild and domestic ungulates by four wolf packs in the Abruzzo, Lazio and Molise National Park (PNALM), central Italy, Jan 2006−Mar 2009, reported at the annual and seasonal (summer vs winter) scale (sample size refers to the number of equivalents, see text). Consumption of prey species are reported according to percentage of occurrence (number of equivalents) and biomass ingested (Weaver, 1993), averaged across packs, seasons and years, and sorted by annual biomass of main categories.

| | Annual (n = 1029) | | Summer (n = 455) | | Winter (n = 574) | |
|---|---|---|---|---|---|---|
| | Frequency[a] | Biomass | Frequency[a] | Biomass | Frequency[a] | Biomass |
| **Domestic ungulates** | 48.3 ($\pm$6.6) | 63.3 ($\pm$14.2) | 51.2 ($\pm$7.9) | 66.3 ($\pm$15.7) | 45.5 ($\pm$4.7) | 60.3 ($\pm$12.9) |
| Cattle (*Bos taurus*) | 17.2 ($\pm$9.4) | 31.2 ($\pm$14.7) | 22.4 ($\pm$15.4) | 36.0 ($\pm$17.5) | 14.9 ($\pm$11.8) | 27.5 ($\pm$18.5) |
| Horse (*Equus callabus*) | 14.3 ($\pm$7.5) | 23.8 ($\pm$13.0) | 16.2 ($\pm$13.7) | 22.8 ($\pm$17.0) | 15.8 ($\pm$9.1) | 24.6 ($\pm$9.9) |
| Sheep (*Ovies aries*) | 7.5 ($\pm$3.5) | 4.7 ($\pm$2.4) | 6.6 ($\pm$1.7) | 4.4 ($\pm$2.0) | 8.8 ($\pm$4.9) | 5.0 ($\pm$3.0) |
| Goat (*Capra hircus*) | 5.7 ($\pm$1.0) | 3.1 ($\pm$0.6) | 6.0 ($\pm$3.2) | 3.2 ($\pm$1.2) | 6.0 ($\pm$1.7) | 3.9 ($\pm$0.8) |
| **Wild ungulates** | 51.7 ($\pm$8.5) | 36.7 ($\pm$5.3) | 48.8 ($\pm$9.7) | 33.7 ($\pm$6.3) | 54.5 ($\pm$10.6) | 39.7 ($\pm$7.1) |
| Wild boar (*Sus scrofa*) | 19.2 ($\pm$11.1) | 13.0 ($\pm$8.1) | 12.5 ($\pm$5.5) | 7.9 ($\pm$5.2) | 27.1 ($\pm$16.3) | 18.1 ($\pm$13.6) |
| Roe deer (*Capreolus capreolus*) | 18.4 ($\pm$9.3) | 11.7 ($\pm$7.2) | 25.1 ($\pm$17.0) | 16.3 ($\pm$14.7) | 12.9 ($\pm$6.6) | 7.1 ($\pm$5.3) |
| Red deer (*Cervus elaphus*) | 9.9 ($\pm$8.4) | 10.7 ($\pm$9.9) | 9.7 ($\pm$7.1) | 8.7 ($\pm$7.3) | 11.2 ($\pm$9.9) | 12.8 ($\pm$13.4) |
| Apennine chamois (*Rupicapra pyrenaica ornata*) | 2.0 ($\pm$1.3) | 1.3 ($\pm$0.8) | 1.6 ($\pm$2.2) | 0.8 ($\pm$1.1) | 3.3 ($\pm$2.6) | 1.7 ($\pm$1.4) |

[a] Based on the number of equivalents.

**Table 2**

Model coefficients, standard errors and P-values including dietary and non-dietary effects as from the most supported log-linear model of prey consumption by wolves in the Abruzzo, Lazio and Molise National Park, central Apennines, Italy (Oct 2006–Sep 2008). See Table S5 for model structure and selection.

| Variable[a] | β | SD | P-value |
|---|---|---|---|
| Villa[b] | −1.06 | 0.23 | 0.0008 |
| Orsara[b] | −0.59 | 0.20 | 0.0031 |
| Mainarde[b] | −1.14 | 0.24 | 0.0003 |
| Winter[c] | −0.68 | 0.20 | 0.0011 |
| Roe deer[d] | −1.24 | 0.25 | 0.0001 |
| Wild boar[d] | −1.93 | 0.33 | 0.0001 |
| Red deer[d] | −2.15 | 0.37 | 0.0008 |
| Sheep/goats[d] | −1.19 | 0.24 | 0.0001 |
| Winter x Mainarde | 1.11 | 0.34 | 0.0012 |
| Winter x Orsara | 0.44 | 0.32 | 0.1675 |
| Winter x Villa | 0.68 | 0.35 | 0.0562 |
| Villa x Roe deer | 1.59 | 0.36 | 0.0001 |
| Villa x Wild boar | 1.80 | 0.45 | 0.0007 |
| Villa x Red deer | 1.92 | 0.48 | 0.0007 |
| Villa x Sheep/goats | 1.23 | 0.37 | 0.0012 |
| Orsara x Roe deer | 1.26 | 0.34 | 0.0002 |
| Orsara x Wild boar | 1.39 | 0.43 | 0.0013 |
| Orsara x Red deer | 1.88 | 0.44 | 0.0002 |
| Orsara x Sheep/goats | 0.26 | 0.39 | 0.5090 |
| Mainarde x Roe deer | 0.79 | 0.42 | 0.0648 |
| Mainarde x Wild boar | 1.48 | 0.48 | 0.0021 |
| Mainarde x Red deer | 0.67 | 0.62 | 0.2780 |
| Mainarde x Sheep/goats | 0.99 | 0.40 | 0.0143 |
| Winter x Roe deer | −0.53 | 0.50 | 0.3027 |
| Winter x Wild boar | 0.68 | 0.49 | 0.1686 |
| Winter x Red deer | −0.30 | 0.70 | 0.6697 |
| Winter x Sheep/goats | −0.42 | 0.48 | 0.3849 |
| Winter x Villa x Roe deer | −1.61 | 0.78 | 0.0407 |
| Winter x Villa x Wild boar | −0.29 | 0.63 | 0.6499 |
| Winter x Villa x Red deer | −1.54 | 0.98 | 0.1171 |
| Winter x Villa x Sheep/goats | 0.50 | 0.62 | 0.4286 |
| Winter x Orsara x Roe deer | −0.19 | 0.64 | 0.7625 |
| Winter x Orsara x Wild boar | 0.27 | 0.60 | 0.6534 |
| Winter x Orsara x Red deer | 0.17 | 0.80 | 0.8354 |
| Winter x Orsara x Sheep/goats | 1.44 | 0.62 | 0.0207 |
| Winter x Mainarde x Roe deer | 0.09 | 0.69 | 0.8965 |
| Winter x Mainarde x Wild boar | 0.29 | 0.63 | 0.6495 |
| Winter x Mainarde x Red deer | −0.36 | 1.01 | 0.7250 |
| Winter x Mainarde x Sheep/goats | −0.34 | 0.66 | 0.6077 |

[a] Non-dietary effects (e.g., Winter, Orsara, Winter x Villa) account for difference in sample size across sampling units.
[b] Reference = Iorio pack.
[c] Reference = summer.
[d] Reference = cattle/horses.

wild boar and roe deer (Table S7); wild boar kills (n = 7) comprised 85.7% of juveniles (6–12 months old), whereas fawns and calves represented 20% of both roe (n = 5) and red (n = 10) deer winter kills, respectively. Social affiliation did not affect feeding activity (Table S8), as scavenging predominated both in floaters and pack members (88.0% and 66.7%, respectively) and both scavenged livestock (72.7% and 75.0%, respectively) more frequently than wild prey carcasses (Fig. 5).

## 4. Discussion

The PNALM, a critical stronghold for wolves in Italy when they were most exposed to extinction risk (Zimen and Boitani, 1975), adopted since the 1970s farsighted conservation measures aimed to enhance the ecological conditions for wolves; these included the strict protection of the Apennine chamois and the reintroduction of the previously extirpated roe and red deer (Tassi, 1976). This, in addition to the hunter-assisted releases and successive expansion of wild boar throughout the region, facilitated the re-establishment of the rich and diversified wild prey community to which wolves are currently exposed. Accordingly, we confirmed that roe deer, wild boar and red deer are all actively predated by wolves in the PNALM. Nevertheless, beyond our expectations, we also revealed that livestock, and in particular carcasses of cattle and horses, largely affected wolves' feeding behavior and predominated their diet in terms of biomass.

The consumption of wild ungulates by wolves in the PNALM underscores a remarkable difference with the feeding ecology of the species documented in the central Apennines a few decades ago, when wolves essentially fed at garbage dumps and their only live prey were occasionally livestock (Macdonald et al., 1980; Boitani, 1982; Ciucci et al., 1997). However, the
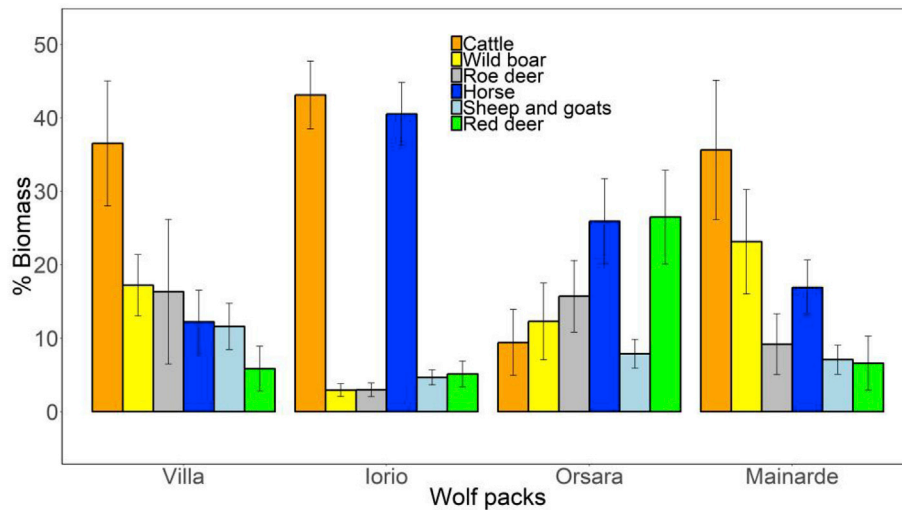
**Fig. 2.** Consumption of main prey categories by 4 wolf packs in the Abruzzo, Lazio and Molise National Park (central Apennines, Italy) based on scat analysis (2005–2007). Biomass is estimated from the number of equivalents according to Weaver's (1993) model. Data are pooled across years and results expressed as mean (±SD) percentages across each sampling unit (i.e., pack/year).

situation we reported for the PNALM did not substantially change with respect to the early 80s when domestic and wild ungulates were consumed by wolves in similar amounts (Patalano and Lovari, 1993), if not for the greater consumption of wild boar and roe deer that we revealed and possibly due to the recent increase in both ungulate species. This indicates that the increase in abundance of wild ungulates in the PNALM ecosystem since the early 80s did not translate into their expected preference over livestock by local wolf packs, nor into a marked reduction in wolf-livestock conflicts (see below). Preference for wild prey over livestock, associated to the natural recovery or reintroduction of wild prey populations, has been observed in wolf populations both in Italy and elsewhere in Europe (Meriggi and Lovari, 1996; Zlatanova et al., 2014; Newsome et al., 2016). In the PNALM, however, even though wild prey and livestock were consumed at comparable frequencies, livestock predominated in terms of biomass, ranging on average 44%–87% in the Orsara and Iorio packs, respectively, and exceeding 50% in three out of the 4 packs we studied. Nevertheless, the diversified wild ungulate community deeply shaped the food-habits of wolves in the PNALM, with wild boar, roe deer, and red deer contributing comparable amounts of biomass to the wolves' diet, even though with marked differences among packs. Although we could not contrast consumption by wolves of the different wild ungulate species with their relative abundance at the pack scale, it is likely that these differences affected prey selection patterns to some extent; this is suggested by the highest and lowest consumption of red deer in the Orsara and Iorio packs, respectively, whose territories hosted the highest and lowest red deer density, respectively, among the four packs we studied (see Study Area). However, other factors may possibly compound prey selection by wolves (e.g., pack size and composition, hunting traditions, habitat features; Mech and Peterson, 2003) to the extent that assessing selection patterns exclusively through indices of wild prey relative abundance could be overly simplistic and possibly misleading (Huggard, 1993); this is particularly true in our specific case, as scat analysis would have further confounded predation with scavenging, which largely dominated wolf feeding behavior. Additionally, we believe the frequent provision of large livestock carcasses would have likely confounded any quantitative inference of selection patterns on wild ungulates. In fact, wild boar, red deer and roe deer were consumed more in wolf packs where cattle and/or horse consumption was lower (Villa, Orsara and Mainarde packs), and a similar trend also held for sheep and goats. This suggests that large livestock consumption by wolves, most likely through scavenging, altered their predatory behavior reducing the necessity to kill wild ungulates. The chamois, likely due to its clustered distribution in areas rich of escape terrains, was consumed in negligible amounts by all wolf packs, as expected based on a Type-III functional response (Huggard, 1993).

We reported a remarkable consumption of juveniles of both wild and domestic ungulates by wolves in the PNALM during summer, a pattern largely documented elsewhere (Olsson et al., 1997; Mattioli et al., 2004). In line with previous reports both in Italy (e.g., Gazzola et al., 2005; Ciucci et al., 2018) and elsewhere in Europe (Nores et al., 2008), wild boar piglets, in particular, were an important component of the wolf's diet, likely due to their greater vulnerability compared to adults (Ciucci et al., 2018). Similarly, red deer calves and roe deer fawns represented during summer a consistent proportion of the occurrences of these prey species in the wolf's diet. Calves and fawns require minimal handling, and the risks of injury upon attack are negligible; thus, they are expected to maximize energy gain over handling time (Stephens and Krebs, 1986). In particular, cattle calves are largely available to wolves in the PNALM since the very first weeks of life as births are delivered without any control in free-ranging herds (Fico et al., 1993), at predictable locations often on pastures overlapping or in close proximity to wolf dens and rendezvous sites (P. Ciucci, unpublished data).
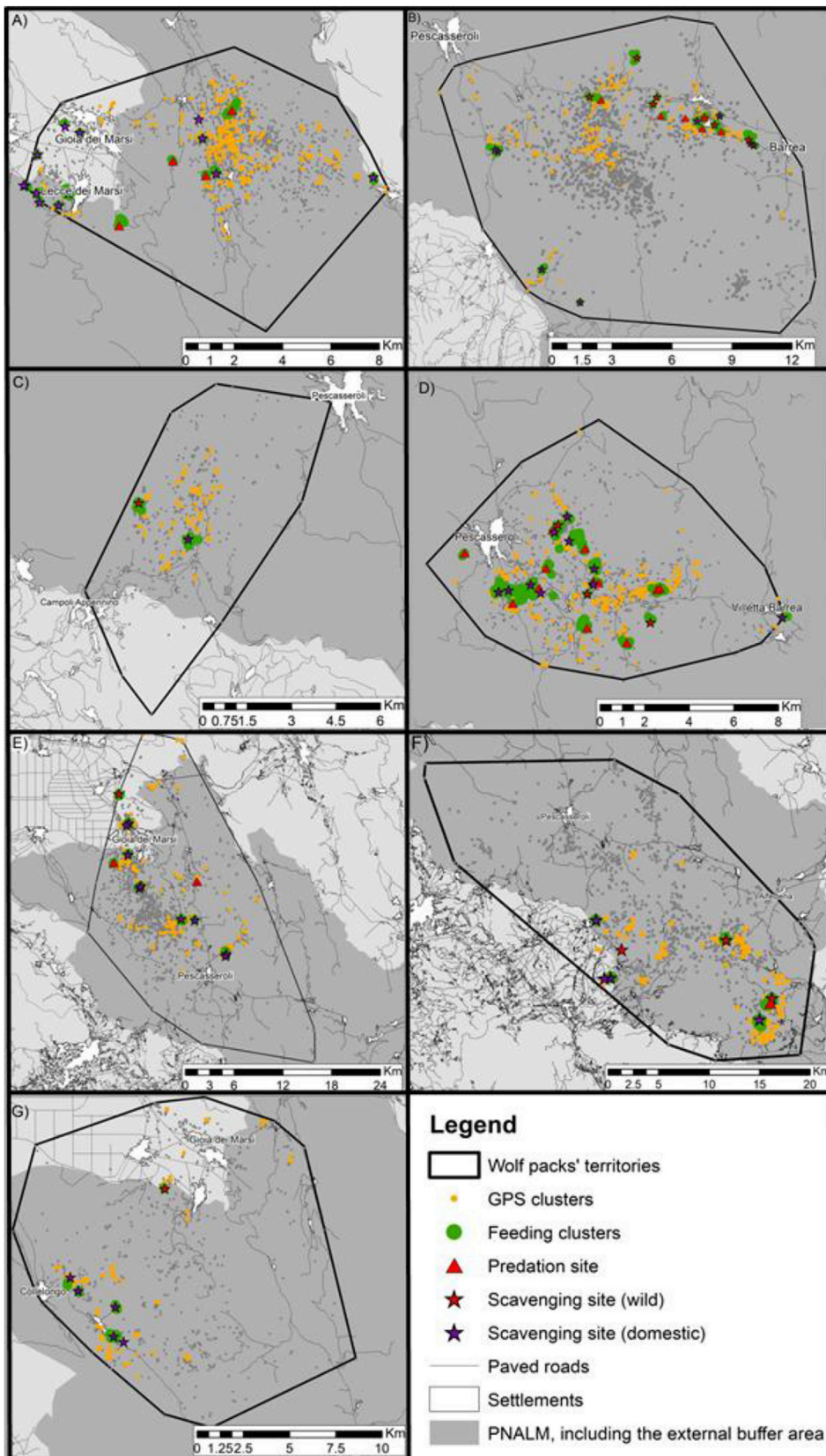
**Fig. 3.** Distribution of feeding sites (i.e., scavenging and predation sites) as determined by field investigation of clusters of Global Positioning System (GPS) locations of 7 adult wolves, including 4 pack members (A: Bisegna pack; B: Canneto pack; C: Iorio pack; D: Orsara pack) and 3 floaters (E: wolf F21; F: wolf F29; G: wolf M22) tracked during winter (Oct−Mar, 2008−2010) in the Abruzzo Lazio and Molise national park (see Fig. 1). In each panel, grey dots represent single GPS locations and thick outlines the wolf pack's territories (pack members) or the maximum area used (floaters), delineated through the Minimum Convex Polygon method (MCP; note that scale varies across panels). In panel C, the MCP delineates the maximum area used by wolf M27, as the limited tracking period (17 Nov 2009−4 Jan 2010) was insufficient to estimate the pack's territory.
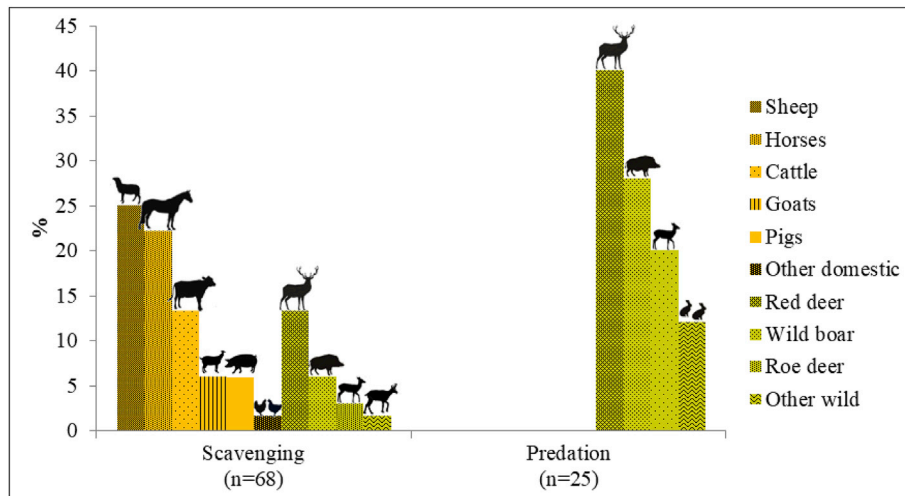
**Fig. 4.** Distribution of prey species by feeding behavior determined from field investigations of clustered and single Global Positioning System locations of 7 adult wolves tracked during winter (Oct–Mar) in the Abruzzo Lazio and Molise national park (2008–2010).
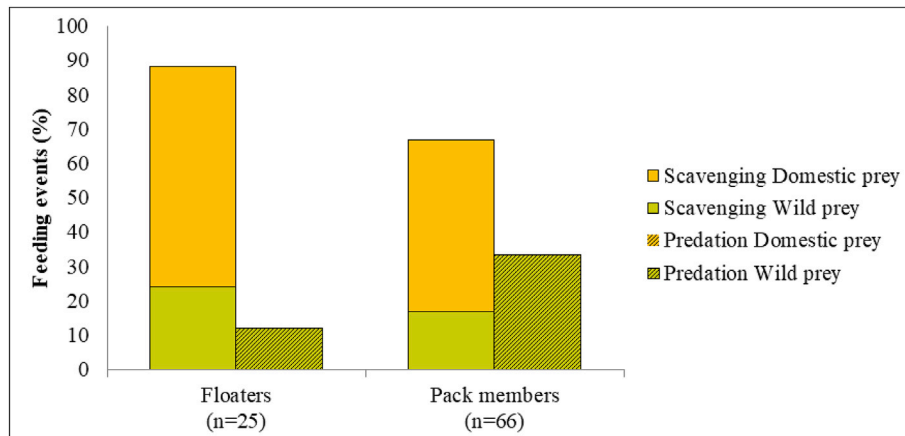


**Fig. 5.** Feeding behavior of wolves toward domestic and wild ungulates based on feeding sites (n = 91) detected through field investigations of clustered and single Global Positioning System locations of 7 adult wolves during winter (Oct–Mar) in the Abruzzo Lazio and Molise national park (2008–2010).

Several other studies in Italy reported an important use of livestock by wolves in different ecological settings (e.g., Meriggi et al., 1996; Capitani et al., 2004; Gazzola et al., 2005, 2008; Ciucci et al., 2018). Compared to single prey systems, where temporary fluctuations in the main prey may cause increased pressure on livestock (e.g., Salvador and Abad, 1987; Meriggi et al., 1996; Ciucci et al., 2018), multi-prey systems may present wolves with buffer species in seasons and years when the main prey is less accessible (Sidorovich et al., 2003; Mattioli et al., 2011; Meriggi et al., 2011, 2015), therefore potentially reducing predation by wolves on livestock (Meriggi and Lovari, 1996). Accordingly, the enrichment of wild prey communities would be expected to alleviate predation on livestock. Based on this rationale, reintroductions of cervids (i.e., red and roe deer) had been conducted decades ago in the PNALM to reduce wolf dependency on livestock (Tassi, 1976; Boscagli, 1985). However, our findings, in line with previous studies elsewhere in Italy (e.g., Capitani et al., 2004; Meriggi et al., 2015; Imbert et al., 2016), indicate this is not necessarily the case, as livestock availability and accessibility to wolves, including carcass subsidies, appears to be the main determinant of wolf dependency on livestock, also if abundant and diversified wild prey communities are available (Salvador and Abad, 1987; Sidorovich et al., 2003; Gazzola et al., 2005; Migli et al., 2005). In rare situations where wolves in human-modified landscape thrive almost entirely on a wild ungulate community (e.g., Mattioli et al., 2004, 2011), local availability and accessibility of livestock appears to be markedly reduced. These conditions are not met in the PNALM, where the replacement of sheep grazing in favor of an economically more profitable production of free-ranging cattle and horses took place over the past years, along with the gradual loss of traditional livestock husbandry and defense practices (Fico et al., 1993; Latini et al., 2005; Galluzzi, 2014). Currently, the high density of livestock farms and heads, the large overlap between livestock grazing areas and critical wolf habitat and, in particular, the frequent abandonment of

large livestock carcasses on the ground, all tend to explain the marked consumption of livestock by wolves in the PNALM, despite a long-restored and abundant community of four wild ungulate species.

Scavenging was largely prevalent over predation by wolves in the PNALM during winter, when we revealed that wolf feeding behavior was markedly driven towards scavenging domestic ungulates; although to a lesser extent, scavenging also involved wild prey, in particular red deer. Notably, we never found livestock being predated by wolves during winter, indicating the large availability of livestock carcasses due to other mortality causes (e.g., disease, climatic conditions, injuries in rough terrain, starvation). In accordance with their highest density in the PNALM, sheep were scavenged more frequently than other livestock species; horses, however, even if occurring at a lower density compared to cattle, were scavenged more frequently than cattle (Fig. 4) and contributed a greater or comparable amount of annual dietary biomass compared to cattle in 2 of 4 packs (Fig. 2). Free-ranging horses are very frequent in the central and southern Apennines and, more than cattle, are abandoned in mountain pastures throughout the year also in very harsh climatic conditions during winter; in addition older females, valued by farmers more for their reproductive potential than for their meet, are left in the herds until they are able to reproduce. Both these conditions may possibly make free-ranging horses more susceptible to natural mortality causes than cattle, therefore increasing the availability of their carcasses to wolves and other scavengers. However we caution that the overall frequency of scavenging on the different livestock species that we revealed did not account for differences in livestock species distribution and density at the pack scale, and further study is needed to quantitatively assess the effect of these variables in shaping scavenging patterns by wolves.

Contrarily to our prediction involving social affiliation (2.a), scavenging by wolves in the PNALM was comparably common between pack members and solitary floaters, suggesting that, given the large availability of livestock carcasses we documented, cooperative hunting in wolf packs does not seem to provide an added value in enhancing wild prey accessibility to pack members. Although these findings pertain to the winter season only, they provide a clear indication of how livestock carrion subsidies can depress the predatory behavior of wolves, therefore reducing their ecological role through top-down effects on the local wild ungulates populations. Nevertheless, predation by wolves still accounted for 27.5% of feeding events during winter and was uniquely directed at wild prey; we verified predation on all wild ungulates in the PNALM with the exception of the chamois. Because during winter both pack members and floaters killed only wild prey, possibly reflecting a relatively lower accessibility of livestock compared to summer, we could not test our second prediction (2.b), and a larger, multi-seasonal sample of predatory events would be necessary to test for the effect of social affiliation on the predatory patterns of wolves.

Based on a complementary approach using scat analysis and GPS cluster checks, our findings have implications on wolf feeding ecology that go beyond our specific case study. First, on methodological grounds, they remind us that interpreting prey remains in the scats in terms of predation is faulty and possibly largely misleading (Peterson and Ciucci, 2003), especially if prey use by wolves is quantitatively compared with prey abundance to make inferences on prey selection patterns. Wolves are efficient predators but, given the chance, are also proficient scavengers, as carrions of large ungulates provide a great amount of edible biomass at no energetic cost or risk of subduing prey. Second, from an ecological standpoint, a consistent availability of large livestock carrions may divert wolf feeding behavior towards scavenging, therefore reducing predation and hampering the potential cascading effects of wolves. Large livestock carcasses are often abandoned on pastures in our study area due to the inaccessibility of the sites and the high costs associated with their removal (Fico et al., 1993), but we argue that the ecological costs of this practice may far exceed those deemed acceptable within a national park. Third, related to wolf-livestock conflict, the availability of livestock carcasses on pastures may attract wolves thus reinforcing their dependency on livestock (i.e., depredation conservatism). Accordingly, even though the PNALM is adopting compensation schemes since the early 70s, wolf impact on livestock remains substantial and compensation consistently absorbs a relevant share of conservation funds (Latini et al., 2005; Galluzzi, 2014). During the years of our study, an average of 390 (±128 SD) claimed wolf depredations were verified by the park personnel each year, corresponding to about 628 depredated livestock heads (60.5% sheep, 16.1% goats, 13.7% cattle, 9.7% horses) and 130,496 € (±38,453 €) compensated by the park authority (Galluzzi, 2014).

Prevalent research on trophic cascades by apex predators pertains to relatively pristine and intact ecological settings, but in human-modified landscapes the ecological role of apex predators may be profoundly altered by anthropogenic effects (Dorresteijn et al., 2015; Kuijper et al., 2016). In particular, human-provided food subsidies are markedly problematic for conservation (Gompper and Vanak, 2008; Newsome et al., 2015). Either in the form of human waste, easily accessible livestock, butchery remains, or large mammal carrions, anthropogenic food subsidies are all expected to exert profound impacts at both the individual and population level, with reflections at the community and ecosystem scales (Oro et al., 2013). Accordingly, we speculate that the large availability of large livestock carrions for wolves in the PNALM not only affects their feeding and hunting behavior, by may also expectedly alter their density, demography, social relationships, as well as territorial behavior and dispersal, with both profound ecological and evolutionary implications. Additionally, availability of livestock carrions has the potential to maintain a permanent state of wolf dependency on livestock, generating high levels of depredations and, in turn, increasing the risk of human-caused wolf mortality due to retaliatory killing (Newsome et al., 2015). About 54% of wolves retrieved dead in the PNALM and adjacent areas from 2003−2013 (n = 80, minimum known mortality) had been intentionally or incidentally killed by humans, 62.6% of which poisoned or shot (L. Gentile, pers. comm.). Furthermore, the availability of large livestock carcasses, coupled with disruption of the social cohesion in wolf packs due to human-caused mortality (Rutledge et al., 2010), may also facilitate affiliative encounters between wolves and dogs, contributing with two additional sources of anthropogenic interference; namely, enhanced chances of introgressive

hybridization between wolves and dogs, a daunting and increasing threat to wolf conservation both in Italy (Galaverni et al., 2017; Salvatori et al., 2019) and elsewhere in Europe (Salvatori and Ciucci, 2018), and a greater potential for the diffusion of diseases typically hosted by domestic dogs (Corrain et al., 2007), as also recently documented in the PNALM (Di Sabatino et al., 2014; Molnar et al., 2014).

## 5. Conclusions

Wolves in the PNALM markedly relied on human-provided livestock carrion subsidies and livestock, despite a long re-established and abundant wild prey community. This raises a question regarding the effectiveness of conservation within national parks to facilitate the ecological role of apex predators. In human-modified landscapes, we argue that the conservation of apex predators should be assessed not only in terms of presence or demography (e.g., wolf density) but possibly also according to their ecology and behavior, especially within national parks where the ecological role of apex predators should be nurtured and facilitated to the greatest extent possible (Dorresteijn et al., 2015; Newsome et al., 2015). Conservation-wise, heavy reliance by apex predators on anthropogenic food subsidies is an indicator of ecosystem degradation (Newsome et al., 2017). In these conditions, asserting to ensure the ecological role of apex predators is an unsupported argument that stems from conservation policies essentially focused to ensure the mere occurrence of predators rather than facilitating ecosystem functioning (Newsome and Ripple, 2015b). By emphasizing how livestock husbandry practices may affect wolf conservation, our findings call for a re-consideration of conservation goals of apex predators in national parks. In particular, we contend that conservation policies and rules regarding livestock management ought to be deeply re-visited, including (but not limited to) livestock carrion removal. Especially in national parks within human-modified landscapes, minimizing accessibility to livestock and other anthropogenic food subsidies by apex predators has to be considered a priority in order to more effectively preserve their ecological role. In this perspective, it would be fundamental to monitor the short and long-term effect of the proper removal of livestock carcasses, as their decreased availability is expected to trigger functional responses in wolves of ecological and management relevance.

## Declaration of competing interest

None.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00841.

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