

## Article

# Scavenger Activity and Anti-Predator Behaviour in an Apennine Wolf Area

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**Abstract:** Scavenging guilds often have several trophic levels with varying dominance and intra-guild predation, competition, and interaction. Apex predators can control subordinate predators by limiting their numbers and affecting behaviour but also supply a continuous food source by abandoning carcasses. Camera traps monitored the scavenger guild in Alpe di Catenaiia, Tuscan Apennine, for three years to determine intraguild interactions and the behaviour response. Wild boar visited most feeding sites but only scavenged in 1.4% of their visits. Red fox was the most frequent scavenger, traded vigilance and feeding equally, and selected low vegetation density, while marten invested more in feeding than vigilance. Marten was the prime follower, appearing within the shortest time after another scavenger had left the site. Red fox occasionally looked upwards, possibly to detect birds of prey. Badger showed scarcely any vigilance, did not feed much on carcasses but scent-marked abundantly. Wolves showed the highest vigilance in proportion to feeding at carcasses among the scavengers. Sites with good visibility were selected by all scavengers except martens who selected poor visibility and new moon illumination. Scavengers were mostly nocturnal, showed weak responses to twilight hours or lunar illumination, and all but red fox avoided human disturbance areas.

**Keywords:** intraguild predation; feeding site selection; following behaviour; time partitioning; lunar illumination



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## 1. Introduction

The presence of large predators is not only a predation risk for intermediate predators [1] but can also be beneficial, as large predators abandon incompletely consumed carcasses, allowing for food acquisition through scavenging. By inducing the distribution and abundance of carrion availability throughout the year, they facilitate an even acquisition of food for scavengers, as in the case of wolves [2]. This positive influence, however, is not a general rule within large predators and can have a variable impact on scavengers' community [3]. Conservation actions seeking to apex predator populations should therefore consider the potential for apex predators to have a direct and facilitative influence on more species belonging to the scavengers' community. They are also strong predictors of mesopredator occurrence, suggesting that mesopredators track wolves for scavenging [4]. Scavenging on carcasses avoids energy costs for hunting and potential injuries, but risks injuries or predation from larger intraguild members. The risk allocation hypothesis predicts that prey are expected to adjust key anti-predator behaviours such as feeding time selection and vigilance to tempo-spatial variation in risk [5]. It has been suggested that smaller, subordinate species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources [6–11]. Nevertheless, in a review at a continental and global scale of carnivore community studies by Prugh and Sivy [12], instead of facilitating mesocarnivore populations, carrion provided by large carnivores may facilitate suppression. Spatial partitioning can be applied when avoiding direct confrontation with larger predators by only feeding at carcasses, while resting,

hunting, and social behaviours are performed at other locations [13]. Predation by top predators on intermediate predators may not only reduce competition through a numerical effect on the intermediate predators but can also lead to a change in behaviour with increased vigilance of the targeted species [14]. Smaller intraguild members will trade off foraging for increased vigilance at feeding sites [15] since the act of feeding represents both competition and predation pressure from larger predators who may be interested in the resource being consumed as well as the individual consuming it [16]. Moreover, vigilance should also function to decrease the risk of predation and injury from interspecific interference competition [17]. Members of a scavenger guild can also follow others to new feeding sites, feed on carcasses simultaneously, and share dens as seen in previous studies [15,18,19]. Temporal partitioning is not only regulated the day and night hours spent on feeding activity, but also by moonlight and the lunar cycle, effecting both predator and prey activity patterns [20–22]. Linley et al. [23] suggest a possible trade-off between increased activity and elevated predation risk during periods of low nocturnal illumination. partitioning of carcass consumption is also determined by the feeding site characteristics. In addition to the intraguild predation risk, season, habitat composition, cause of death, and consumption level of carcasses also influence scavengers' choice of feeding site [15,24–26]. Anthropogenic stressors such as climate change, ecotoxicology, and the conversion of forests to agro-grazing systems also affect carcass availability and the landscape characteristics for scavengers [27]. In Europe, there have been some studies of scavenger behaviour in wolf territories in Northern Europe, but none in the Apennine mountains in Italy, which is why we wanted to compare latitudinal behavioural differences as the body sizes of both wolves and their main prey species differ [28]. The very low presence of avian scavengers in the Tuscan Apennines also affects the carcass consumption process, as the predation risk by birds of prey is consequently lower for mesopredators. We investigated the scavenger guild members' behaviour at carcasses and feeding sites, their intraguild interference and predation, as well as eventual tempo-spatial predator avoidance strategies, including activity in the different lunar phases. We predicted that (1) wild boar, being the wolf's main prey, would show the highest vigilance at feeding sites; (2) the opportunistic red fox would be the most active follower of other scavengers to carcasses/feeding sites; and (3) illumination and feeding site characteristics would affect smaller-sized scavenger behaviour by avoiding larger-sized tempo-spatial selection of feeding sites.

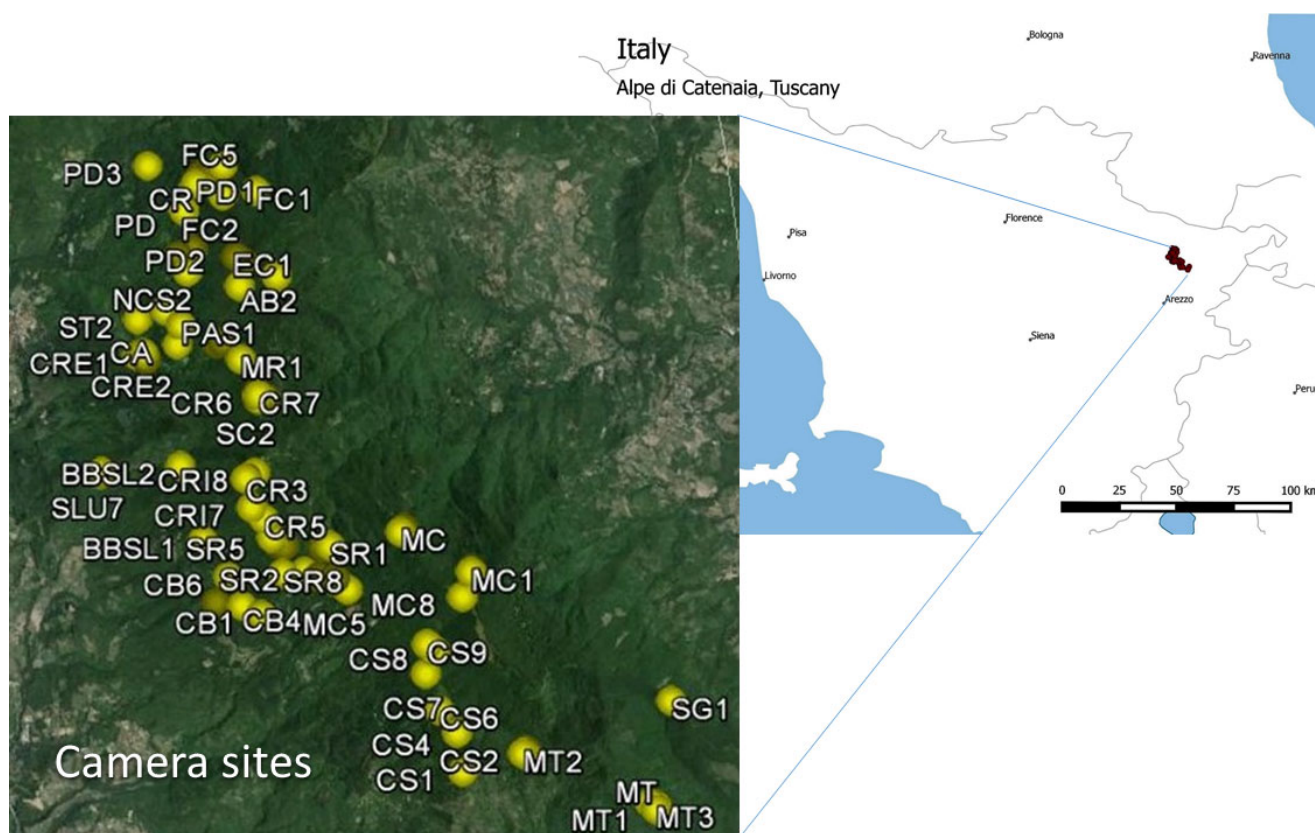
## 2. Material and Methods

### 2.1. Study Area

Data were collected from July 2010 to May 2013 in Alpe di Catenaia (43–48° N, 11–43° E), in the Arezzo Province located in north-central Italy, at an altitude of 490–1414 m above sea level (Figure 1). Camera monitoring of scavenging species was approved by Arezzo Province. The study area is 120 km<sup>2</sup> and includes a small, protected area of 27 km<sup>2</sup> in the centre, where locked gates prevent public access by car.

The climate is continental and characterised by high humidity. There is more than 80% forest cover with coppice, high trunk forests of Turkey oak (*Quercus cerris*) and chestnut (*Casanea sativa*) at lower elevations, and of beech (*Fagus sylvatica*) at upper ranges. Moreover, conifers such as pine and black pine (*Pinus nigra*), white spruce (*Abies alba*), and Douglas fir (*Pseudotsuga* spp.) are interspersed into deciduous woods or form small patches of pure forests. Temperatures drop below freezing in winter, with heavy snowfall occurring. The mean temperature is 11.6 °C (summer 17.5 °C and winter 8 °C). Precipitation is approx. 1000–1600 mm/year. Resident species are roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), European hare (*Lepus europaeus*), pine marten (*Martes martes*), stone marten (*Martes foina*), European badger (*Meles meles*), wolf (*Canis lupus*), crested porcupine (*Hystrix cristata*), wildcat (*Felis silvestris*), common buzzard (*Buteo buteo*), goshawk (*Accipiter gentilis*), sparrow hawk (*Accipiter nisus*), hooded crow (*Corvus cornix*), and European jay (*Garrulus glandarius*). The

average weights of the main scavenging mammalian predators are wolf (31.7 kg), badger (7–17 kg), red fox (5–7 kg), and marten (0.9–2.5 kg).



**Figure 1.** Movement- and heat-triggered camera sites in Alpe di Catenia, Tuscany.

## 2.2. Carcasses and Feeding Sites

Wild boar is the main prey for wolves in Tuscany [28] and camera traps were located at ungulate carcasses and baiting sites. Carcasses were found and reported from the forestry service or hunters. Twenty-seven carcasses of wild boar, roe deer, fallow deer, and red deer were used, weighing 12–49 kg. Moreover, we prepared 110 feeding sites 10–20 metres from wildlife trails using bone and hide of ungulates dissected in a veterinary study, deaths by car collisions or hunting injuries.

## 2.3. Movement- and Heat-Triggered Camera Systems

Movement- and heat-triggered camera systems, henceforth called camera traps or camera sites, were placed at carcasses killed by wolves or deaths of other causes [15], i.e., random allocation, and the simulated carcass sites had deliberately biased placement as similar to the former, year round. Five different camera trap systems were used: 20 DVREye™ Wireless PIR Model DVR, PixController Inc., (Export, PA, USA), 20 Multipir-12, Tecnofauna Ziboni s.r.l. (Rogno, Italy), 20 Bushnell HD Trophy Cam, Bushnell Outdoor (Kansas City, KS, USA), 1 BolyGuard SG550M, Boly Media Communications Ltd. (Shenzhen, China), and 1 Uovision UM565 Uovision Australia (Huntingdale VIC, Australia). Cameras were programmed to take a sequence of video film, or in the BolyGuard SG550M, 1–3 photos per second with one second of interval when triggered by movement. Camera traps were placed between 0.5 and 2 m above the ground on tree stems, depending on site location and terrain ruggedness [29] as well as risk of scavenger interference, 2 and 10 m from carcasses. The movement detectors were not triggered by scavenging birds smaller than jays or by mammals smaller than squirrels. The date and time were stamped on every film/photo. Many mammal species reacted to the visible infrared red light used in the DVREye camera when taken during dark hours, which is why we replaced them with the

other four brands after the first six months (no statistically determined difference in the behavioural distribution shown). Camera sites were checked, and memory cards and/or batteries were changed every 2–6 weeks, except for the BolyGuard SG550M and Uovision UM565, which used GPRS/MMS transmission, and the latter had a solar cell panel as an energy source since they were located in remote areas with no access during periods of high snow levels.

#### 2.4. Data Analysis

All films and photos were visually analysed and categorised by camera ID, video result (activity), location, date, time, duration, species, number of individuals, and behaviour. Other data classifications:

*A visiting occasion*—as scavengers, once they arrived at the carcass, very rarely left the site for more than 10 min, we classified a visiting occasion when there was  $\geq 11$  min between two feeding bouts.

*Interactions*—for establishing guild member interactions or interference, we recorded “*following behaviour*” when a specie visited a feeding site where another specie had been 0–180 min earlier.

*Behaviour*—defined as *Feeding*—chewing, *Vigilant*—a head lift which interrupts feeding activity on the carcass, followed by visual scanning of the environment [30], *Looking upwards*—raising head and looking toward the tree canopy or sky, *Scent-marking*—urinating, excavating, or rubbing the side of the head and/or neck on ground or vegetation, *Looking at camera*—eyes focusing directly on the camera, *Other*—inspecting, searching, social interaction (mainly wild boar and fox), moving, grooming (mainly fox and marten). Each species time spent on different behaviours and proportion of behaviours were then tested against the other scavenger guild members.

The 24-h activity at feeding sites were pooled in six time periods: 00:00–03:59, 04:00–07:59, 08:00–11:59, 12:00–15:59, 16:00–19:59, 20:00–23:59.

*Seasonal activity*—summer: May–October; early winter: November–December; mid-winter: January–February; late winter: March–April.

*Visibility*—estimated from the four cardinal points sideways of carcasses by measuring the distance from where it could be detected. Visibility was then calculated as the average of all distances in the four directions taken at a height of approx. 50–60 cm, categorised as 0–14 m (poor) or  $\geq 15$  m (good), for estimating the probability of detection of and by competitors or predators.

*Human disturbance*—camera sites located  $< 1$  km from farms, forestry service, or other human activity were used to evaluate the effect of human disturbance.

*Illumination*—visits were recorded as occurring during light or dark hours, as well as dawn and dusk. Crepuscular periods were classified as dawn starting 30 min before sunrise, and dusk starting at sunset and ending 30 min after. Nocturnal visits at full moon and new moon  $\pm 72$  h were recorded.

*Vegetation density*—*low*: open grass/herbal meadows with no or low quantities of shrub; *medium*: approx. 2–8 trees and/or bushes per 100 m<sup>2</sup>; *high*: dense forest with  $\geq 10$  trees and/or bushes per 100 m<sup>2</sup> with rich understorey.

*Carcass cause of death*—wolf-killed, traffic collision, natural, or human.

*Carcass consumption level*—0–85%, 90–95%, or 100%. Wolf-killed carcasses (or those killed by other causes) were often highly consumed when detected, as no radio-collared wolf was available in the area.

To assess the effect of *feeding site characteristics* on scavenger behaviour unrelated to competition or predation within the guild, we used modelling in the linear family to see if one particular independent variable changes the relationship of another particular independent variable. We used the backward elimination procedure (with  $p = 0.05$  as a threshold) to build and compare sets of generalised linear mixed models (GLMM) to test the effect on each scavenger species with the camera site fitted as a random factor and (1) season, (2) cause of death, (3) consumption level, (4) vegetation density, (5) visibility,



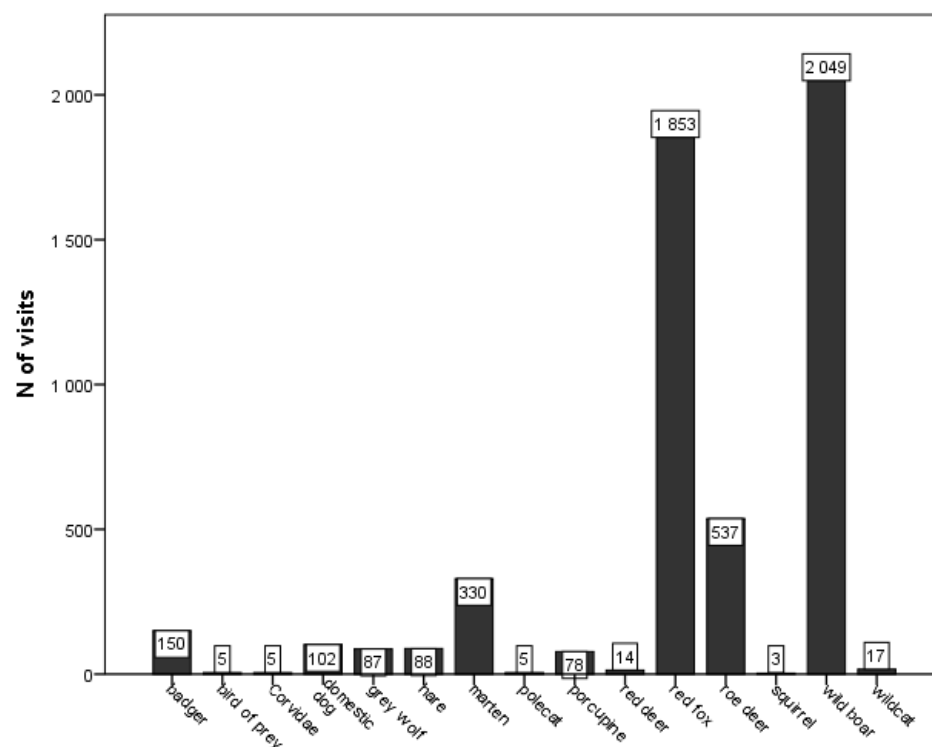
(6) distance to human disturbance, and (7) snow presence as fixed effects [31]. We used GLMM to enable the modelling of variables measured at multiple time scales with an unbalanced design. When data were normally distributed, statistical significance was tested with a single-factor ANOVA and post-hoc Tukey HSD test. When not normally distributed, statistical significance was tested with the nonparametric Mann–Whitney and Kruskal–Wallis test. Data were analysed using IBM SPSS Statistics 21.

### 3. Results

Cameras recorded at 137 carcasses/feeding sites (Figure 1) between 4 and 291 days (mean 63 days per site), 24 h/day, all year round from July 2010 to May 2013 (35 months). Over 17 species in 10,085 films/photos (9922 films, 163 photos) with 263 h of film were recorded for 5556 days and nights. In 3026 films, there were two or more individuals simultaneously. Camera sites mainly consisted of beech or mixed forest. Visibility at 54.8% of the carcasses/feeding sites was >15 m in at least three cardinal point directions. Vegetation density was high in 15.0%, medium in 40.5%, and low in 44.5% of the camera sites. At 73% of the camera sites, the recordings took place when there was no snow on ground, 18% when it was covered with snow, and 9% temporarily with or without snow.

#### 3.1. Scavenger Guild Members

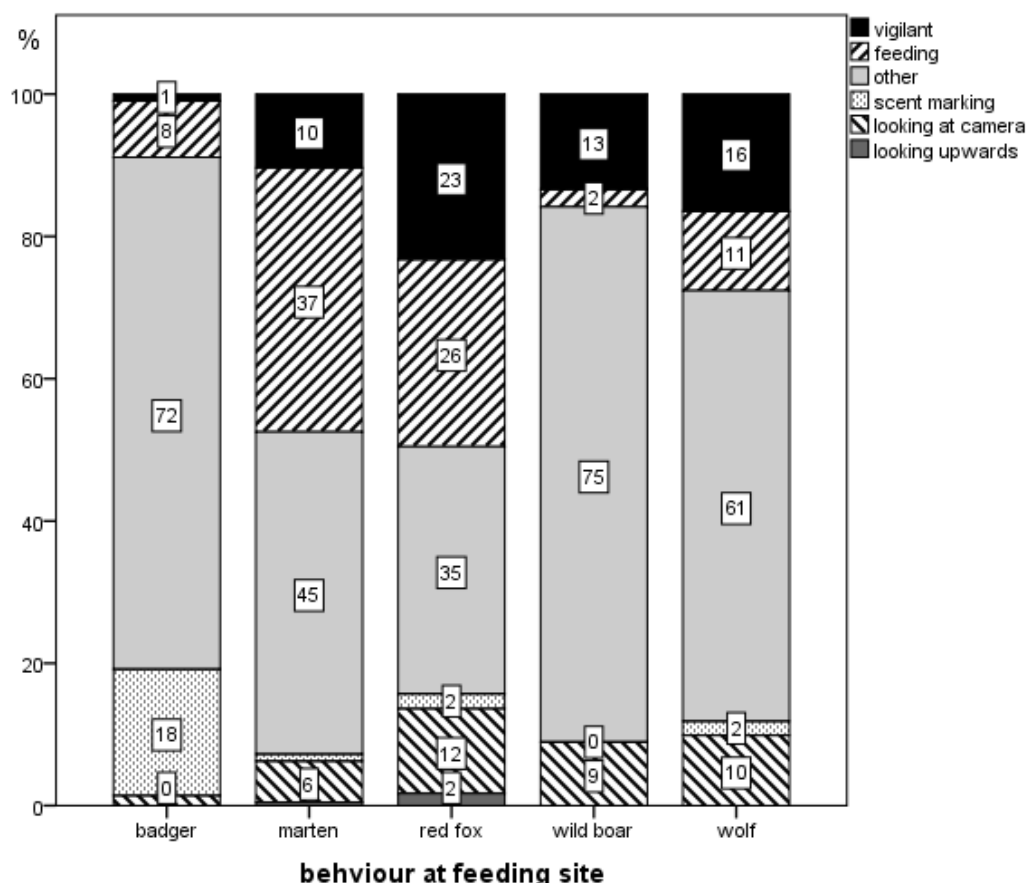
In total, 5366 visiting occasions were calculated whereof scavengers: wild boar 38.2%, red fox 34.5%, marten 6.1%, badger 2.8%, domestic dog (*Canis familiaris*) 1.9%, wolf 1.6%, *Corvidae* spp. 0.09%, bird of prey 0.09%, polecat (*Mustela putorius*) 0.09%, and nonscavengers: porcupine 1.5%, wildcat 0.3%, roe deer 10%, red deer 0.3%, hare 1.6%, and red squirrel (*Sciurus vulgaris*) 0.03% (Figure 2). Domestic dogs were mainly present at feeding sites during daytime in autumn and winter, in correspondence with wild boar hunting season. However, there were two free-roaming dogs that were present in the area and consumed entire carcasses on at least two occasions. Birds of prey and corvids were very rare. It was visually impossible to distinguish between pine marten and stone marten, so both were classified as “marten” (Figure 2).



**Figure 2.** Visiting occasions by all species at carcasses/feeding sites in Alpe di Catenia, 2010–2013.

### 3.2. Scavenger Behaviour at Feeding Site

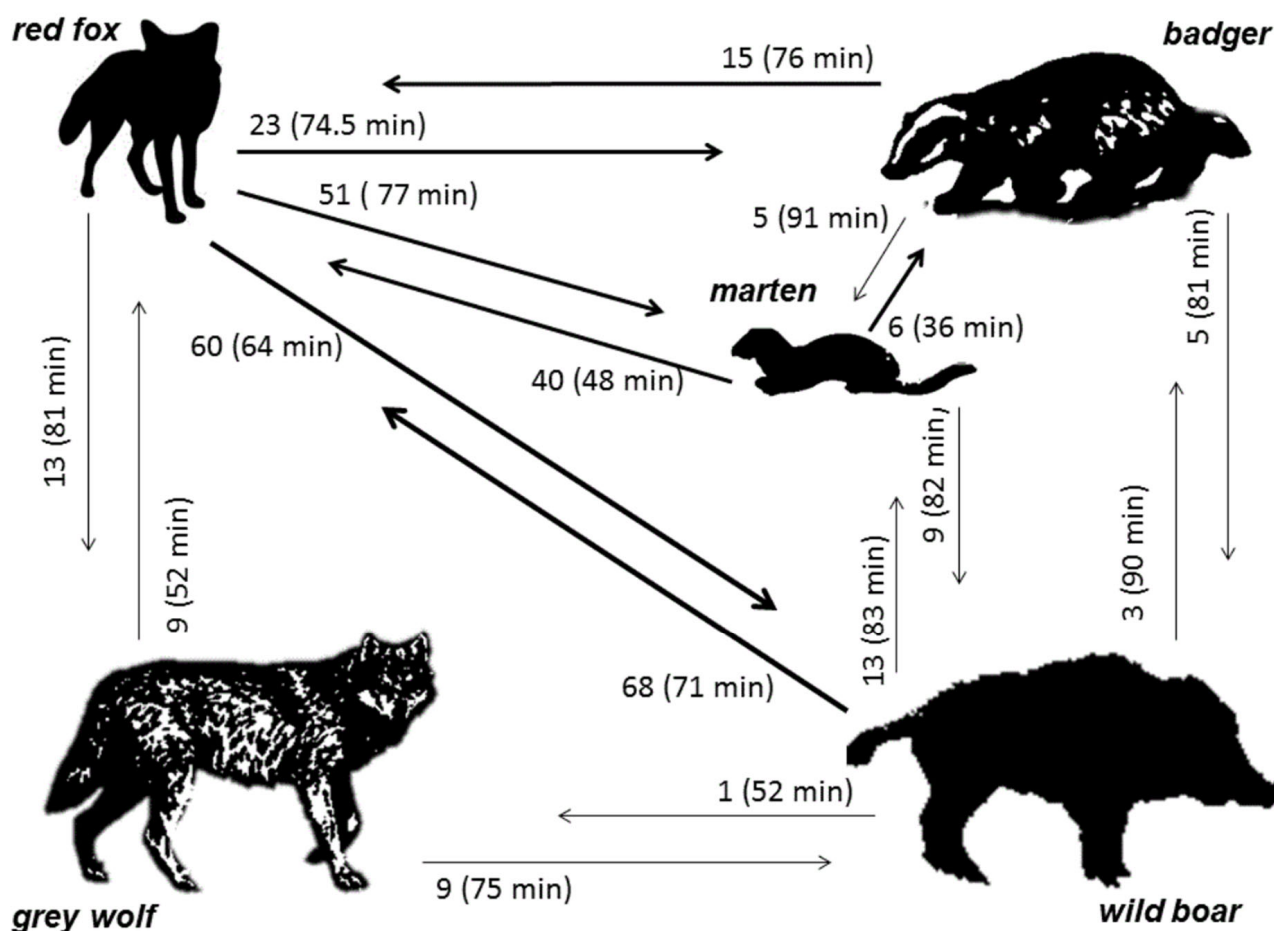
A Kruskal–Wallis test shows a significant difference in the scavenger species behaviours at feeding sites:  $H = 11.96$ ;  $n = 8072, 214, 1104, 152, 4031$ ;  $p = 0.018$ . Each scavenger's distribution of different behaviours is visually demonstrated by the percentage of total behaviour at feeding sites in Figure 3. Wild boar fed on the carcass itself in only 1.4% of their visits. A major part of their feeding was on insects and arthropods around the carcass. With *a posteriori* Tukey HSD test, red fox shows significant difference in behaviour compared to badger ( $p = 0.033$ ) and wolf ( $p = 0.031$ ) but no significance to marten or wild boar.



**Figure 3.** Scavenger behaviour at feeding sites were defined as *Vigilant*—a head lift which interrupts feeding activity on the carcass, *Feeding*—chewing, followed by visual scanning of the environment, *Other*—inspecting, searching, social interaction (mostly wild boar and fox), moving, grooming (only fox and marten), *Scent-marking*—urinating, excavating or rubbing side of head and/or neck on ground or vegetation, *Looking at camera*—eyes focusing directly on the camera, *Looking upwards*—raising head towards tree canopy or sky.

### 3.3. Scavenger Guild Members' Interaction or Interference

Two or more individuals of different species visited the sites simultaneously on only five occasions with fox and wild boar, twice with fox and marten, and once with fox and wolf. Marten and fox withdrew immediately when the superior scavenger appeared, but fox and wild boar did not react noticeably to each other. The highest interaction between the most common scavenging (thus excluding wild boar) species—red fox, badger, marten, wolf—were between red fox and marten, as seen in Figure 4.

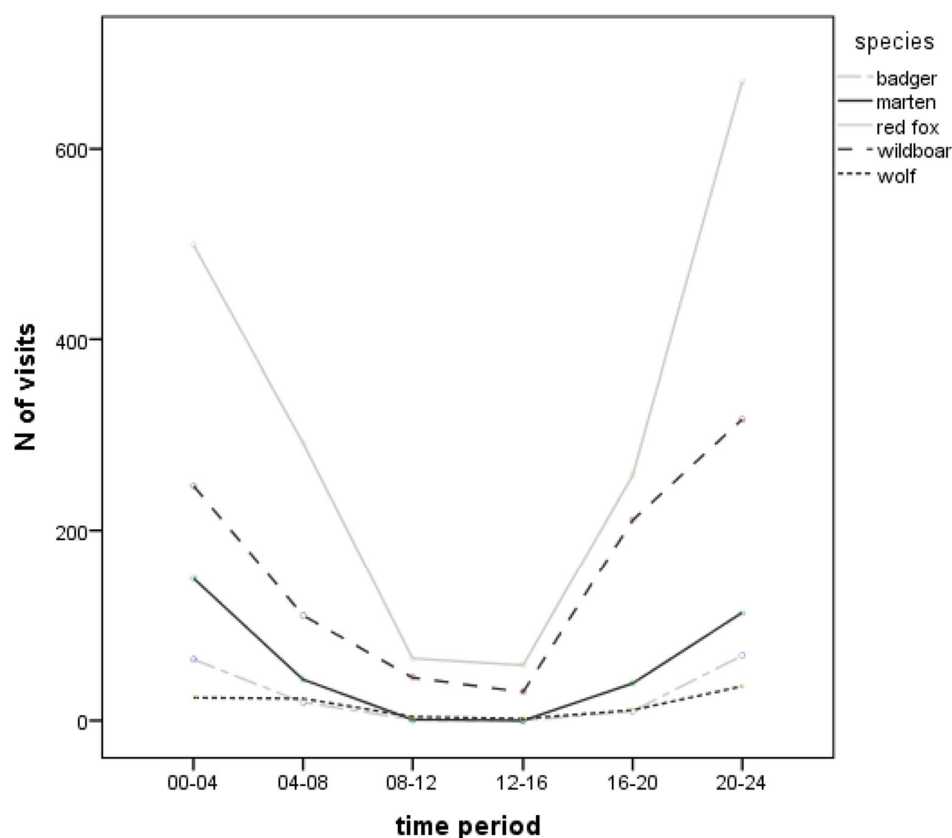


**Figure 4.** Number of observations when scavengers follow other scavengers and average minutes after the previous visitor has left the carcass/feeding site.

Foxes followed marten on 51 occasions, between 0 and 168 min after marten had left (average 77 min), but martens followed foxes on 40 occasions, from 0 to 134 min (average 48 min), showing a significantly shorter following time (Mann–Whitney test:  $U = 761.5$ ,  $n = 51, 40$ ,  $p = 0.039$ ). Also tested: badger followed fox ( $n = 15$ , average 76 min), fox followed badger ( $n = 23$ , average 74.5 min), marten followed badger ( $n = 6$ , average 36 min), badger followed marten ( $n = 5$ , average 91 min), wolf followed fox ( $n = 9$ , average 52 min), fox followed wolf ( $n = 13$ , average 81 min), and wolf followed wild boar ( $n = 6$ , average 61 min) but all of these were NS.

### 3.4. Temporal Partitioning and Illumination

A two-factor ANOVA without replication showed significant differences in behaviour between the five species ( $F_{4,20} = 9.921$ ,  $p < 0.001$ ) and between the time periods ( $F_{5,20} = 4.518$ ,  $p = 0.006$ ) (Figure 5). A two-factor ANOVA without replication showed no significant temporal variation between visits in relation to illumination by the five species ( $F_{4,4} = 3.785$ ,  $p = 0.113$ ) and the crepuscular periods ( $F_{1,4} = 2.909$ ,  $p = 0.163$ ). A two-factor ANOVA without replication also showed significant differences in behaviour between the five species ( $F_{4,8} = 19.863$ ,  $p < 0.001$ ) and between full moon, new moon, and other monthly moon phases ( $F_{2,8} = 5.0956$ ,  $p = 0.037$ ).



**Figure 5.** Scavenger guild visiting numbers and time periods over 24 h.

Table 1 shows all visiting wildlife species in relation to illumination in percentage. Avian scavengers appeared most of all scavengers near human activity, whilst red fox was the most common mammal with 39.2% of all their visits to feeding sites being <1 km from human disturbance. A two-factor ANOVA without replication showed NS between the five species ( $F_{4,4} = 5.876$ ,  $p = 0.057$ ) as well as between proximity or further distance from human disturbance ( $F_{1,4} = 4.350$ ,  $p = 0.105$ ). Within the scavenger guild, 1423 of the visits occurred <1 km from human disturbance and 3454 > 1 km.

**Table 1.** Percentage of diurnal, nocturnal, and crepuscular activities at sunrise −30 min and sunset +30 min, activity in illumination by full moon and new moon  $\pm 72$  h, by the most frequently visiting species (domestic dog excluded).

	Diurnal		Crepuscular		Nocturnal	Lunar Cycle	
	light	dawn	dusk		dark	full moon	new moon
badger ( <i>Meles meles</i> )	6.7				93.3	17.4	24.0
bird of prey	75.0				25.0	20.0	20.0
corvids <i>Corvidae</i> spp.	80.0	20.0					
grey wolf ( <i>Canis lupus</i> )	11.0	8.2			80.8	21.1	15.8
hare ( <i>Lepus europaeus</i> )						23.5	18.4
marten ( <i>Martes martes</i> , <i>Martes foina</i> )					100.0	14.5	27.6
porcupine ( <i>Hystrix cristata</i> )			3.4		96.6	15.8	20.0
red deer ( <i>Cervus elaphus</i> )	66.7				33.3	28.6	7.1
red fox ( <i>Vulpes vulpes</i> )	4.4	1.4	1.0		93.2	28.9	23.9
roe deer ( <i>Capreolus capreolus</i> )	60.0	4.3	6.7		29.1	22.4	17.7
wild boar ( <i>Sus scrofa</i> )	3.9	1.4	0.7		94.0	28.5	21.0

### 3.5. Carcass/Feeding Site Characteristics

Marten showed significant preference for traffic-killed carcasses compared to deaths by natural causes ( $p = 0.014$ ) and completely consumed carcasses compared to consumption level 90–95% ( $p = 0.055$ ). Red fox selected low vegetation density significantly more than



medium ( $p = 0.031$ ). Wild boar visited carcass sites significantly more often in summer compared to late winter ( $p = 0.016$ ). Wolf selection was NS, and badger was excluded as they did not visit carcass sites in early or midwinter seasons, being scarcely active at these times. Visits to camera traps <1 km from human disturbance occurred in 10.4% of the total visits in badger (17/147), 11.9% in wolf (14/104), 17.8% in marten (61/282), 39.2% in red fox (756/1172), and 24.7% in wild boar (545/1664) (Table 2).

**Table 2.** Parameter estimates ( $\beta$ ) of season, carcass cause of death, consumption stage, vegetation density, visibility, distance to human disturbance, and snow coverage of visits by marten, red fox, wolf, and wild boar at carcass/feeding sites during ten-day periods ( $n = 134$ ). Badger was excluded due to NS. <sup>a</sup> This coefficient is set to zero because it is redundant. The column for  $p$ -values has a light grey background.

95% Confidence Interval								
Species	Variables	$\beta$	SE	t	p	Exp Coef	Lower	Upper
MARTEN								
	season							
	summer	1.51	1.461	1.034	0.36	4.525	0.078	261.05
	late winter	−0.856	1.55	−0.552	0.61	0.425	0.006	31.451
	mid-winter	0	1.414	0	1	1	0.02	50.728
	early winter	0.000 <sup>a</sup>						
	cause of death							
	wolf-killed	0.000 <sup>a</sup>						
	traffic	1.51	0.365	4.136	0.014	4.525	1.643	12.465
	natural	0.000 <sup>a</sup>						
	human	0.000 <sup>a</sup>						
	consumption level							
	1	2.773	1.031	2.69	0.055	16	0.915	279.914
	90–95%	0.000 <sup>a</sup>						
	0–85%	0.000 <sup>a</sup>						
	vegetation density							
	low	0.000 <sup>a</sup>						
	medium	0.000 <sup>a</sup>						
	high	0.000 <sup>a</sup>						
	visibility	0.000 <sup>a</sup>						
	poor	0.000 <sup>a</sup>						
	good	0.000 <sup>a</sup>						
	human disturbance							
	>1 km	0.000 <sup>a</sup>						
	<1 km	0.000 <sup>a</sup>						
	snow cover							
	yes	0.000 <sup>a</sup>						
	no	0.000 <sup>a</sup>						
RED FOX								
	season							
	summer	0.643	0.458	1.403	0.167	1.901	0.757	4.778
	late winter	0.538	0.489	1.099	0.277	1.712	0.64	4.581
	mid-winter	0.589	0.454	1.296	0.201	1.802	0.722	4.496
	early winter	0.000 <sup>a</sup>						
	cause of death							
	wolf-killed	−0.347	0.583	−0.596	0.554	0.707	0.219	2.283
	traffic	0.239	0.376	0.636	0.528	1.27	0.596	2.706
	natural	0.162	0.494	0.328	0.744	1.176	0.435	3.177
	human	0.000 <sup>a</sup>						
	consumption level							
	1	−0.709	0.717	−0.989	0.328	0.492	0.116	2.081
	90–95%	−0.484	0.764	−0.634	0.529	0.616	0.132	2.867
	0–85%	0.000 <sup>a</sup>						

Table 2. Cont.

95% Confidence Interval								
Species	Variables	$\beta$	SE	t	p	Exp Coef	Lower	Upper
WOLF	<i>vegetation density</i>							
	low	1.354	0.609	2.223	0.031	3.874	1.138	13.191
	medium	0.971	0.573	1.695	0.097	2.641	0.834	8.364
	high	0.000 <sup>a</sup>						
	<i>visibility</i>							
	poor	−0.37	0.419	−0.883	0.382	0.691	0.297	1.605
	good	0.000 <sup>a</sup>						
	<i>human disturbance</i>							
	>1 km	0.397	0.437	0.908	0.368	1.488	0.617	3.587
	<1 km	0.000 <sup>a</sup>						
	<i>snow cover</i>							
	yes	−0.177	0.428	−0.413	0.681	0.838	0.354	1.981
	no	0.000 <sup>a</sup>						
WILD BOAR	<i>season</i>							
	summer	0.654	1.28	0.511	0.611	1.924	0.149	24.88
	late winter	−24.031	390,269.2	0	1	0	0	
	mid-winter	−0.752	1.526	−0.493	0.624	0.472	0.022	9.967
	early winter	0.000 <sup>a</sup>						
	<i>cause of death</i>							
	wolf-killed	25.734	352,113.8	0	1	1.50 E+11	0	
	traffic	1.772	1.291	1.372	0.175	5.88	0.445	77.742
	natural	−24.007	476,795.3	0	1	0	0	
	human	0.000 <sup>a</sup>						
	<i>consumption level</i>							
	1	26.306	0.949	27.718	0	2.66E+11	3.98E+10	1.77E+12
	90–95%	25.816				1.63E+11		
	0–85%	0.000 <sup>a</sup>						
	<i>vegetation density</i>							
	low	−1.426	672,826.6	0	1	0.24	0	
	medium	23.313	473,917.0	0	1	1.33E+10	0	
	high	0.000 <sup>a</sup>						
	<i>visibility</i>							
	poor	24.147	352,113.8	0	1	3.07E+10	0	
	good	0.000 <sup>a</sup>						
	<i>human disturbance</i>							
	>1 km	−0.167	1.312	−0.127	0.899	0.846	0.061	11.665
	<1 km	0.000 <sup>a</sup>						
	<i>snow cover</i>							
	yes	0.421	1.095	0.384	0.702	1.523	0.17	13.608
	no	0.000 <sup>a</sup>						
WILD BOAR	<i>season</i>							
	summer	1.068	0.429	2.488	0.016	2.911	1.233	6.868
	late winter	−0.033	0.501	−0.065	0.948	0.968	0.355	2.638
	mid-winter	0.021	0.494	0.042	0.967	1.021	0.38	2.742
	early winter	0.000 <sup>a</sup>						
	<i>cause of death</i>							
	wolf-killed	−0.106	0.615	−0.173	0.864	0.899	0.263	3.078
	traffic	0.385	0.408	0.945	0.348	1.47	0.65	3.324
	natural	−0.049	0.498	−0.099	0.921	0.952	0.352	2.576
	human	0.000 <sup>a</sup>						
	<i>consumption level</i>							
	1	0.563	0.7	0.803	0.425	1.755	0.433	7.122
	90–95%	0.284	0.75	0.379	0.706	1.328	0.297	5.95
	0–85%	0.000 <sup>a</sup>						
	<i>vegetation density</i>							
	low	0.777	0.609	1.275	0.207	2.175	0.643	7.358
	medium	0.311	0.542	0.574	0.568	1.365	0.461	4.039
	high	0.000 <sup>a</sup>						

Table 2. Cont.

Species	Variables	95% Confidence Interval			<i>p</i>	Exp Coef	Lower	Upper
		$\beta$	SE	<i>t</i>				
	<i>visibility</i>							
	poor	−0.547	0.415	−1.32	0.192	0.578	0.252	1.325
	good	0.000 <sup>a</sup>						
	<i>human disturbance</i>							
	>1 km	0.653	0.464	1.405	0.165	1.92	0.759	4.86
	<1 km	0.000 <sup>a</sup>						
	<i>snow cover</i>							
	yes	−0.456	0.448	−1.018	0.313	0.634	0.259	1.553
	no	0.000 <sup>a</sup>						

## 4. Discussion

### 4.1. Test Predictions

The results from this study showed that wild boar and red fox were the most active visitors to carcasses/feeding sites in the Alpe di Catenaiia, albeit that wild boar very rarely scavenged. Our first prediction, that wild boar was the most vigilant being wolf's main prey, turned out to be false, as red fox showed the highest level of vigilance, followed by wolf. A plausible explanation can be that wild boar are socially aggregated in group living and kin-selected cooperation, which in this case means more sets of sense organs scanning the environment and a greater probability of detecting predators [32]. The high level of vigilant behaviour shown by wolves can be explained by the high level of human persecution suffered by this species: out of 77 dead wolves recovered in Tuscany in the last 20 years whose mortality cause was determined, 30 were deliberately and illegally killed by humans either by shooting or by poisoning [33]. These data also explained the reluctance of wolves to use carcasses that were not the outcome of their predator activity. The high vigilance of foxes has probably the same origin, as foxes are legally persecuted for 5 months a year in the ordinary hunting season (from September to January), and further killed in specific shooting control actions in the spring. Furthermore, marten, in spite of being the smallest scavenger, showed the least vigilance, except for the next largest, badger. When comparing vigilance behaviour with Sweden in northern Europe [15], red fox (Sweden 19% and Tuscany 23%) and badger (0% and 1%) were rather similar, while marten (37% and 10%) and wolf (7% and 16%) differed noticeably. Wolves show higher vigilance in Italy than in Sweden, neither being subject to any predation risk by other carnivores but being subject to poaching by poison and shooting in both countries [34]. All large carnivore species are highly persecuted by humans, regardless of whether they are legally protected or not, due to poaching [35]. Overlap between large carnivores and humans is increasing in regions with large carnivore recovery [36], which in turn has resulted in human-induced fear and risk-foraging trade-off in large carnivores [37]. EU wolves were protected by the Habitat and Species Directive from 1996 until 2010, when the Swedish government introduced quota hunting. Poaching is a difficult problem in both Sweden and Italy [38,39]; nonetheless, wolf vigilance in Tuscany is higher than in Sweden [15]. Within the canid species wolf, domestic dog, and fox, there is a niche overlap between wolves and domestic dogs and between domestic dogs and foxes, but in both cases, the interference competition is dependent on the domestic dog's body size. In this study, domestic dogs were smaller than wolves, with the exception of two much larger individuals (mastiffs). Martens in Sweden show higher vigilance, which may be explained by the higher predation risk by birds of prey. However, in Alpe di Catenaiia, red fox (3%) and marten (0.7%) looked upwards towards the tree canopy or sky when visiting feeding sites despite the lack of avian predators, which was surprising.

Our second prediction that the opportunistic red fox would be the most active follower showed virtually the opposite result in this study; the next largest scavenger, badger, visited feeding sites <180 min after a previous scavenger had left in 12% of their total visits. Wolf, which is the largest, followed others in 9.8%, marten followed others in 6.4%, and red fox

followed others in 1.9% of their total visits. Wild boar group members varied vastly in weight, but they followed others in 2.7%. However, marten was the quickest to arrive after other species with an average of 42 min, wolf 57 min, while red fox had an average of 77 min, wild boar 80 min, and badger 83 min, suggesting that marten is the optimal follower of the scavenging guild in Alpe di Catenia wolf territories. Correspondingly, with Swedish pine marten and red fox [15], marten follow red fox within a shorter time than vice versa.

Our third prediction, that illumination and feeding site characteristics affect smaller-sized scavenger behaviour by avoiding larger sized scavengers' tempo-spatial selection of feeding sites, was not clearly supported in this study. There are mainly two characteristic features when classifying diurnal, nocturnal, crepuscular, and lunar illumination selection: marten's selection of the new moon with low moon illumination and wolf selection of morning twilight. Wolves' visits at dawn (8.2%) were consistent with the activity peak shown by ungulates in the same area at that time and at dusk [40]. Moreover, red deer and wild boar were more active in full moon illumination rather than new moon, which may also be the reason why wolves were more active in full moon illumination. Rasmussen and Macdonald [41] suggested that light availability at night may influence the activity patterns of wild dogs and cheetahs, and that nocturnal activity may be more pronounced than previously thought, thus questioning the real role of lions and hyenas in influencing the activity patterns of subordinate species. The red fox shows a somewhat higher selection of full moon than new moon and is most likely the highest predation risk factor for martens. This may be a reason for martens choosing new moon rather than full moon illumination. Linley et al. [23] found that there may be trade-offs between predation risk and foraging when clouds decrease moon illumination, and as we did not record cloudiness in this study, we would highly recommend measuring exact illumination regardless of moon phase for future studies. Smaller scavengers showed the same temporal activity as larger ones, all being nocturnal, with only red fox and wild boar appearing to a lesser extent between 08:00 and 16:00. There was no significant correlation between larger and smaller scavengers regarding seasonal activity, cause of death of carcasses, consumption level, vegetation density, visibility, or snow coverage. Red fox and wild boar showed the highest tolerance of human disturbance, which may well be related to being the most abundant visitors at feeding sites. As we only classified visits at feeding sites less than one kilometre from human disturbance as a reference point, future research should evaluate scavenging behaviour at a range of different disturbance intensities.

#### 4.2. Feeding Time and Anti-Predator Investment in the Main Scavenger Species

##### 4.2.1. Red Fox

Red fox was clearly the main scavenger with the most visiting occasions during the three-year study period. It showed the highest vigilance and apprehension, reflected in the behaviour of observing the camera trap most often of all the scavengers. Noticeable was also the behaviour of looking upwards towards the tree canopy or sky, most often combined with a high level of vigilance, despite the very low density of avian predators in the Tuscan Apennines. This vigilance behaviour indicates that red fox home range may cover urban areas outside the mountain area where avian predators are present, but this is beyond the scope of this study. Red foxes are known to kill martens [42], but this behaviour appeared most often even when no martens had been observed before or after red fox visits. Climbing trees only occurred in 0.4% of the marten visits at feeding sites in this study. Red fox followed all other scavengers, selected feeding sites in the forest with low vegetation density (also confirmed in the GLMM), good visibility, less snow, and, of all mammalian scavengers, nearest human activity. Refuge by subordinate carnivores against interference by larger carnivores in urban areas was observed by Moll et al. [43], and this way of using a "human shield" effect may have been the strategy used by the red foxes, as they showed the highest number of visits to feeding sites near human disturbance. They were mainly nocturnal but showed no attraction to crepuscular hours or lunar illumination, even if somewhat more in full moon than new moon. Predation risk in this study was from wolves,

dogs who occurred much less at carcasses/feeding sites, and human hunters/poachers. Aggregation with high numbers of subordinate species has been seen to defend or take over carcasses [25], but this was never observed in Alpe di Catenaiia. Red foxes and domestic dogs were never observed simultaneously or within short time intervals at the feeding sites; nevertheless, domestic dogs could be a potential risk, as they occurred just as much as wolves but mainly in daytime during the hunting seasons. Moreover, several red fox individuals showed injuries such as limps and lost legs and eyes, which may indicate that they live under high predation pressure from both wolves and domestic dogs. Injuries may also have arisen from interspecific combat as well as shooting injuries. In studies of sympatric canids, the clear trend is for larger species to kill or displace smaller ones, resulting in habitat partitioning [44]. The higher red fox density shown by higher visits at feeding sites may explain that even if red fox avoid proximity to wolves and domestic dogs, it is not enough to avoid the predation risk entirely; therefore, they have to trade other behaviours off for vigilance.

#### 4.2.2. Pine and Stone Marten

Martens were the second most active scavenger and they followed, and were followed, by red foxes and badgers. They were, however, the only other scavenger looking up at the canopy, even if this was rare. They arrived at feeding sites more rapidly than other scavengers after the previous visitor had left. They spend most of their time feeding, and, next after badger, are the least vigilant but nonetheless smallest scavenging species. Moreover, they selected low vegetation with grass and shrubs with poor visibility. Snow was avoided and they moderately visited sites near human activity. They are exclusively nocturnal and seem to prefer the darkness of new moon rather than full moon illumination. Contrasting to other studies where foraging is restricted and adjusted due to predation pressure [45], marten did not express a trade-off in foraging and anti-predator behaviour compared to other scavengers. They spent more time feeding than the others and, apart from badgers, less time being vigilant. This is the direct opposite of pine marten and red fox behaviour at carcass sites in Sweden [15], suggesting that marten has a latitudinal variation in anti-predator behaviour.

#### 4.2.3. Badger

Badgers have been classified as extreme specialist [46] to generalist [47] as well as adjustable to latitudinal variation [48]. In Alpe di Catenaiia, badgers did not feed on carcasses often, lacked vigilant behaviour as the only superior scavenger and possible predators are wolves and humans, but scent-marked more than any other scavenger. They often scent-marked over other species markings, which can be explained by the fact that the territories are defended by occasional fighting and by a system of scent-marking with latrines at their border [49]. Badger followed red fox, which has been seen in previous studies [50], and marten on a few occasions. Low vegetation density, good visibility, less snow, and avoided human activity most of all scavengers. Mostly nocturnal and showed no attraction to crepuscular hours or new moon illumination. On the contrary, they visited carcasses/feeding sites more during new moon.

#### 4.2.4. Grey Wolf and Domestic Dogs

Wolf was the fifth most active scavenger; however, domestic dogs (hunting dogs), who were slightly more active, appeared very intensely during daytime, primarily during the hunting season. In addition, there were urban and rural free-ranging dogs that could affect the scavenger guild through competition, predation, and transmission of diseases [51–53]. Among these, there were two large dogs (~70–80 kg), which may have caused wolves high interference and competition, including spatiotemporal impact, kleptoparasitism, and possibly direct killing [54]. Ethiopian wolves (*Canis simiensis*) are denied potential food resources, such as ungulate carcasses, as they are quickly monopolised by dogs [55], and this was also shown in our study by these two large dogs. Wolf followed only red fox



and wild boar on a few occasions, and it is difficult to determine whether it was in search of carcasses in the case of red fox, or after prey, as wild boar is the main prey in Alpe di Catenaiia [28,56]. Wolf do kill red fox that scavenge on their prey [57], but the red fox may follow the wolf for abandoned kill leftovers [24]. Wolves scavenged moderately (11.2%) compared to the other scavengers in this study and to Swedish wolves (37.2%) (Ståhlberg, unpublished). They were next after red fox, the second most vigilant scavenger, most likely due to poaching [39]. They selected low vegetation density with good visibility and avoided human activity. They were mainly nocturnal but also active during the morning twilight until noon.

As a final point, there is a risk of increased pathogen transmission when humans, agriculture, and wildlife share a landscape. The facultative scavengers in this study provide an essential ecosystem service in the reforested Alpe di Catenaiia wolf area by reducing potential sources of disease [58,59], signifying the importance of future research within biodiversity and conservation ecology.

## 5. Conclusions

The lack of avian scavengers results in a clear mammalian-dominated scavenger guild in the wolf territories in Alpe di Catenaiia. Even though wild boar showed the highest number of visiting occasions at the feeding sites, they barely scavenged, which makes red fox the most common scavenger, followed by marten, badger, domestic dog, and wolf. Many factors shape the interactions in scavenger guilds in wolf territories. At carcass sites in Alpe di Catenaiia, pine and stone marten balance the trade-off between feeding and vigilance in the most beneficial structure. The scavenger guild also provides an essential ecosystem service in this reforested Tuscan Apennine mountain range, which is highly significant for biodiversity and conservation.

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