

Kleptoparasitism and Scavenging Can Stabilize Ecosystem Dynamics

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ABSTRACT: Scavenging is ubiquitous in nature, but its implications have rarely been investigated. We used camera traps on wolf kills to investigate the role of scavenging on predator and multiprey dynamics in a northern Apennine system in Italy. In contrast to North American systems, the omnivorous wild boar successfully competes with wolves for the meat of their kills. We developed a deterministic, multitrophic web model (wolf, vegetation, deer, and wild boar), tunable through a parameter that governs the impact of prey sharing between wolves and wild boar. When prey sharing is scarce, populations oscillate, but above a threshold value the trophic web is stabilized, with the regime solution becoming a fixed, stable point. Both deer and wild boar then increase as a function of prey sharing, and the impact of herbivores on the vegetation increases. When prey sharing exceeds another threshold, the system collapses due to the extinction of both wolves and wild boar. Our analysis shows that scavenging is crucial for the dynamics of this ecosystem, and thus it should not be overlooked in food web modeling. The exploitation of wolf kills by wild boar may allow juveniles and yearlings to obtain high-quality resources that are not usually available, helping the wild boar to compensate for losses caused by hunting. This is likely to make them even more invasive and difficult to control.

Keywords: wild boar, wolf, multitrophic web, scavenging, kleptoparasitism, population dynamics.

Introduction

In the last few decades, many European forest ecosystems have been characterized by remarkable increases in the number of large herbivores and by the return of large carnivores (Chapron et al. 2014). Even though the ability of large carnivores to affect the overall dynamics of terrestrial ecosystems has been well demonstrated in North America (Ripple and Beschta 2012), it has been overlooked in European ecosys-

tems. Kuijper et al. (2013) were the first to suggest the presence of a trophic cascade in Białowieża, Poland, but the evolution of trophic cascades in human-dominated systems (Hebblewhite et al. 2005; Dorresteijn et al. 2015) appears more difficult to predict compared to pristine environments (Peterson et al. 2014). In North American ecosystems with recovering wolf populations, most large herbivores are ruminants, but throughout Europe, wolf habitats are dominated by a nonruminant scavenger: the omnivorous wild boar (Ballari and Barrios-Garcia 2014).

Scavenging is a specific form of high-quality detritus feeding in which a carcass is consumed. Most if not all mammal predators are facultative scavengers (Wilson and Wolkovich 2011). The importance of scavenging in food webs has often been overlooked, perhaps because for humans, scavenging denotes a less than noble lifestyle (DeVault et al. 2003). There are technical difficulties in discriminating scavenged and preyed food in scat analysis, but recently some studies exploiting camera traps have quantified the impact of scavenging in terrestrial ecosystems (Selva et al. 2003; Wilmers et al. 2003; Wikenros et al. 2013; Allen et al. 2015). Scavenging may result from kleptoparasitism, a form of competition that involves the stealing of already procured prey from other species (Iyengar 2008). There are well-known examples; for instance, hyenas kleptoparasitize large cats in Africa. In northern ecosystems, wolves are the apex predators and brown bears (*Ursus arctos*) can usurp their kills and may decrease wolves' kill rates (Tallian et al. 2017; but cf. Hebblewhite and Smith [2010] for a different view). Coyotes (*Canis latrans*) and wolverines (*Gulo gulo*) scavenge wolf kills, but they do it at risk of retaliation (Berger and Gese 2007). In Eurasia, very little is known about the importance of wild boar scavenging on wolf-prey systems, and ecologists do not currently have general models of the effects of scavenging on predator-prey dynamics.

A way to improve predictions of ecosystem dynamics is to develop mathematical models and test them for plausible parameter values. Several studies (May 1976; Hastings

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and Powell 1991; Scheffer and Carpenter 2003) have shown that ecosystems may be characterized by multiple stable states. The effects of trophic cascades should be investigated not only on population abundances but on their dynamic stability, which influences ecosystem resilience.

In this article, we document scavenging by wild boar to investigate its effects on a multitrophic model, based on the northern Apennine ecosystem (NAE) but applicable throughout Eurasia. We focus on wolf, deer, and wild boar dynamics. We have no precise information about the behavioral interactions among boar and wolves. For simplicity, we assume that resource stealing (whether scavenging or kleptoparasitism) always entails a cost for the predator that is independent of the scavenger's aggression and that there is no deadly retaliation by the predator against the scavenger. Two main approaches are available to model predator-prey relationships: prey- and ratio-dependent functional responses (Abrams and Ginzburg 2000). Since we have no information about the wolf/deer functional response in NAE, the simpler prey-dependent processes are considered.

Our analyses comprise four steps. First, we investigate the extent to which wild boar scavenge kills made by wolves. Second, motivated by the findings of a field study, we develop a multitrophic model of the NAE. This model includes one scavenger species. We study how the long-term dynamics of the ecosystem were modified with respect to a tritrophic (vegetation-prey-predator) model (Hastings and Powell 1991). The stabilizing property of scavenging is investigated, and critical transitions between oscillatory and stable solutions are highlighted. Third, we investigate whether scavenging can initiate in this ecosystem a trophic cascade able to affect the other components of the trophic web (i.e., vegetation and herbivores). Finally, we discuss the dynamic effects of trophic cascades on the long-term conservation of the NAE, an ecosystem where the impact of human activity is significant.

Material and Methods

Study Area

The NAE includes the entire north Apennine range of Tuscany, Emilia-Romagna, and Liguria, Italy. The wolf (*Canis lupus*) is the apex predator in this ecosystem. Caniglia et al. (2012) showed that in a large sector (10,000 km²) of the NAE, the wolf population has increased by 5% per year, with a maximum of 0.246 wolves/km². Wolf predation in the NAE has been analyzed by scat analyses (Mattioli et al. 2011; Bassi et al. 2012; Milanesi et al. 2012). Wolves focused on roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), and for the latter, most predation is on young individuals (for instance, Bassi et al. [2012] report 27% of >35-kg wild boar in the scats).

The estimates of ungulate populations in the NAE between 1998 and 2004 were reported by Carnevali et al. (2009): wild boar estimates were not available, but the harvest bag counts showed a 40% increase. Roe deer had increased by 27%, with densities generally >10 individuals/km² and locally attaining >40 individuals/km²; fallow deer (*Dama dama*) are patchily distributed and could attain >30 individuals/km². Wolves preyed on both roe and fallow deer, whose proportion in the diet varied from place to place. From scat analyses, the two resources seem to be substitutable (but there are no formal analyses) because where fallow deer are abundant, roe deer are usually scarce, with the predator shifting to the most abundant species even if catchability and handling times can be different. Hereafter, this combination is referred to as deer, for simplicity. The wild boar has classically been thought of as an herbivore, but it is more properly considered an omnivore (Ballari and Barrios-Garcia 2014). It is worth noting that wild boar are strongly gregarious, and animals may cooperate in food gathering (Focardi et al. 2015).

The study of the carcasses was performed in a section of the NAE north of Firenze over an area of about 200 km². The area included both protected and hunting zones. Elevations were usually below 1,000 m, and the landscape was a patchwork of cultivated areas, pastures, and forests. Cultivation was more common in the valley floors, while forests cover >80% of the territory at higher elevation. The forest's main species were beech (*Fagus sylvatica*), oak (*Quercus pubescens*, *Quercus cerris*), sweet chestnut (*Castanea sativa*), spruce (*Picea abies*), and black pine (*Pinus nigra*).

Camera Trapping

To study the scavenging by wolves and wild boar on ungulate prey killed by wolves, we placed movement-triggered cameras near the carcasses and filmed the activity of the scavengers. Camera trapping has often been used to document scavenging (e.g., Wikenros et al. 2013). Camera trapping was performed opportunistically when someone (usually rangers, hunters, or breeders) reported the presence of an ungulate carcass within the study region. The cause of death was determined according to Fico et al. (2005) by methods also currently used for forensic assessment of predation in Italy. This approach has been independently validated by Caniglia et al. (2013) via molecular identification. Inspection of the carcass allowed us to determine whether wounds occurred prior to or after death, and the putative predator was determined by inspection of tracks and scats and with the help of camera traps eventually available in the area. Only animals killed during the previous night and not scavenged were considered. The approximate time since death was evaluated by observation of the eye, rigor mortis, and color of the tissues. Wolves first bite the abdominal cavity and consume

some organs, such as liver, heart, and lungs, but not the guts. On the contrary, the wild boar eats the guts and attacks the carcass without a standardized order so that the consumption and the bites are present on the whole carcass. Because of the different teeth, the bites of the wild boar look different from those of the wolf. The foraging of other small scavengers eventually present in the study area (such as foxes [*Vulpes vulpes*] or buzzards [*Buteo buteo*]) could not be detected on our first visit to the carcass.

A camera trap with LED infrared flash activated by a passive infrared sensor (Scout Guard 550, IR Plus 640 × 480) was positioned near the carcass (often tied to a tree, approximately 3–5 m distant and 2–3 m high to reduce the disturbance to the animals). The video recording was triggered by the presence of an animal for 60 s, and it was reactivated if an animal was present after a second delay time. The portion of consumed biomass was visually estimated during the camera setup, at each visit made to replace the battery and memory card (approximately once per week), and by observation of the videos. A four-level ordinal index of consumption (CI) was used to score the extent of consumption of the j th species (absent = 0, scarce = 1, medium = 2, high = 3; cf. Vucetich et al. 2012; Ray et al. 2014 for similar approaches). We analyzed each recorded video, also including the duration and time of permanence of the different species (i.e., the difference between arrival and departure times). Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p8j38> (Focardi et al. 2017).

Statistical Analysis

The cutting yield (i.e., the amount of meat one can obtain from the carcass, excluding skin, bones, and viscera) was known for both domestic and wild ungulates (Ponzetta et al. 2001; D. Berzi, personal communication). The cutting yield (here computed with respect to the live weight) was 48.9% for fallow deer, 55% for sheep (*Ovis aries*), and 40% for asses (*Equus asinus*). For red deer (female yearling) and roe deer, we used the same cutting yield as for fallow deer. We computed the meat available in a carcass by multiplying the average live weight recorded in the Apennines by the cutting yield. Yields (Y) are hence 24.5 kg for fallow deer, 13 kg for adult roe deer, 50 kg for red deer, 46 kg for sheep, 60 kg for asses, and 15 kg for goats (*Capra hircus*).

We observed that the consumption of the carcass was not a continuous process: each species consumed a meal and then left the carcass. Meals were indexed by $k = 1, 2, 3, \dots$, where $k = 1$ refers to the first meal (always by wolves) immediately following the predation event. Denoted $CI_{\text{tot}} = \sum_k CI_k$, the weight of meat removed at each k th meal is estimated by $W_k = Y \times CI_k / CI_{\text{tot}}$, where the summation counts all meals recorded for the carcass. The overall mass

of meat removed by the j th species from a carcass reads $W_j = \sum_k W_{k,j}$. We used Kruskal-Wallis statistics for evaluating the overall differences in W_j among species. The differences of meat mass removed by wolves and wild boar on different meals for $k > 1$ were evaluated by a paired t -test. All statistics are given \pm SE. Statistical analyses were performed in SAS 9.3 (SAS Institute 2011).

The Model

The trophic web used to investigate the dynamics of the NAE is displayed in figure 1. Wild boar of all ages (B) and deer (D) consume the vegetation, which, according to the literature on multitrophic systems (Hastings and Powell 1991), is assumed to be a single resource (V ; although there are differences between the diet of deer and wild boar). In the absence of herbivores, the vegetation growth is logistic with rate r_0 up to a carrying capacity K_0 . We assumed that wolves (W) actively prey on both deer and young wild boar (hereafter, piglets $P = \beta B$, β being the juvenile and yearling ratio), but they do not prey on the $(1 - \beta)B$ adults. According to our field observations, wild boar scavenged carcasses produced by wolves, but here for simplicity we did not consider carcasses produced by other causes (e.g., roadkill). Moreover, the quantity ψ is introduced to refer to the fraction

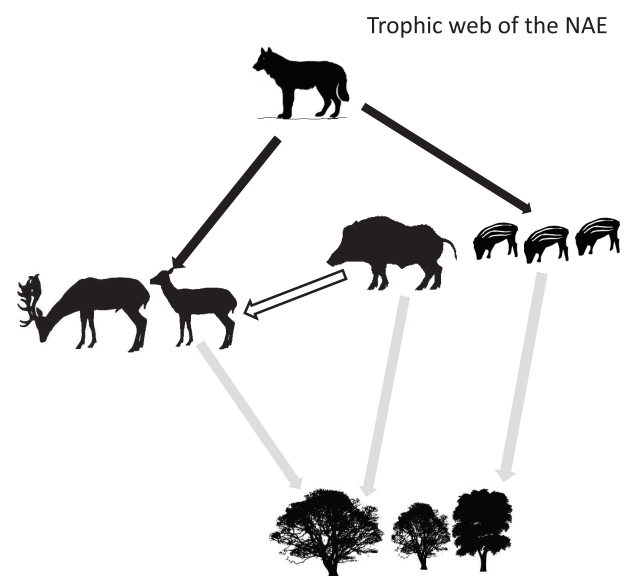


Figure 1: Trophic web of the northern Apennine ecosystem (NAE). Black arrows indicate predation, the open arrow represents scavenging, and light gray arrows represent grazing. Both deer (here pictured as fallow deer) and wild boar forage on plants, but wild boar can exploit carcasses of deer killed by wolves. Piglets are subject to predation by the wolf.

of deer carcasses actually consumed by wolves, while $1 - \psi$ is the fraction consumed by wild boar.

The model is a system of differential equations that reads

$$\begin{cases} \dot{V} = R_0 V \left(1 - \frac{V}{K_0}\right) - f_{VD}(V)D - f_{VB}(V)(1 - \beta)B - f_{VP}(V)\beta B, \\ \dot{D} = C_{VD}f_{VD}(V)D - f_{DW}(D)W - \Delta_D D, \\ \dot{W} = \psi C_{DW}f_{DW}(D)W + C_{PW}f_{PW}(P)W - \Delta_W W, \\ \dot{B} = C_{VB}f_{VB}(V)(1 - \beta)B + C_{DB}(1 - \psi)f_{DW}(D)W \\ \quad - f_{PW}(P)W - \Delta_B(1 - \beta)B - \Delta_P \beta B, \end{cases} \quad (1)$$

where the functions $f_{XY}(X)$, $\beta(V, W)$, $\psi(W, B)$, $A_{DW}(D, B)$, and $A_{PW}(D, B)$ are defined as follows:

$$\begin{cases} f_{XY}(X) = \frac{A_{XY}X}{B_{XY} + X}, \\ \beta(V, W) = \frac{\beta_0 V}{1 + \eta V + kW}, \\ \psi(W, B) = \frac{W}{W + \alpha(1 - \beta)B}, \\ A_{DW}(D, B) = \frac{A_{DW}^{(0)}D}{a_p \beta B + D}, \\ A_{PW}(D, B) = \frac{A_{PW}^{(0)}\beta B}{a_D D + \beta B}. \end{cases} \quad (2)$$

The function $f_{XY}(X)$ represents a generic Holling type II functional response where X denotes the prey and Y the predator (Holling 1966). The biological meaning of the model's parameters and their values are reported in table 1. The following features are of special relevance in model (1).

Age Structure. The wild boar population is split into two age classes, piglets P and adults B - P . Piglets are not a system variable, but they are derived from the adult boar as a fraction of the entire population, namely, $\beta(V, W)$. Thus, βB and $(1 - \beta)B$ represent the number of piglets and adults, respectively. Here, $\beta(V, W)$ depends on the available vegetation and the wolf population. From the expression of β in equation (2), it follows that $\beta \rightarrow 0$ if $W \rightarrow \infty$, while $\beta(V, W) \rightarrow \beta_0/\eta$ if $V \rightarrow \infty$. The first property derives from the assumption that all the piglets are killed by wolves when $W \rightarrow \infty$. The second property instead assumes that for overabundant vegetation, the ratio of piglets to adults attains the maximum allowed by the biology of this species. The other populations are considered homogeneous pools.

Numerical Response. The coefficients C_{VD} and C_{VB} represent, respectively, the number of deer and wild boar produced per unit of vegetation. We do not have a similar term for piglets, as we assume reproduction only of adults. Similarly, C_{DW} and C_{PW} represent the number of wolves produced per deer and per piglet, respectively. In the term $C_{DB}(1 - \psi)f_{DW}W$ of the fourth equation of system (1), C_{DB} represents a conversion factor from deer to wild boar, and $f_{DW}W$ represents the number of deer killed by wolves.

Interference. The term $1 - \psi$ is the portion of the kills stolen by wild boar, and it is assumed (see third equation in model [2]) a function of an adult wild boar $(1 - \beta)B$, multiplied by a constant α that represents the ability of the wild boar to exploit wolf kills (i.e., the interference coefficient between wild boar and wolves). More specifically, $\alpha^{-1} = (1 - \beta)B$ represents the number of adult boar necessary to steal half of the kills. There is no kleptoparasitism for $\alpha = 0$.

Predation Rates. The term

$$A_{PW}(D, B) = \frac{A_{PW}^{(0)}\beta B}{a_D D + \beta B}$$

represents the wolf's predation rate on piglets, and

$$A_{DW}(D, B) = \frac{A_{DW}^{(0)}D}{a_p \beta B + D}$$

represents the predation rate on deer. To represent the wolf's diet selection, A_{PW} and A_{DW} are set as functions of the other prey via parameters a_p and a_D , respectively. Thus, the predator tends to choose the most common prey (Garrott et al. 2007). When coefficients $A_{DW}(D, B)$ and $A_{PW}(D, B)$ are inserted into the response functions, they reduce to

$$f_{DW}(P, D) = \frac{\gamma_{DW}D^2}{1 + g_{DW}(P)D + \gamma_{DW}h_{DW}D^2},$$

$$f_{PW}(P, D) = \frac{\gamma_{PW}P^2}{1 + g_{PW}(D)P + \gamma_{PW}h_{PW}P^2},$$

given the following conventions:

$$\begin{cases} \gamma_{DW} = \frac{A_{DW}^{(0)}}{a_p B_{DW}}, & \gamma_{PW} = \frac{A_{PW}^{(0)}}{a_D B_{PW}}, \\ h_{DW} = \frac{1}{A_{DW}^{(0)}}, & h_{PW} = \frac{1}{A_{PW}^{(0)}}, \\ g_{DW}(P) = \frac{P}{B_{DW}} + \frac{1}{a_p}, & g_{PW}(D) = \frac{D}{B_{PW}} + \frac{1}{a_D}. \end{cases} \quad (3)$$

It is worth observing that f_{DW} and f_{PW} are sigmoid response functions with coefficients depending on the other resource

Table 1: Parameters from the multitrophic predator-prey-scavenger-vegetation model used to test for dynamic stability properties of scavenging in a wolf, boar, and deer system in the northern Apennines, Italy

Parameter	Meaning and constraints	Value
R_0	Regrowth rate of vegetation at $V = 0$	4.00
K_0	Carrying capacity of vegetation	10.00
A_{VD}	Per-capita ingestion of resources by D for overwhelming V (must be >2.5); the handling time of D on V is A_{VD}^{-1}	3.00
B_{VD}	Half-saturation density of V in the browsing of D	10.00
C_{VD}	Mass-specific conversion factor from the consumed resource V to D	.25
Δ_D	Inverse of the half-life of deer (in the absence of food)	.20
A_{VB}	Per-capita ingestion of resource V by B for overwhelming V ; the handling time of B on V is A_{VB}^{-1}	2.50
B_{VB}	Half-saturation density of V in the browsing of B	10.00
C_{VB}	Mass-specific conversion factor from the consumed resource V to B	.30
Δ_B	Inverse of the half-life of adult wild boar (in the absence of food)	.20
A_{VP}	Per-capita ingestion of resource V by P for overwhelming V	1.00
B_{VP}	Half-saturation density of V in the browsing of P	5.00
Δ_P	Inverse of the half-life of piglets (in the absence of food)	.01
$A_{PW}^{(0)}$	Per-capita ingestion of resource P by W for overwhelming P and in the absence of D ; the handling time of W on P is $h_{PW} = A_{PW}^{(0)-1}$	2.30
B_{PW}	Half-saturation density of piglets in wolves' preying (in the absence of deer)	4.50
a_D	Ad hoc constant, involved in $g_{PW}(D) = B_{PW}^{-1}D + a_D^{-1}$ (that regulates how fast the search rate of piglets by wolves saturates) and in $\gamma_{PW} = A_{PW}^{(0)}(a_D B_{PW})^{-1}$.1
C_{PW}	Mass-specific conversion factor from the consumed resource P to W	.30
$A_{DW}^{(0)}$	Per-capita ingestion of resource D by W for overwhelming D and in the absence of P (must be <2.3); the handling time of W on D is $h_{DW} = A_{DW}^{(0)-1}$	1.50
B_{DW}	Half-saturation density of deer preyed on by wolves (in the absence of piglets)	7.00
a_P	Ad hoc constant, involved in $g_{DW}(P) = B_{DW}^{-1}P + a_P^{-1}$ (that regulates how fast the search rate of deer by wolves saturates) and in $\gamma_{DW} = A_{DW}^{(0)}(a_P B_{DW})^{-1}$.5
C_{DW}	Mass-specific conversion factor from the consumed resource D to W (must be $>.3$)	.35
Δ_W	Inverse of the half-life of wolves (in the absence of food)	.20
α	Wolf and wild boar interference coefficient	Variable
C_{DB}	Mass-specific conversion factor from the consumed resource D to B (must be $<.35$)	.25
η	Ad hoc constant: in the absence of wolves, the half-saturation density of V for the piglets-to-boar ratio is η^{-1}	5
β_0	Ad hoc constant: in the absence of wolves, the limit ratio of the piglets-to-boar ratio for overwhelming resource V is $\eta^{-1}\beta_0$	5
k	Ad hoc constant: for a fixed value of V , the limit ratio of the piglets-to-boar ratio for overwhelming resource V is halved to $\frac{1}{2}\eta^{-1}\beta_0$ as W reaches $k^{-1}(1 + \eta V)$	40

Note: The table reports the parameter, the biological meaning of the model's parameter, and the values used in simulations.

(Joly and Patterson 2003). In multiprey systems, type II functional responses turn into type III sigmoid when the predators select the most common prey (Huggard 1993).

The coefficients in equation (3) are referred to as prey-predator encounter rate (γ) and handling time (h), while g measures how fast the response function saturates. We do not assume any form of compensatory mechanisms in wolves to buffer the effect of scavenging, which, to our knowledge, has never been demonstrated in this species. Finally, Δ_D , Δ_W , and Δ_B represent the mortality rates of the three populations due to causes not explicit in model (1).

Parameter Estimate and Sensitivity Analysis

A significant challenge in developing a mathematical model of an ecological system is to obtain a behavior resembling

the original process. To tackle this issue, we have used the following approach. First, we set the best-documented parameters (survival and reproductive rates) according to the values from the literature. Moreover, we identified the parameter sets that were able to reproduce asymptotic behaviors matching the available field observations, on a per km² scale. The remaining parameter values were chosen to avoid both chaotic and spiked time series. We also assumed that deer were more efficient than wild boar in exploiting vegetation, so that if wolves are absent, then wild boar are driven to extinction by exploitation competition. However, since the mean predation rates on deer are chosen to be larger than those on wild boar, in the presence of predators, both populations can coexist. Vegetation is expressed as biomass density, according to the regrowth equation of Turchin and Batzli (2001) where biomass is expressed in normalized values with respect to its carrying capacity K_0 .

Finally, a standard sensitivity analysis was carried out by building statistics about the behavior of the model around the nominal parametric configuration (Bendat and Piersol 2010). The results used to plot the bifurcation diagrams were collected by randomly varying each parameter inside an interval of amplitude 4% centered on its nominal value and the mean bifurcation diagram computed over 100 replicates.

Numerical Simulations

Numerical simulations were performed using MATLAB R2013 x64 (MathWorks) on a 2.7 GHz Intel Core i5 processor equipped with 8 GB of 1,600 MHz DDR3 ram memory. The ODE45 solver, featuring the Dormand-Prince method for the Runge-Kutta numerical integration algorithm, was used to solve the ordinary differential equation (ODE) model to understand the temporal evolution of the dynamical system. The simulations covered a span of 40,000 time units to efficiently eliminate the long transients, while the numerical error was contained by integrating with absolute and relative tolerance set to 10^{-7} and 10^{-5} , respectively.

Results

Observations

The pattern of scavenging observed in the NAE is shown in figure 2. Wolves removed a large part of the carrion during the first meal after predation, but they were unable to maintain control over the carcass much longer, such that wild boar could consume most of the remaining meat. The difference between the overall amount of meat consumed by wolves and wild boar is significant (Wilcoxon test: $\chi^2_2 = 8.25$, $p = .02$). Wolves removed a total of 200 kg (50.8%) and wild boar 134 kg (34.1%) of meat from all carcasses in the sample. Smaller amounts were removed by red foxes (4.6%), large birds (9.1%), and martens (1.3%), but, probably given the small number of observations, no difference in the amount of meat consumed can be detected among these small scavengers (Wilcoxon test: $\chi^2_2 = 1.54$, $p = .46$). The wolves and wild boar pattern in carcass usage is depicted in figure 3, which shows that wolves consumed smaller portions than wild boar over successive visits. The relative statistics are reported in table 2. It is

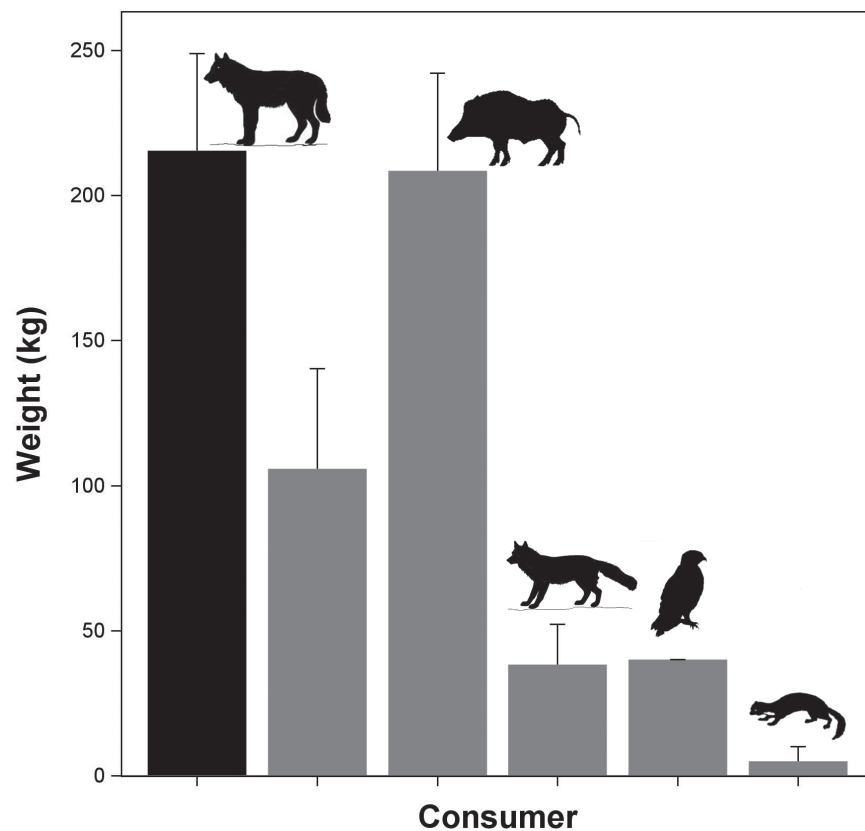


Figure 2: Scavenging patterns of wolf prey in the northern Apennine ecosystem. Black bars show the sum amount of meat (ordinates with vertical bars representing SE) consumed by wolves at $k = 1$. Gray bars show the consumption by wolves at $k \geq 2$ and for other species, the sum amount of meat scavenged.

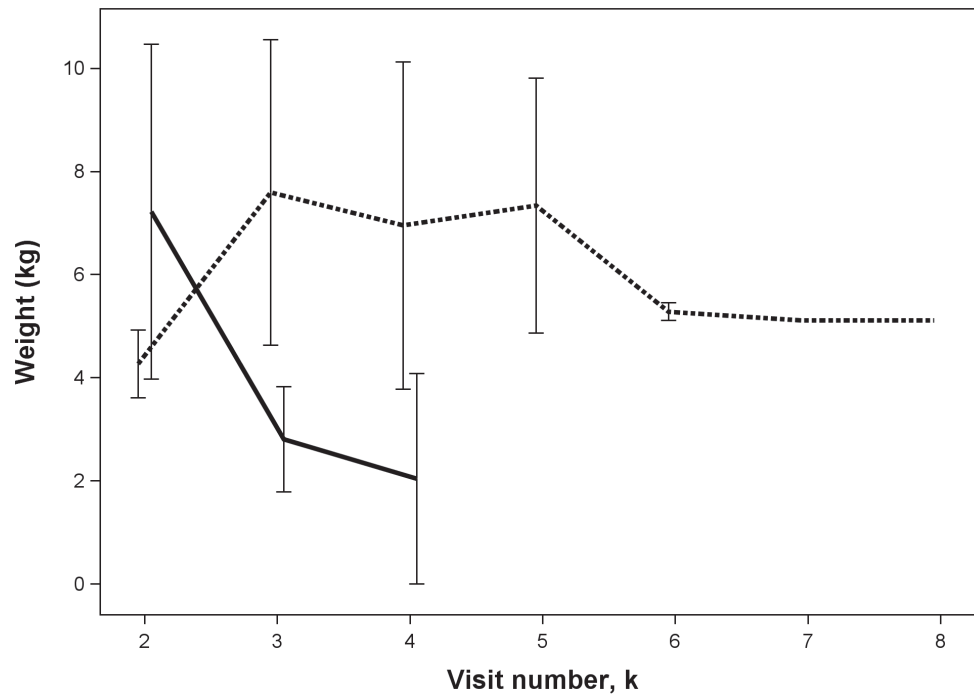


Figure 3: Temporal use of carcasses by wolves (solid line) and wild boar (dashed line) in the northern Apennine ecosystem. The vertical lines represent SE. The abscissae mark the occasion of scavenging (k).

worth observing that there is no significant difference in the overall mass of meat consumed by either species for $k > 1$. However, for later occasions (i.e., $k > 2$), wild boar consumed significantly more meat and remained near the carcass longer than wolves.

Our empirical results showing that wolves cannot exclusively control their kills and prevent scavenging by wild boar are supported by two videos in the supplementary ma-

terial (videos 1, 2, available online). In video 1, wolves left the carcass after 1 h and were replaced by wild boar. Note the long period of occupancy of wild boar near the carcass. This is a general pattern; wild boar remain longer (68 min) than wolves (45 min) near the carcass (Wilcoxon test: $\chi^2 = 7.27$, $p = .007$). Video 2 suggests that the recorded wolf is displaced from the carcass by a group of wild boar. These anecdotal cases support our empirical results that wild boar

Table 2: Comparison of the differences of meat mass consumed by wolves and wild boar in the northern Apennine ecosystem

Variable and sample size	Δ	Student's t	p	Data selection
Consumed meat:				
46	1.4 ± 1.3	1.0	.299	Overall
32	-2.0 ± 1.4	-1.4	.173	$k > 1$
21	-4.2 ± 1.4	-3.1	.006	$k > 2$
Permanence of the carcass:				
32	-19.7 ± 8.5	-2.3	.027	$k > 1$
21	-28.4 ± 12.0	-2.3	.035	$k > 2$

Note: Recall that k indexes the meal, where $k = 1$ refers to the consumption by wolves immediately following predation. Comparisons were performed using all data, after the first consumption by wolves ($k > 1$), and after the second consumption by any of the studied species ($k > 2$). The parameter Δ indicates the difference between the wolf and the wild boar meat consumption, hence negative values indicate a higher wild boar consumption. The overall time of permanence is not computable, because the camera trap was positioned after the predation. Degrees of freedom are given by (sample size - 1).

appear to dominate carcasses and wolves have to exploit their quarry before the wild boar manage to locate it.

The elapsed time between two consecutive visits to the carcass was usually short (almost 30% of cases within 3 h); in only five cases did the carcass remain unvisited for >2 days. In excluding these cases, the mean time between two consecutive visits was 10.7 ± 2.6 h.

Numerical Analysis

Figure 4 reports the stationary equilibrium for $\alpha = 0$. The parameters have been chosen to obtain animal population densities within the ranges typically observed in the NAE. According to the literature on similar systems (cf. Stone and He 2007 and references therein), the dynamics are oscillatory and persistent. Even in the absence of kleptoparasitism, wild boar tend to fluctuate out of phase with respect to deer and be synchronous with vegetation and wolves. In figure 4, we also report three other scenarios for increasing kleptoparasitism. For $\alpha = 0.001$, the solution is similar to the system without kleptoparasitism, while for larger α ($\alpha = 0.003$), oscillations are smoother (i.e., kleptoparasitism stabilizes the behavior of the model). Figure 5 reports the bifurcation diagrams as a function of α , which show oscillations for all the variables at low α values. There exists a threshold value around $\alpha = 0.0055$ such that the system oscillates with decreasing amplitudes as it is approached. This stabilizing process reduces to a fixed-point regime that continues almost unchanged until the critical value $\alpha_0 \cong 0.006$. High kleptoparasitism rates increase the population of wild boar at the expense of the wolves, also favoring the deer, as better highlighted by their median population line.



Video 1: Still image from a video recorded at Badia di Moscheta ($44^{\circ}04'28.3''\text{N}$, $11^{\circ}25'28.4''\text{E}$) on August 4, 2011 (video 1, available online). It displays a predation by wolves on a fallow deer doe and the scavenging of the carcass by wild boar. Note the black wolf.



Video 2: Still image from a video recorded at Villa Ginori ($43^{\circ}50'19.5''\text{N}$, $11^{\circ}13'00.2''\text{E}$) on October 22, 2010 (video 2, available online). A fallow deer doe has been killed by wolves, and later the carcass has been scavenged by a large number of wild boar.

The increase of both herbivores depresses vegetation and strengthens the intensity of competition between wild boar and deer. For even higher α , this results in wolf and wild boar extinction.

The sensitivity analysis shows that this deterministic pattern holds true for small variations of the parameters, and the perturbed solutions remain close to the nominal one, thus implying the intrinsic robustness of the phenomenon. Only near the critical transition at α_0 does the error band increase.

Discussion

It is usually assumed that intraguild competitive interaction is a main force limiting the number of species at each trophic level (Simberloff and Dayan 1991). The main interguild relationship is instead predation, generating energy flows from lower to upper trophic levels. The case examined in this article is unusual because we documented an interguild competitive interaction in which the wild boar competes systematically and successfully with the apex predator. In turn, the wolf is able to exploit the juvenile stage of its competitor. We showed that inclusion of an omnivore in multitrophic food web dynamics provides counterintuitive predictions for population dynamics of predators, prey, and vegetation. In particular, we showed that this process can theoretically generate a trophic cascade: the model predicts that wild boar are able to reduce the impact of wolves on herbivores, which in turn reduces vegetation. Hence, kleptoparasitism results in fewer wolves and more deer and wild boar, the latter resulting in increased kleptoparasitism. This self-sustaining feedback loop reduces resources to wolves if

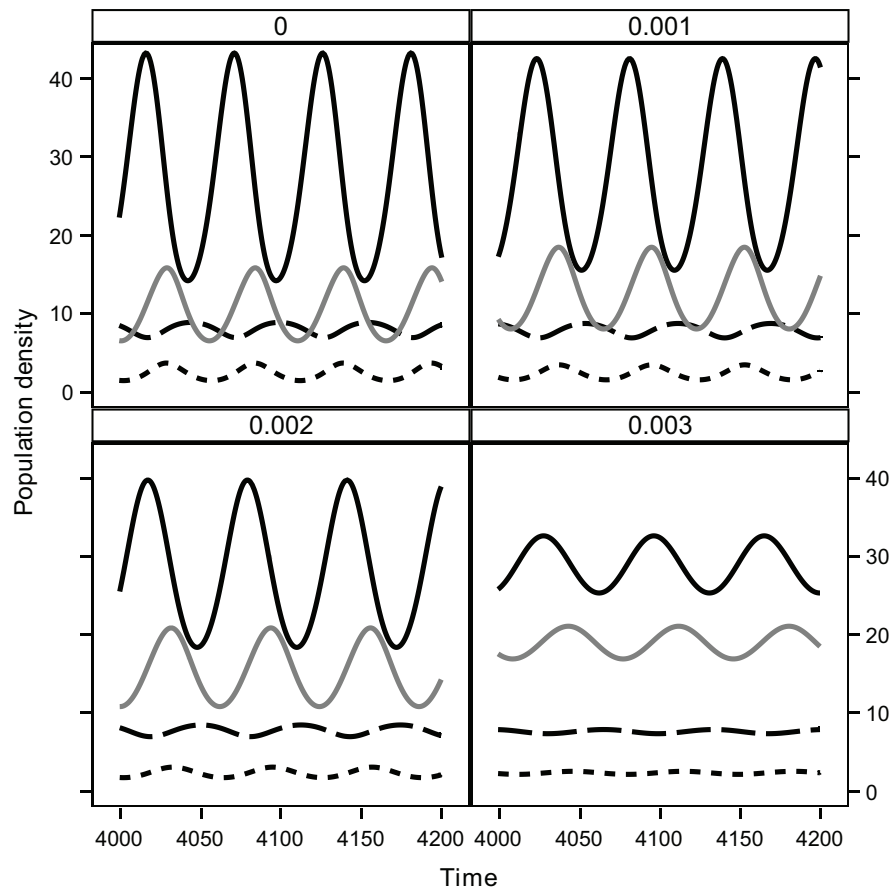


Figure 4: Plot of the equilibrium time series for the four studied populations (solid black line: deer; solid gray line: wild boar; short-dashed black line: wolf; long-dashed black line: vegetation) for four different α values, the parameter that describes interference competition between wild boar and wolves. Note that wild boar and deer are given per km², wolves are given per 10 km², and vegetation is given in a fraction of carrying capacity K_0 .

they are unable to compensate with a larger hunting effort, as we assumed in our model. Such a type of compensation occurs, albeit partially—for instance, when brown bears scavenge lynx (*Lynx lynx*) prey (Krofel et al. 2012)—but it seems not to be present in wolves (Tallian et al. 2017).

In temperate and boreal ecosystems, a situation comparable to that described here may occur between wolves and ursids. A large part of bears' food derives from vegetation (Bojarska and Selva 2012), but black bears (*Ursus americanus*) may be important scavengers in North American ecosystems (Allen et al. 2015), and brown bears scavenge wolves' kills in both North America and Europe (Tallian et al. 2017). Our case, however, is more compelling because typical black bear densities (e.g., around 1/10 km²; Keech et al. 2011) are far smaller than those of the wild boar in Italy (>20/km²; Focardi et al. 2008).

Scavenging by wild boar has been documented even though the amount of meat food in the diet is usually small. Indeed, feral pigs in North America removed 11% of small

mammal carcasses (DeVault and Rhodes 2002), while wild boar were present in only 5.7% of occasions removing bison carcasses in Białowieża (Selva et al. 2003), and they were minor scavengers in the Bavarian National Park (Ray et al. 2014). In contrast, our study shows that wild boar can exploit most of the carcasses of the animals preyed on by wolves, consuming >30% of the whole biomass. Whether naturally dead animals are scavenged similarly to the wolves' prey remains to be investigated.

There are some concerns regarding the sample size used to deduce the pattern of kleptoparasitism in the NAE. Indeed, the use of camera trapping to investigate this phenomenon is in its infancy, and we wish to underline the importance of this methodology. Our field observations, however, are sufficient to highlight the importance of wild boar kleptoparasitism, which is still overlooked in literature. In particular, when wild boar locate a carcass, they are able to steal a good part of it because they are very often gregarious. It would be interesting to verify whether group

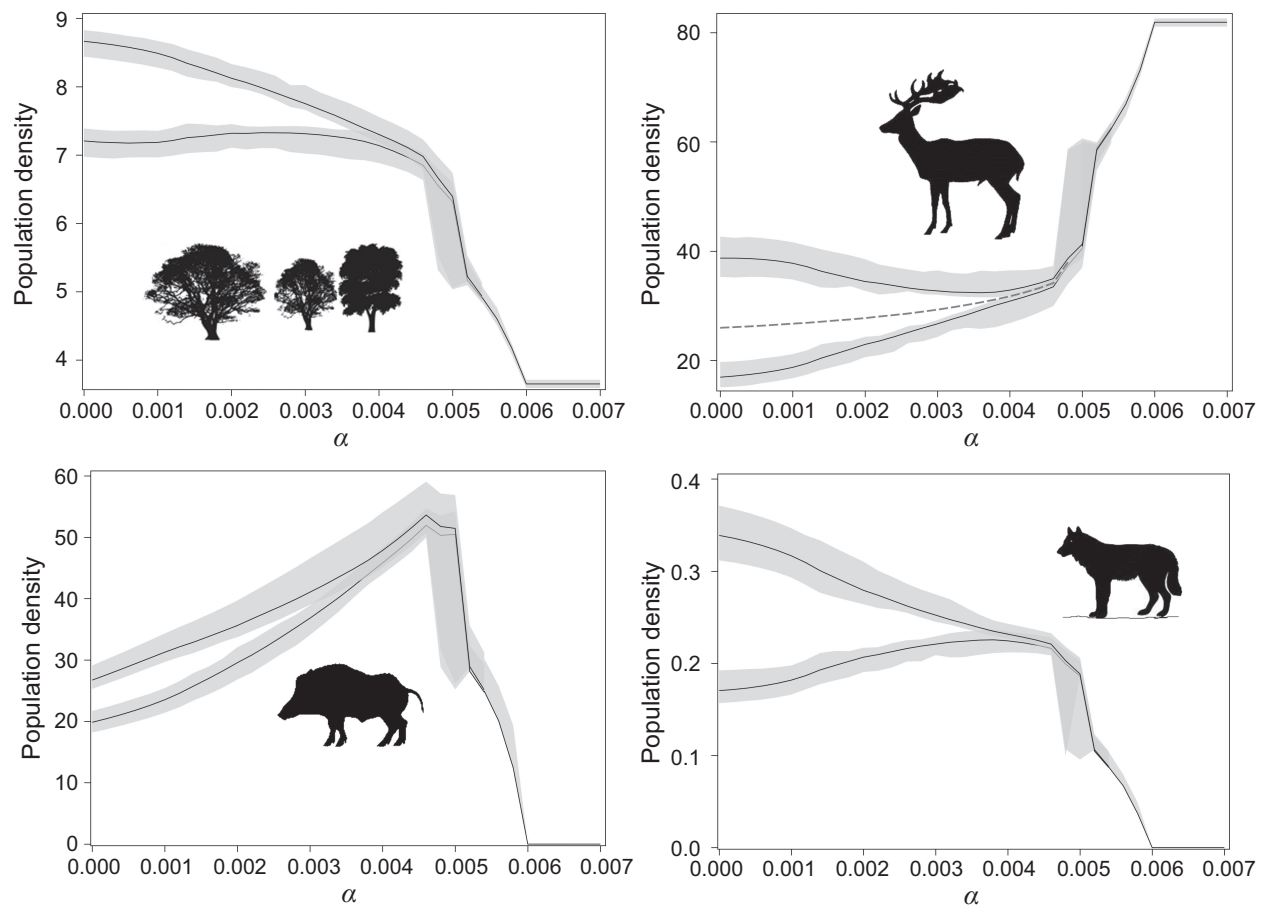


Figure 5: Bifurcation plots reporting the variation of the four studied populations (ordinates, animal populations: individuals/km²; vegetation: units of K_0) as a function of the interference parameter α . The dotted line in the deer plot refers to the median population values. The gray areas represent the variations observed perturbing the values of parameters in model (1) by 4%. For deer, we also report the value of the median values of maximum and minimal values (dashed line).

size increases the probability of detecting and exploiting carrion. The assumption of density-dependent regulation for the access to carrion in the wild boar fits well with our knowledge (Focardi et al. 2015), but this assumption should ideally be tested further. Probably, when the group size increases over a certain extent, wolves are unable to defend their carcass at all.

We stress that our model is completely deterministic even though the wild boar population is affected stochastically by ecological and climatic factors (e.g., mastings and drought) not considered here. However, we expect under actual field conditions that a dynamical equilibrium is still attained as transient among deterministic stationary regimes. The heuristics of the modeling is controversial, since four ODEs are too few to represent in some realistic way any natural ecosystem. For our model, we tried to improve realism by developing the functional responses, the prey-switching mechanics, and the process of the kleptopara-

sitism on the basis of empirical evidence, providing reasonable qualitative predictions. Thus, our study can induce innovative research in ecosystem dynamics by including scavenging in food web theory. We showed that scavenging has the potential for increasing biodiversity and improving ecosystem stability, two cornerstones of modern biodiversity theory (Loreau 2010).

Focardi et al. (2008) proposed that the unusual life-history traits of the wild boar (large size, high fecundity, low and variable adult survival) may depend on the presence of animal food in the diet. Now we can speculate that the use of high-quality food items has selected for kleptoparasitism in the wild boar. While, in the absence of apex predators, wild boar scavenging remains occasional, the presence of wolves can exacerbate these aspects of its life history, enhancing its well-known invasion capacities (Barrios-Garcia and Ballari 2012).

Our study is also relevant for practical ecosystem management. The presence of wolves producing carcasses ex-

plottable by wild boar reduces the chance that control by hunting may be successful for this species, since scavenging may lead to earlier reproduction and larger litter sizes. However, the access of juveniles and yearlings to the carcasses would deserve a specific research, even though we expect that the population can be boosted when these age classes can exploit high-quality resources. Because of the ubiquity of wild boar and wild pigs through all of Eurasia, surrogate species in Africa, and the widespread invasion of North America by wild pigs, we believe our results will have broad implications for terrestrial food webs. In addition, in North America, ursids may play a similar ecological role as wild boar, mediated by the degree of scavenging on carcasses of carnivore-killed prey. Regardless of the large mammal system under investigation, in conclusion, our report strongly suggests that kleptoparasitism needs to be included in ecosystem modeling.

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