



Original Research Article

Kleptoparasitism and complexity in a multi-trophic web

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ABSTRACT

In this work the effects of kleptoparasitism in a multi-trophic food-web, in which an omnivorous species scavenges the kills of a top predator, are investigated. Scavengers are assumed to be able to steal predators' kills by direct interference and aggression. The amount of prey shared depends on the relative competitive abilities of omnivores and predators and on their abundances. To make the proposed model consistent, scavenging is accompanied by other features. First, the predator can prey only on the juvenile life stage of scavengers (i.e. not on adult individuals) as well as on a different species of herbivores. Hence, an age structure is enforced within scavengers, so that they belong to the guild of preys when they are young and vulnerable. Second, predators can switch between prey species selecting the most abundant one. This condition grants the competitive exclusion of the two vegetation eaters, allowing them to co-exist: the omnivore and the herbivore compete for the same vegetation pool but pure herbivores are indeed assumed to be more efficient in its exploitation. The omnivorous species is not able to kill the herbivores, but nonetheless it may exploit their carcasses after they have been killed by predators. Finally, the juvenile/adult ratio of omnivores varies depending on the available resources and predators' amount. In such a scenario it is shown that kleptoparasitism can modify to a large extent the stability of the system, leading either to a regularization or to chaos, depending both on the scavenger's and the predator's functional response. Moreover, an excess of kleptoparasitism is shown to compromise the whole trophic web, making extinct both predators and scavengers. As far as the authors are aware of, this paper is the first one to explicitly introduce kleptoparasitism in trophic web models.

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1. Introduction

The object of the present paper is the mathematical investigation of a particular form of competition between species, referred to as *kleptoparasitism*. This relationship takes place when the individuals of a species use to steal resources collected by another species. This occurs when, for the former species, it is more convenient to steal the prey than to hunt it, or when hunting actively the prey is not possible at all for them. *Kleptoparasitism clearly affects the trophic web topology* of the ecosystem at hand. In the present work its effect on a simple, but realistic, *multi-trophic web* is investigated.

A large number of studies have been dedicated to the dynamics of trophic webs with different topologies (see, e.g., [Krivan and](#)

[Schmitz, 2003](#)). The seminal study of the tri-trophic model with non-linear functional responses by [Hastings and Powell \(1991\)](#) has been modified by introducing a number of different processes, well documented in the experimental ecological literature, such as inter- and intra-specific competition, mutualism ([Krishna et al., 2008](#)), parasitism, omnivory and intra-guild predation ([Pal et al., 2014](#)) which occurs when a top predator preys on mesopredators ([Newsome and Ripple, 2015](#)).

Also, the forms of functional response describing how one species preys on another one have evolved ([Arditi and Ginzburg, 2012](#)): while the linear functional response used in the classic Lotka–Volterra models is deemed too much unrealistic, different functional responses such as Holling's type II, sigmoid, ratio-dependent or Beddington–DeAngelis functions have been introduced ([Turchin, 2003](#)) according to the behavioral processes underpinning predation events in different study cases. For example, the ratio-dependent functional response is aimed to represent interference among predators ([Abrams and Ginzburg, 2000](#)), while sigmoid functions are used to model prey-switching

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(van Baalen et al., 2001). For realism's sake, some authors introduced some behavioral complexity such as predator specialization (van Baalen et al., 2001), as well as a different number of species within each trophic level (see, e.g., Hadley and Forbes, 2009). Some of these evolved features are included in the present model for the biological sake.

In a multi-trophic system, where there is an autotrophic resource (vegetation) along with a first trophic level occupied by herbivores and a second level of predators, kleptoparasitism may be exerted by a predator at the expenses of other predators. A classical example is represented by the behaviour of a pack of hyenas stealing preys from large cats, such as cheetahs and lions (Schaller, 1972). However, there are several other biological examples to which a mathematical model of kleptoparasitism can be applied (Garthe and Huppopp, 1998). Scavenging, indeed, is pervasive in ecological communities where top predators are present (Iyengar (2008)). Other examples in the literature consider the interaction between a large cat and a powerful scavenger, such as the puma (*Puma concolor*) and the black bear (*Ursus americanus*) (Allen et al., 2015), or the lynx (*Lynx lynx*) and the brown bear (*Ursus arctos*) (Krofel et al., 2012). In all the foregoing examples, the top predator and the kleptoparasite belong to the same trophic level. Indeed, kleptoparasitic species usually belong to the predator guild and are often mesopredators, such as hyenas, coyotes, foxes, wolverines and jackals (Pereira et al., 2014).

In the case of predators stealing the kills of top predators, as hyenas do with large cats, the influence of kleptoparasitism is pretty clear: a certain amount of food (depending on the competitive ability of the kleptoparasite) is deviated, and it does not feed the top predator. In this work, instead, we are interested into a kind of kleptoparasitism that is *less apparent and more complicated*. Here, the focus is on the kleptoparasitism exerted by an *omnivorous scavenger*, i.e. a species that is not usually a predator and that, nonetheless, successfully chases predators and steals their kills. This is another form of interaction, never mathematically modeled before in the literature, as far as we know. A biological example is represented by the social scavenging of wild boar (*Sus scrofa*) exerted on wolf's (*Canis lupus*) kills (Berzi priv. comm., Focardi et al., in preparation). One may refer to this kind of kleptoparasitism as *Inter-Level Kleptoparasitism (ILK)*, meaning that the competing species belong to *different trophic levels*. An important difference between ILK and the kleptoparasitism exerted by meso-predators is that in ILK the kleptoparasites compete with (top) predators for carcasses, and also with their preys for the autotrophic resource: the consequences of this difference can not be figured out easily. Therefore, this work is devoted to studying the implications of ILK in the dynamics of multi-trophic webs.

The organization of the paper is as follows. In Section 2 kleptoparasitism is presented as a special kind of scavenging and an overview of the model is traced. In Section 3 its analytical formulation is given in terms of population dynamics described by a set of Ordinary Differential Equations (ODEs). Section 4 reports the results of the numerical bifurcation analysis obtained varying an ILK efficiency parameter, namely α , in four different case studies, which are distinguished by different values of the parameters implying different survival efficiency of the scavenger and of the predator. Conclusions are drawn in Section 5, with some discussion about the future application of the model and its possible improvements.

2. Model overview

Scavenging is a form of high quality detritus feeding and refers to the use of carcasses which are produced by different processes such as senescence, hunting, extreme weather conditions, diseases and predation (Wilson and Wolkovich, 2011; Pereira et al., 2014).

When predation is the cause of death, scavengers may exploit parts of the prey's carcass which are not used by the predator itself. This process represents a form of commensalism, since it does not harm predators' fitness to any extent. As noted by DeVault et al. (2003), the importance of scavenging in a food web is often overlooked because of "human aversion to decomposing matter", but scavenging has a clear favorable impact on biodiversity conservation and increases the overall faunal biomass in the ecosystem (Wilmers and Post, 2006). A classical example of scavenging is represented by the necrophagy, typical of several species of vultures, each one specialized in using different parts of the carcasses, such as bones or skin, which the predator is however unable to exploit (Kendall et al., 2012). Further, in some cases, as showed by the marginal value theorem (Charnov, 1976), partial prey consumption can represent a tactic for long-term foraging maximization by the predator and thus the deserted carcasses represent an empty "trophic niche" for other species (Materassi et al., 2013). However, in many cases, when the population of predators is close to its carrying capacity, the predator uses the most of the carcass and prey sharing may occur only in the presence of kleptoparasitism, a behavioral adaptation where a competitor is stealing the carcass by interference and overt aggression (Iyengar, 2008). From an ethological point of view, active competition through physical aggression is the distinctive element of kleptoparasitism with respect to scavenging. In terms of the mathematical representation of the system, instead, kleptoparasitism is an interaction *subtracting biomass to the predator's balance to an extent depending on the relative strength and abundance of the two competing species*. How scavenging can give rise to kleptoparasitism should definitely be matter of biological and ethological investigation.

In the literature it has already been showed that detritus feeding tends to stabilize trophic webs (see, e.g., Moore et al., 2004), and so does scavenging. However, to our knowledge, until now nobody has previously investigated the impact of scavenging and/or kleptoparasitism on food web dynamics in more quantitative terms (see Previtte and Hoffman, 2013 for further reading), namely through the *bifurcation analysis* of suitable dynamical systems. In order to mathematically model the kleptoparasitism, we have considered an ecosystem that includes the minimal number of species allowing for ILK to occur: there is a primary autotrophic resource V ; a herbivorous prey D ; an omnivorous scavenger B acting as the kleptoparasite; and a top predator W , that preys both on D and on a fraction of B . Our goal is to understand how this illustrative multi-trophic web has its dynamics influenced by the presence of the competition between B and W for the carcasses of D killed by W . Then, a *deterministic space-independent population dynamic model* has been conceived and represented through a system of ODEs. The *dynamical variables* of the system are the biomasses of the species V , D , B and W , respectively indicated as V , D , B and W . Some important features are considered in the proposed trophic web, that are included in the equation formulation in order to render the system more sensible.

The omnivorous scavenger B is assumed less efficient than the herbivorous D in exploiting the autotrophic resource V . Since we also assume that D and B compete for the same kind of vegetation, the in absence of the predator W , B is doomed to extinction because D collects all the resources. In order for B to survive, the predator W must be present, but it can not prey independently on D and B , otherwise only a frail (unstable) stationary equilibrium between D and B could be reached. Rather, W is assumed at each instant to mostly prey on the species that is prevailing, until the other becomes strong enough to turn the tables. This predator's behaviour is commonly referred to in the literature as "prey switching" (Murdoch, 1969). It is worth stressing that the specializing predator not only renders it possible for the two prey

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