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An overview of understudied interaction types amongst large carnivores

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ABSTRACT

Among the many different ways in which large carnivores interact with other organisms, predation and competition are those most studied and investigated. Studies on these topics have led to the creation of well-known models and theories (e.g. Lotka-Volterra's prey-predator equations, Paine's keystone species concept, or mesopredator release theory) used to explain ecosystem structure and food web dynamics. However, many other interaction types exist between mammals, birds and reptiles, including mutualism, commensalism and parasitism. Symbiosis and amensalism also occur. These interactions can be strong and ecosystem-structuring, yet they are seldom considered in large carnivore science. Here, we provide a brief overview of these interaction types, giving examples of their occurrence in nature, in an attempt to encourage greater scientific study of their role in food webs containing large mammalian carnivores.

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1. Introduction

No species lives in isolation, and each one can be potentially influenced by others, including those at distant trophic levels (Begon et al., 2006). Species interactions play key roles in the ecological and evolutionary structuring and dynamics of groups, populations, communities, ecosystems and entire food webs (Barbosa and Castellanos, 2005). In the field of large carnivore science, recent research has mainly focused on the cascading effects of apex predator removal or addition, highlighting the important roles of predation and predation risk on ecosystem structure, function and stability (Estes et al., 2011; Ripple et al., 2014). Competition between carnivores is also known to have substantial influence on ecosystems (Ritchie and Johnson, 2009). However, predation and competition are but two of many interaction types capable of strongly driving ecosystem structure and function. Is large carnivore science overlooking some of these other interaction types, and could their consideration help explain some of the conflicting results often reported in large carnivore studies (Allen et al., 2017)?

Investigating and quantifying the strength and value of these interactions is not easy, but ignoring them risks the oversimplification of food webs, which could lead to the development of poor or unsuccessful management strategies for carnivores. The aim of this study is to briefly review a few types of alternative species interactions – besides predation and competition – that could assist in better understanding the role of large carnivores in food web dynamics.

Species interactions have traditionally been categorized by their effect on the species involved, for example positively, negatively or neutrally (+, − or 0) (Dickman, 1992). Effects are characterised in this way by the change that they produce in the equilibrium population

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size of the interacting species. While predation (+ −) and competition (− −) among vertebrates and carnivores have been widely investigated, mutualism (+ +), commensalism (+ 0), amensalism (0 −) and parasitism (+ 0) have largely been considered mainly in microbial, fungal and invertebrate systems (Dickman, 1992). Despite this, mixed groups of interacting fish, bird, reptile and mammal species have long been noted and, among these classes, a variety of interaction types have been documented (Dickman, 1992; Chapman and Chapman, 2000). Beyond their effects, these interactions could be considered strong on the basis of the duration of the relationship between the involved organisms. For example, short-lived interactions could be typical of predation, while extended or permanent ones are more likely to be symbiotic (Combes, 2001). Symbiosis, originally and restrictively considered equivalent to mutualism, has recently gained a broader and accepted meaning. According to the widely used 'de Bary' definition, the term symbiosis refers to mutualistic, commensalistic and parasitic interactions between species (Bradford and Schwab, 2012 and references therein). Thus, in this review, symbiosis will not be explicitly considered. We consider only mutualism and commensalism, parasitism (including kleptoparasitism), and amensalism, and describe a theoretical example of how these may operate in a food web inclusive of mammalian carnivores.

2. Mutualism and commensalism

Cooperation among organisms can produce a variety of advantages. In mutualistic associations, organisms of different species interact to their mutual benefit (+ +) (Begon et al., 2006). Mixed species groups occur in many different habitats and are very different in duration, frequency, activities and structure. Functional reasons for these groups usually fall into two categories: foraging advantages and predator avoidance (Clutton-Brock, 2009). Several examples of polyspecific mutual interactions are available in the literature, including the very well-known example of cooperation between pollinators and plants (Landry, 2010). Birds, small carnivores (e.g. foxes, beech martens, polecats, badgers, stoats) and other mammals (hedgehogs) can be important seed dispersers (Hernández, 2008).

Mutualisms among vertebrates and carnivores are also known (Fig. 1). For example, the dwarf mongoose joins hornbills or fork-tailed drongos during its feeding activities. The little carnivore flushes little mammals or invertebrates from cover allowing the birds to feed on them. The drongo and the hornbill, to keep the hunters safe, cry havoc when a possible larger predator is near. Interestingly, these birds learn to alert the mongooses even when an exclusive mongoose predator is nearby (Dickman, 1992; Sharpe et al., 2010). Similarly, the yellow mongoose and the cape ground squirrel use each other to emit alarm calls in response to predators (Makenbach et al., 2013). Furthermore, species that receive foraging benefits preserve the second species not from predators, but from parasites. This kind of mutualism is well represented by interactions between ungulates and oxpeckers (Dickman, 1992).

Mutualisms can be characterized by apparent asymmetry in benefits received by the two sides of the interaction. In these cases, it is possible to talk about 'commensalism' or, if the asymmetry becomes exacerbated, of parasitism (Hoeksema and Bruna, 2000). In fact, the term 'parasitism' is used for the form of predation, in which the consumer usually feeds on its host disadvantaging it (+ −), whereas the term 'commensalism' is usually used for cases in which one organism (the host) provides resources for another organism, but the host itself suffers no tangible ill effects and does not gain any benefits (+ 0) (Begon et al., 2006). Some species of birds (e.g., pied babblers) or mammals (e.g., squirrel monkeys) eavesdrop on the alarm calls of other species (e.g., scimitarbills or capuchins monkeys), while screech owls prefer to nest in association with blind snakes that eat nest parasites. Owls gain clear benefit from the presence of the snakes but there is no clear evidence that snakes do better in nests than if they had remained in the soil (Dickman, 1992). Muskrats often use beavers lodges (Nielsen et al., 2013), and aardvarks and rabbits, given their burrowing activities, benefit many species which make use of their holes for shelter and rearing of young. In addition, aardvarks' predation of ant and termite nests provides additional food for other myrmecophagous as aardwolves, little African carnivores (Taylor and Skinner, 2000).

Involving species ascribed to different Families and Orders, the study of amensalism and commensalism represents a useful key to more deeply understand the interactions among carnivores belonging to the middle trophic levels, and to better inspect the dynamics of carnivore communities.

2.1. Parasitism

Interactions among organisms are not cooperative in a large number of cases (Raffel et al., 2008). In parasitic interactions for example, one organism benefits from the association while the second one is disadvantaged (+ −). Historically considered a specialized form of predation, predators and parasites are rather overlapping classes of natural enemies, distinguished by the interaction with the prey (respectively consumption of prey tissue, and symbiosis with a host organism) (Raffel et al., 2008). Parasitism is defined as a symbiosis in which the parasite harms the host, using it as a habitat and depending on it for resource acquisition (Roberts and Janovy, 2000).

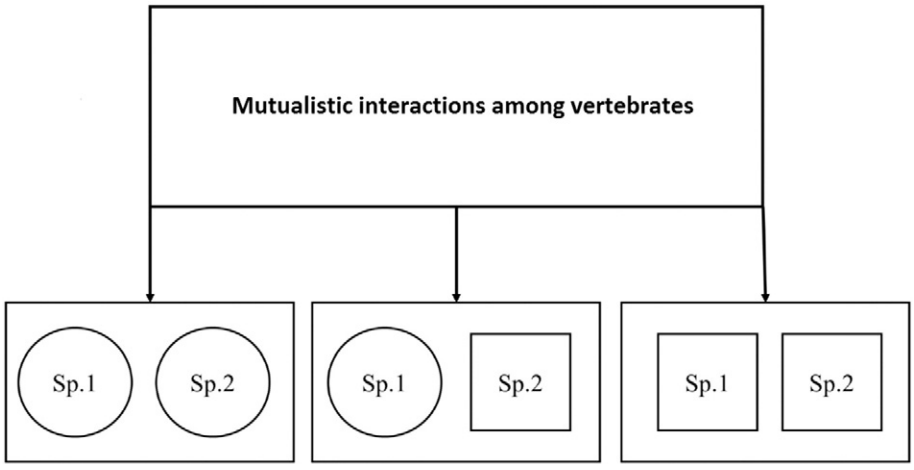

Fig. 1. Schematic representation of the mutualistic interactions among vertebrates. The circle represents the foraging advantage and the squares the protection from predators (detecting and avoidance) or parasites. Species involved in the cooperation have the same benefit or each species receives a different one.