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Indirect effects of primary prey population dynamics on alternative prey

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ABSTRACT

We develop a theory of generalist predation showing how alternative prey species are affected by changes in both mean abundance and variability (coefficient of variation) of their predator's primary prey. The theory is motivated by the indirect effects of cyclic rodent populations on ground-breeding birds, and developed through progressive analytic simplifications of an empirically-based model. It applies nonetheless to many other systems where primary prey have fast life-histories and can become superabundant, thus facilitating impact on alternative prey species and generating highly asymmetric interactions. Our results suggest that predator effects on alternative prey should generally decrease with mean primary prey abundance, and increase with primary prey variability (low to high CV)—unless predators have strong aggregative responses, in which case these results can be reversed. Approximations of models including predator dynamics (general numerical response with possible delays) confirm these results but further suggest that negative temporal correlation between predator and primary prey is harmful to alternative prey. Finally, we find that measurements of predator numerical responses are crucial to predict – even qualitatively – the response of ecosystems to changes in the dynamics of outbreaking prey species.

1. Introduction

Many predators have a preferred prey item, or primary prey, which is eaten more frequently when all prey types are equally available (Murdoch, 1969). Such preference can occur because of higher encounter rates with primary prey, lower handling times, or active prey selection based on energetic content. An integration of these factors is provided by the classical prey model of optimal foraging theory, where the diet breadth of consumers increases when primary prey density is low, and shrinks again at high primary prey density (Emlen, 1966; Schoener, 1971; Pulliam, 1974; Charnov, 1976; Pyke et al., 1977; Stephens and Krebs, 1986). Whatever the reason for predator preferences, predators eat more than proportionally their primary prey when abundant, and increase the ratio of alternative prey species in the diet when the primary prey becomes scarce.

For community dynamics, this implies that alternative prey species are influenced by the dynamics of the primary prey through the predator's functional (Oaten and Murdoch, 1975) and numerical (e.g. Holt and Kotler, 1987; Wilson and Bromley, 2001) responses to shifts in primary prey abundance. Predator numerical responses can be aggregative through movements (Turchin and Hanski, 1997), or demographic through reproductive changes; in most cases, a mixture of both. However, changes in functional and aggregative/demographic responses following an increase in primary prey have opposite effects on alternative prey. When the primary prey increases in numbers, individual predators tend to eat less of alternative prey species, but predators also tend to be more numerous, which potentially increases the overall impact of predators on alternative prey populations. The impact of predators on alternative prey (i.e., change in population size and probability of persistence) results from a balance between the numerical and functional components of the predator response,

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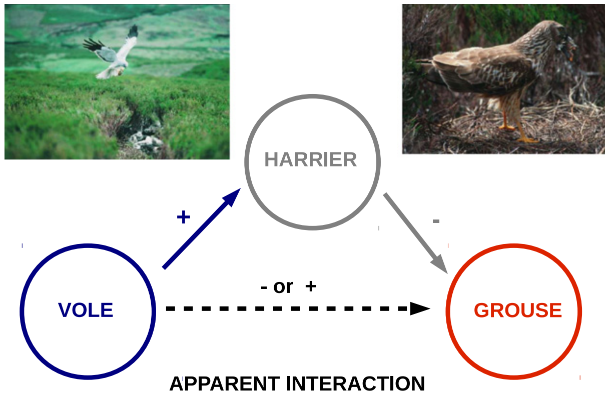

Fig. 1. The asymmetric apparent interaction module. A primary prey (vole) is eaten by the predator (harrier), which reacts both numerically (aggregative response) and through its functional response, i.e. the amount of both vole and grouse eaten as a function of their densities. The predator also has a negative effect on the alternative prey (grouse) density, as it eats grouse chicks. The combination of both arrows, i.e. the indirect effect of voles on grouse, can be positive or negative, depending on the strength of the predator numerical response. Top left picture: Male harrier bringing back a vole to the nest. Top right picture: Female harrier with a grouse chick in its beak. Pictures: S. Redpath, E. Donnelly.

which determines whether the primary prey has a positive or negative impact on the alternative prey. If the predator numerical response is strong, classic theory predicts that the impact will be negative (Holt, 1977). However, if the numerical response is weak and the functional response saturates, the impact of primary on alternative prey can be positive (Holt, 1977; Holt and Kotler, 1987; Holt and Lawton, 1994). Apparent interactions can therefore take the form of competition or mutualism (Abrams et al., 1998; Bêty et al., 2002; Brassil and Abrams, 2004), or even amensalism (0/−) versus commensalism (0/+), if the primary prey has greater impact on the secondary prey than the reverse, which often seems to be the case because of differences in maximum biomass and life histories (Sinclair, 2003; DeCesare et al., 2010; Holt, 2012).

Primary prey are often species that are easy to catch, which usually corresponds to r-strategists that invest heavily in reproduction and less in survival. Such fast-reproducing species are strongly influenced by environmental variability, and therefore tend to have dynamics that are both highly variable (Sæther et al., 2002; Sinclair, 2003) and nonstationary (e.g., Angerbjörn et al., 2001). The influence of variability and nonstationarity of primary prey dynamics on alternative predation is not yet well developed in the otherwise abundant apparent competition/mutualism literature (Holt and Lawton, 1994; Abrams et al., 1998; Brassil and Abrams, 2004; Brassil, 2006; Schmidt and Ostfeld, 2008), despite its relevance to a number of species of scientific and conservation importance (see Schmidt and Ostfeld, 2008 for examples). In this paper, we investigate how the interplay between the mean and variability of primary prey abundance affect alternative prey species demography. An alternative prey is, according to our definition, a prey that is eaten less frequently when both prey are equally available. We further restrict the definition of alternative prey in two ways in this article. First, it is a species that – unlike the primary prey – is either not available or not nutritious enough for the predator to specialize on it year-round. Second, which might be a corollary of the first, the alternative prey cannot drive the aggregative/numerical response of the predator, which is mostly influenced by the primary prey (e.g. New et al., 2011, 2012). These restrictions make the interaction highly asymmetric, i.e. prey 1 indirectly affects prey 2 but not the other way around (Fig. 1). It seems that such asymmetric subsets of the food web (trophic modules) are not only quite widespread (e.g., DeCesare et al., 2010; Stouffer et al., 2012; Holt, 2012), but also important to consider from a functional or conservation perspective (Wittmer et al., 2013; McKinnon et al., 2013; Nolet et al., 2013), and correspond well to the empirical examples below.

A typical terrestrial example of highly variable primary prey are rodents such as voles and lemmings (subfamily *Arvicolinae*), that exhibit large-amplitude cycles, especially in boreal and arctic regions. These cycles are often non-stationary, because rodent vital rates react to trends in climatic variables (Kausrud et al., 2008). As Lack (1946) remarked early on, rodents are preyed upon by an important guild of avian and mammalian predators. This guild includes foxes and mustelids, on the mammalian side, and on the avian side, raptors and some other birds such as skuas and corvids. All these rodent-eating predators have the habit of including more alternative food sources in their diet when the rodent cycle is at a trough; often such alternative prey consists of eggs and juveniles of gamebirds, waterfowl, etc. (see Valkama et al., 2005, for more details). Thus, the breeding success of many bird species is severely impacted by the population dynamics of rodents (Lack, 1946; Summers et al., 1998; Wilson and Bromley, 2001; Blomqvist et al., 2002; Bêty et al., 2002; Valkama et al., 2005; Schmidt and Ostfeld, 2008; McKinnon et al., 2013; Nolet et al., 2013). It has even been hypothesized that bird breeding habitat in the Arctic is partly determined by association with cyclic rodents (Blomqvist et al., 2002; Gilg and Yoccoz, 2010).

Other examples of key primary prey whose dynamics influence alternative prey species range from hares (*Lepus* sp.) in boreal landscapes (Krebs, 2011) to wildebeest (*Connochaetes* sp.) in the Serengeti (Sinclair, 2003); or in marine ecosystems, from sandeels (family *Ammodytidae*; Matthiopoulos et al., 2008) to small, overabundant pelagic fishes that create so-called "wasp-waist" ecosystems (Cury et al., 2000). Though such species are sometimes referred to as "keystone" (e.g. Cornulier et al., 2013), their importance is largely due to their large maximal biomass at peak densities, unlike keystone species which have a disproportionate effect on the ecosystem per unit of biomass (Power et al., 1996). Hence, we refer to rodents and their r-strategist counterparts in other ecosystems simply as "key" prey species.

In a previous paper, Matthiopoulos et al. (2007) developed a model for predation by harriers (*Circus cyaneus*) on red grouse chicks (*Lagopus l. scoticus*, an alternative prey to voles *Microtus agrestis*) in Scottish moors, for different levels of abundance of voles and pipits (*Anthus pratensis*), both of which are important in the harriers' diet. This was done using empirically measured multispecies functional and aggregative responses. The study was largely motivated by management of a human—wildlife conflict; hunters typically want to shoot more grouse and see less harriers, while conservationists wish to protect the hen harrier, an endangered raptor in the UK (Thirgood and Redpath, 2008). The impact of harriers on grouse is managed through a number of techniques, that range from the illegal killing of raptors to diversionary feeding (Redpath et al., 2001). A modelling assessment of the various management techniques is given in New et al. (2012). We use this system as a key empirical example to motivate general theory rather than the object of study per se. Red grouse corresponds well to our abovementioned definition of alternative prey.

Field vole numbers – the primary prey of harriers – were assumed for simplicity to be a constant in Matthiopoulos et al. (2007). However, vole abundance can vary greatly from year to year, and harriers can react numerically (aggregatively) to these variations (Redpath et al., 2002). The model we develop here relaxes the assumption of constant vole primary prey availability. The way we represent primary prey dynamics is akin to a resource pulse (Holt, 2008; Schmidt and Ostfeld, 2008). Through a series of progressive approximations of the detailed, empirically-based model of vole–harrier–grouse dynamics, we formulate a simplified